The drive to control : how affect and motivation regulate cognitive control

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Humor and Conflict Adaptation: a Neural Mechanism

> "One happiness scatters a thousand sorrows."
>
> Chinese proverb

This chapter is based on:

van Steenbergen, H., Band, G.P.H., Hommel, B., Rombouts, S.A.R.B., & Nieuwenhuis, S. (submitted for publication). Keep smiling! Humor reduces neurocognitive adjustments to conflict.

Abstract

Positive emotional states are known to reduce the impact of cognitive demands and information-processing conflict on human behavior, but the underlying neural mechanism of this modulation is unknown. We used functional magnetic resonance imaging to examine how pleasure induced by funny cartoons regulates behavioral control and neural adaptations to cognitive conflict. Humor activated hedonic hotspots in the basal ganglia, which attenuated the rostral anterior cingulate cortex (ACC) response to conflict. This reduced subsequent conflict adaptation as observed in behavior and monitoring-related dorsal ACC activation. Our observations reveal the neural mechanism by which positive emotions regulate adaptive goal-directed behavior.

Introduction

Positive emotions do not only feel good, they may also help to counter the impact of stressful events on our behavior and health (Garland et al., 2010). The claim that pleasure reduces the impact of events evoking information-processing conflict and negative performance outcomes (Gendolla, 2000; Botvinick, 2007) is supported by physiological measures, subjective evaluations, and behavioral adjustments to such events (de Burgo & Gendolla, 2009; Mayer, Gaschke, Braverman, & Evans, 1992; van Steenbergen, Band, & Hommel, 2010). An important aim of neuroscience is to understand how pleasure-related neuromodulation produce adaptive behavior (Kringelbach & Berridge, 2009). Neuroimaging studies suggest that hedonic tone attenuates demand-related conflict signaling in the anterior cingulate cortex (ACC; Luu et al., 2000; van Wouwe et al., 2011), a brain region in which cognitive and affective information converge (Botvinick et al., 2001; Paus, 2001; Bush et al., 2000). Here we provide evidence that pleasure-induced ACC attenuation regulates behavioral adjustment to conflict, and that this modulation is driven by subcortical reward systems.

Pleasant emotions may regulate cognitive-control optimization to behavioral demands via neural interactions between ACC and the basal ganglia. According to an influential neurobiological theory, the ACC supports adaptive behavior to the situational value at hand via dopaminergic teaching signals from the basal ganglia (Holroyd & Coles, 2002). Several observations in humans confirm the involvement of such interactions between cortex and basal ganglia: nucleus accumbens recordings have revealed a negative functional coupling with monitoring-related ACC activity (Munte et al., 2008), pharmacological studies have found that elevated baseline dopamine levels reduce conflict-related ACC activity (Jocham & Ullsperger, 2009), and lesion studies have demonstrated that ACC activity depends on intact basal ganglia (Ullsperger & von Cramon, 2006). Neuromodulatory projections to the ventral striatum (VS) and the ventral pallidum (VP) – the central components of the neural reward circuit (Haber & Knutson, 2010) – may allow hedonic states to modulate this network. Earlier studies have shown that stimulation of the VS and VP can generate hedonic 'liking' reactions in the rat. fMRI studies in humans have also strongly implicated these regions in the processing of reward and positive emotions (Kringelbach & Berridge, 2009).

To investigate the impact of pleasant emotional states on conflict processing, we used fMRI to record brain activation while measuring participants' behavioral adjustments to a demanding conflict task. Pleasure was induced by funny cartoons; stimuli that are known to increase hedonic tone (Abel & Maxwell, 2002) and to activate the reward system (Mobbs, Greicius, bdel-Azim, Menon, & Reiss, 2003). Following cartoon presentation, participants performed the arrow-flanker task, an established paradigm for inducing and measuring reactive cognitive control adjustments to conflict (Gratton et al., 1992; Egner, 2007; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; see Figure 1A and 1B). In each flanker trial, a central target indicates whether the left or right-hand response is required, and flanking distracters introduce either no conflict (compatible information) or conflict (incompatible information). Because conflict trials are more demanding than no-conflict trials, responses in these trials are commonly slower; this compatibility effect can be taken as an index of attentional interference. The critical

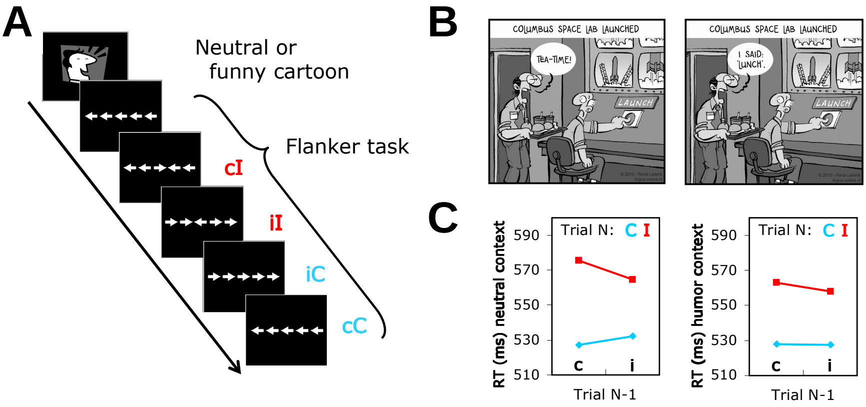

***Figure 1**. **A.** Example of a trial. Neutral and funny cartoons were presented in random order. Each cartoon was followed by a block of five randomly selected flanker trials being either compatible (C) or incompatible (I). Sequential-effect analyses compared Trial N compatibility (as indicated by upper-case letters C and I) as a function of the compatibility of the preceding trial (Trial N-1; indicated by lower-case letters c and i). **B.** Example of a funny cartoon (right) and the same cartoon with funny cues omitted presented as neutral cartoon (left). © 2010 René Leisink, reprinted with permission. **C.** Standard conflict-driven behavioral adjustment was observed following neutral cartoons (left). This effect was cancelled out by humor (right).*

moment of adaptation in this task occurs on trials that follow conflict trials, in which the compatibility effect is reduced (Figure 1C, left panel). This indicates that conflict detection leads to reactive increases in cognitive control in the subsequent trial (Egner, 2007; Gratton et al., 1992). Previous studies have suggested that this often-replicated behavioral post-conflict adjustment is driven by ACC activation (Botvinick et al., 1999; Kerns et al., 2004) and is reduced when hedonic tone increases (van Steenbergen et al., 2010). We tested whether such affective regulation of conflict adaptation depends on modulation of ACC, driven by pleasure-related activation of VS and VP.

Methods

Participants

Twenty-two healthy right-handed volunteers (age 18 - 29) with normal or corrected-to-normal vision participated in the study. In order to optimize the detection of humor-induced reward circuit activation, we tested only females. Earlier studies have shown stronger mesolimbic reward responses to funny cartoons in females than in males (Azim, Mobbs, Jo, Menon, & Reiss, 2005). The volunteers gave written informed consent for participation in the study, and they received a monetary incentive. The experiment was approved by the medical ethics committee of the Leiden University Medical Center.

Stimuli

Thirty-two funny cartoons were selected from a set of approximately 130 cartoons, on the basis of funniness ratings and simplicity ratings (i.e., how easy the jokes were to comprehend) provided by participants matched to the age and background of the experimental subjects. Adopting the same approach as earlier studies (Azim et al., 2005; Mobbs et al., 2003), a closely matched set of 32 non-funny, neutral cartoons was created by omitting funny cues of humor cartoons through visual and/or textual changes. Both gray-scaled sets were matched on visual clarity, geometrical complexity and mean luminosity. All cartoons were presented once during the experiment.

Task and procedure

Before entering the MRI scanner, participants were informed about the task to perform. They were encouraged to enjoy the content of the funny cartoons even during subsequent flanker trials and to avoid head movements. Instructions emphasized fast and accurate responses to the direction of the central target arrow of the flanker task. Optical response-button boxes (positioned on the upper leg) recorded index finger responses of the left and right hand. Participants performed two practice trials with performance feedback before the experiment started. Experimental data were then acquired in two consecutive runs of 32 trials.

Stimuli were presented against a black background (1024 x 768 pix). Funny and neutral cartoons (500 x 500 pix) were presented in a quasi-random order for 6 seconds each. Following each cartoon, a fixation cross (jittered duration between 2-6 seconds), a block of five flanker trials and another fixation cross (1 second) were presented. Each trial in the block consisted of an imperative flanker stimulus (a row of five black arrows pointing either left or right; 100 x 7 pix), presented for 1 second, followed by a fixation cross (jittered, 3 – 5 seconds). In order to provide an index of neural distracter-related activation measurable in the visual motion area of the brain, the flankers were always moving vertically (using a triangle function with T = 200 ms and A = 10 pix). We used the same number of compatible (flankers in same direction as the central target) and incompatible (flankers opposite to central target) trials. A quasi-random trial sequence was created, ensuring that all possible sequential combinations occurred equally often during the experiment. Data were collected in one test session including two consecutive runs, each lasting about 20 min. In a final functional scan a motion localizer task was presented. Participants passively viewed moving flanker trials and still flanker trials in 12 alternating runs of 15 seconds, separated by 10-seconds fixation periods. In each of these localizer runs, 15 random flanker stimuli were presented for 800 ms, separated by an inter-stimulus interval of 200 ms.

After the scan session, participants rated the funniness of each cartoon they saw in the scanner (9-points scale). Participants were fully debriefed at the end of the experiment.

Behavioral data analysis

Inspection of the post-experimental ratings revealed that a few cartoons were given funniness ratings that did not match the intended funny/nonfunny category. Cartoons with such extreme outlier ratings (more than 3 interquartile ranges below/above the 25/75th percentile; on average 1.8 cartoons per participants) and its subsequent block of flanker trials were marked as rating outliers and were excluded from all analyses. On initial inspection of the behavioral flanker task data, two participants turned out to have made more than 5% response omissions. These participants were excluded from further analyses.

Correct reaction time (RT) and error rate were analyzed with repeated measures ANOVAs that included the factors current-trial compatibility (Compatible vs. Incompatible; abbreviation: C vs. I), previous-trial compatibility (compatible vs. incompatible; abbreviation: c vs. i), and humor context (funny vs. neutral cartoon). Standard sequential compatibility effects (i.e., the conflict-adaptation effect), for both RTs and error rates and separately for both humor contexts, were calculated by subtracting the compatibility effect following a correct incompatible (conflict) trial (i) from the compatibility effect following a correct compatible (no-conflict) trial (c) (i.e., (cI – cC) – (iI – iC)). The first trial of each block, trials following errors, trials following cartoons with outlying ratings, and behavioral outlier trials (RT > 2 SD from the condition-specific means, calculated for each participant separately) were excluded from all analyses.

fMRI data acquisition

Scanning was performed with a standard whole-head coil on a 3-T Philips Achieva MRI system (Best, The Netherlands) in the Leiden University Medical Center. For both task runs 532 T2*-weighted whole-brain EPIs were acquired, including two dummy scans preceding each scan to allow for equilibration of T1 saturation effects (TR = 2.2 sec; TE = 30 msec, flip angle = 80°, 38 transverse slices, 2.75×2.75×2.75 mm(+10% interslice gap)). During the motion localizer task, 141 of these EPIs were acquired. Visual stimuli were projected onto a screen that was viewed through a mirror at the head end of the magnet. After the functional runs, a high-resolution EPI scan and a T1-weighted anatomical scan were obtained for registration purposes (EPI scan: TR = 2.2 msec; TE = 30 msec, flip angle = 80°, 84 transverse slices, 1.964×1.964×2 mm; 3D T1-weighted scan: TR = 9.717 msec; TE = 4.59 msec, flip angle = 8°, 140 slices, .875×.875×1.2 mm, FOV = 224.000×168.000×177.333).

fMRI data analysis

Data analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.FMRIb.ox.ac.uk/fsl (Smith et al., 2004). The following pre-statistics processing was applied: motion correction (Jenkinson, Bannister, Brady, & Smith, 2002), non-brain removal (Smith, 2002), spatial smoothing using a Gaussian kernel of FWHM 8.0 mm, grand-mean intensity normalization of the entire 4D data set by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100.0 seconds). Functional scans were registered to high-resolution EPI images, which were registered to T1 images, which were registered to standard MNI space (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

In native space, the fMRI time series were analyzed using an event-related approach in the context of the general linear model with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Models were high-pass-filtered (Gaussian-weighted least-squares straight-line fitting, with sigma=100.0 seconds). All regressors used square-wave functions to represent stimulus duration and were convolved with a canonical HRF and its temporal derivative.

Exactly equivalent to the trials included for RT analysis, a first model analyzed trial-to-trial adaptation in conflict-related ACC activation by comparing iI and cI trials following neutral and funny cartoons. This model included all eight possible combinations of current-trial compatibility (Compatible vs. Incompatible), previous-trial compatibility (compatible vs. incompatible), and humor context (trials following neutral cartoons vs. following funny cartoons) as separate regressors. Additional confound regressors included funny cartoon and neutral cartoon presentation, as well as events representing the first flanker trial of each block, errors, trials following errors, and outliers.

In order to reveal modulating effects of pleasure on the conflict trials preceding adaptation, we ran a second model that included regressors for incompatible (conflict) trials and compatible (no-conflict) trials (i.e., irrespective of subsequent-trial compatibility) as well as for cartoon presentations. These events were modeled separately for both humor contexts. Separate confound regressors included events of the last flanker trial of each block, errors, trials before errors, and trials before outliers.

Two additional variants of the previous model were also analyzed. One analysis examined whether ACC activity during conflict trials predicted trial-to-trial adjustments in the subsequent conflict trial. This model included all eight possible combinations of current-trial compatibility (Compatible vs. Incompatible), subsequent-trial compatibility (compatible vs. incompatible), and humor context (neutral vs. funny cartoons). These events were added as two series of eight regressors. The first series used standard fixed weights to account for invariant BOLD responses to stimulus presentation. The second series of regressors used a weighting vector determined by condition-specific standardized RT values of the subsequent trial. This allowed us to reveal any conflict-related BOLD responses in the

ACC that predicted subsequent adaptation in iI trials. All remaining events were modeled as confound regressors.

The second variant modeled interactions in functional connectivity between subcortical reward areas and ACC during conflict trials. Two psychophysiological interaction (PPI) analyses Friston et al., 1997 were run separately for the ventral striatum (VS) seed and the ventral pallidum (VP) seed. Physiological regressors used the extracted time-course information from the VS (2, 20, -4) and the VP (14, -10, -8), based on a sphere of radius 4 mm around the peak-activation voxel in the respective region using the funny vs. neutral cartoon contrast. The convolved psychological regressor represented the contrast incompatible trials after funny cartoons (FI) – incompatible trials after neutral cartoons (NI). In order to mop out shared variance, a FI + NI regressor was also added. Compatible trials following funny and neutral cartoons were modeled separately. The PPI regressor was computed as the product of the demeaned physiological timecourse and the centred psychological regressor. Again, all remaining events were modeled as confound regressors.

For all analyses, the relevant contrasts were combined across the two runs on a subject-by-subject basis using fixed-effects analyses (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). Second-level contrast images were submitted to third-level mixed-effects group analyses. All resulting statistical parametric images were thresholded using clusters determined by $Z > 2.3$ and a cluster-corrected significance threshold of $p < 0.05$ (Worsley, 2001). Given the a priori hypotheses about conflict-related ACC activation triggered by incompatible flanker stimuli, analyses for these contrasts were constrained to an anatomical mask defining the anterior cingulate cortex proper (using the anterior division of the cingulate cortex as defined by the Harvard-Oxford structural atlas, 70%-likelihood threshold). ROI analyses used individual mean z-scores from second-level analyses extracted with Featquery.

Table 1. *Behavioral data*

	After neutral cartoon				After funny cartoon			
	RT (ms)		Error rate		RT (ms)		Error rate	
Trial Type	Mean	SD	Mean	SD	Mean	SD	Mean	SD
cC	527	67	0.2%	0.7%	528	68	0.5%	1.2%
cI	576	72	2.2%	3.5%	563	75	2.9%	3.8%
iC	532	69	0.8%	2.1%	527	67	0.5%	1.3%
iI	565	65	1.3%	2.1%	558	66	1.2%	1.7%
Compatibility effect =								
((cI + iI) - (cC + iC)) / 2	40	18	1.3%	2.4%	33	18	1.5%	1.7%
Conflict-adaptation effect =								
(cI - cC) - (iI - iC)	16	27	1.5%	2.6%	4	26	1.7%	4.5%

Note: The table reports mean response times (RTs), error rates, and the corresponding flanker compatibility effects and conflict-adaptation effects. cC = compatible trials following compatible trials; cI = incompatible trials following compatible trials; iC = compatible trials following incompatible trials; iI = incompatible trials following incompatible trials.

Results

Behavioral results

The flanker task produced robust current-trial compatibility effects in reaction time (F(1,19) = 116.7, $p < .001$, MSE = 455.7), indicating that it successfully induced performance conflict. An interaction between current-trial and previous-trial compatibility, indicating standard conflict adaptation, was observed in the neutral condition (F(1,19) = 7.0, $p < .02$, MSE = 182.6), but not in the humor condition (F(1,19) = 0.5, p = .50, MSE = 173.0) (Figure 1C). Thus, in line with predictions and replicating earlier findings (van Steenbergen et al., 2010; van Steenbergen et al., 2009), participants adjusted their behavior in response to conflict only in the neutral, low-pleasure condition: incompatible trials preceded by incompatible trials (iI) were faster than incompatible trials preceded by compatible trials (cI), presumably because the preceding conflict trial evokes increased cognitive control (effect = 11 ms, t(19) = 2.2, $p < .05$). (Similarly, compatible trials preceded by incompatible trials (iC) were numerically slower than compatible trials preceded by compatible trials (cC) (effect = 5 ms, t(19) = 1.3, N.S.), probably because increased control decrease flanker facilitation). A planned comparison confirmed that humor reduced the conflict-adaptation effect (t(19) = 1.9, $p < .05$).

Note that humor did not modulate overall flanker interference (t(19) = 1.6, N.S.), suggesting that it did not change general motivation (Gable & Harmon-Jones, 2010b). Furthermore, there were no modulating effects of humor on error rate, indicating that the effects on reaction time cannot be attributed to speed-accuracy tradeoff (Fs(1,19) < 1; see Table 1). Post-experimental cartoon ratings (9-points scale) outside the scanner confirmed that funny cartoons were funnier than their neutral counterparts (M = 6.1 versus M = 2.3, t(19) = 13.0, p < .001).

fMRI results

In keeping with conflict monitoring theory (Botvinick et al., 2001) and previous observations (Kerns et al., 2004; Botvinick et al., 1999), we predicted that behavioral adjustment to conflict on a given trial should concur with reduced cognitive

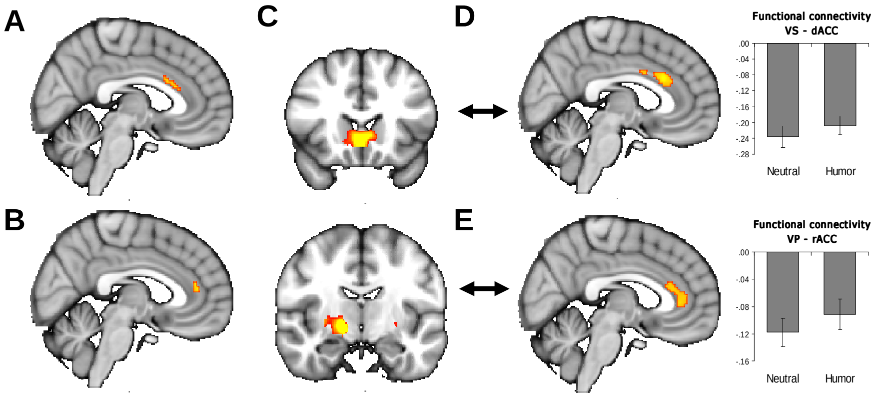

Figure 2. ***A.*** *Trial-to-trial adaptation in dorsal ACC (peak voxel in MNI coordinates: 2, 22, 20) for the cI > iI contrast of flanker trials following neutral cartoons. Confirming behavioral findings, there was no evidence for conflict adaptation in the ACC following funny cartoons, even when lowering the threshold to z = 1 (p = .15, uncorrected).* ***B.*** *Deactivation in the rostral ACC (2, 42, 12) for conflict trials following funny cartoons (versus neutral cartoons).* ***C.*** *In comparison to neutral cartoons, funny cartoons increased reward system activation in the ventral striatum (top slice, 2, 20, -4) and right posterior ventral pallidum (bottom slice, 14, -10, -8). Images are in radiological convention (left hemisphere to viewer's right). Activations in other regions are reported in Table 2.* ***D.*** *Psychophysiological interaction between ventral striatum and dorsal ACC (4, 24, 26) during conflict trials. This region overlaps with the activation cluster displayed in A.* ***E.*** *Psychophysiological interaction between ventral pallidum and rostral ACC (0, 40, 8) during conflict trials. This region overlaps with the activation cluster displayed in B.*

conflict registered in the ACC on the subsequent trial. This trial-to-trial adaptation effect should not be observed in the funny condition, in which behavioral conflict adaptation was cancelled out. Confirming predictions, activity in the dorsal ACC (dACC) decreased during iI as compared to cI trials following neutral cartoons, but not following funny cartoons (Figure 2A). This demonstrates that pleasure eliminates not only the behavioral adjustment to conflict but also the resulting adaptations of conflict monitoring activity in dACC.

To test the hypothesis that this reduction of conflict adaptation originates from general pleasure-driven ACC attenuation during conflict, we compared ACC activity elicited by conflict trials following neutral and following funny cartoons. Pleasure-related deactivation to conflict was observed in the affective, rostral part of the ACC (rACC; Figure 2B), presumably reflecting reduced negative appraisal of conflict when participants are in a hedonic state (Bush et al., 2000; Taylor et al., 2006). To test the hypothesis that rACC under neutral conditions plays a pivotal role in subsequent behavioral adjustment, we used intra-individual fluctuations in behavior adaptation during iI trials as a regressor to model predictive brain activity in the preceding conflict trial. Using an ROI analysis focusing on the dACC and rACC activation clusters, we found that neural conflict-related increases in the rACC were a successful predictor of subsequent behavioral adaptations following neutral cartoons ($t(19) = 2.7$, $p < .02$), but not following funny cartoons ($t(19) = -1.0$, $p = .30$). This suggests that the pleasure-driven reduction of activation in the rACC eliminated the implementation of conflict-driven cognitive control increases observed under normal, emotionally neutral conditions. No predictive brain activation was observed for the dACC ($|t|$s < 0.5).

We compared brain activation related to funny and neutral cartoons to determine the neural antecedents of conflict-related ACC attenuation. Replicating earlier findings (Mobbs et al., 2003), funny cartoons recruited a large network of brain areas involved in the representation of language, semantic, and motor aspects of humor (see Table 2). More importantly, we also replicated the involvement of mesolimbic reward circuitry. As predicted, funny cartoons elicited more activation than neutral cartoons in the VS and VP (Figure 2C) – the only two regions currently known to play a direct causal role in hedonic liking reactions (Kringelbach & Berridge, 2009). To investigate the modulatory role of activity in these regions during conflict processing, we carried out a psycho-physiological interaction (PPI) analysis, which provides a measure of condition-specific functional connectivity between two brain regions. This allowed us to test whether the negative coupling between ventral basal ganglia and ACC, as should be observed during conflict processing under affectively neutral conditions (Holroyd & Coles, 2002; Munte et al., 2008), is attenuated by pleasure. Confirming predictions, a PPI analysis using the VS as seed region revealed the dACC (Figure 2D), overlapping with the region earlier identified as cognitive conflict area (cf. Figure 2A). This network showed reduced conflict-related negative coupling in the funny condition. A similar interaction was observed between the VP and the rACC (Figure 2E), which overlaps with the rACC region identified earlier as being involved in the subjective emotional evaluation of conflict (cf. Figure 2B).

Additional fMRI analysis: breadth of attention

Earlier studies have suggested that conflict-driven behavioral adaptation reflects the neural enhancement of task-relevant information, whereas the behavioral compatibility effect may reflect susceptibility to task-irrelevant information related to increases in attentional breadth (Egner & Hirsch, 2005). Replicating earlier findings (van Steenbergen et al., 2009; van Steenbergen et al., 2010), our data suggest that pleasure can reduce conflict adaptation independently of modulations in the compatibility effect. However, it might still be argued that the small, though non-significant, decrease in the behavioral flanker compatibility effect following funny cartoons indicates that humor tends to reduce the susceptibility to task-irrelevant information. This effect might be driven by changes in motivation that are known to change attentional breadth (Rowe, Hirsh, & Anderson, 2007; Gable

Table 2. *Brain areas activated by funny versus neutral cartoons*

Regions	Left/ Right	Brodmann area	Cluster size (voxels)	Z-score	MNI coordinates		
					X	Y	Z
Temporal pole*, fusiform gyrus, ITG, MTG, STG, MTL, IFG, cerebellum, insula, amygdala, midbrain, thalamus, ventral pallidum	L/R	20, 21, 28, 36, 38, 44, 45, 48	15,238	6.27	-52	8	-20
Supplementary motor area*	L/R	6	462	3.98	-10	4	56
Sensorimotor cortex*	L	3	148	4.46	-48	-16	42
Sensorimotor cortex*	R	3	68	3.63	44	-16	36
Lateral occipital cortex*, angular gyrus, temporo-occipital junction	L	39, 21, 37	5,187	5.53	-42	-72	38
Lateral occipital cortex*, angular gyrus	R	39, 21	1,106	5.10	46	-68	40
Anterior cingulate gyrus*, medial frontal cortex	L/R	10, 24, 32	4,118	5.20	-2	18	24
Posterior cingulate gyrus*, precuneus	L/R	23, 31	2,105	4.47	-12	-52	22
Ventral striatum*	L/R	_	126	3.83	2	20	-4

* Denotes peak activation . Table shows activation clusters for the Funny cartoon > Neutral cartoon contrast, thresholded at $z > 3.1$; $p < 0.001$; > 50 contiguous voxels. Abbreviations: ITG, inferior temporal gyrus; MTG, middle temporal gyrus; STG, superior temporal gyrus; MTL, medial temporal lobe; IFG, inferior frontal gyrus.

& Harmon-Jones, 2010b; Schmitz, De Rosa, & Anderson, 2009). To investigate this possibility we analyzed neural activation in the visual cortex representing distracter-related information. Because the distracters in our flanker task were moving, we could use motion-related brain activity as a neural index of distracter activation.

In order to analyze individual distracter-related brain activation, a motion localizer task was used to identify each subject's MT+ complex, an area in the dorsal visual cortex that has consistently been implicated in human motion processing (Tootell et al., 1995). Epochs of moving flankers and still flankers were compared to identity motion-specific activation. Using this contrast, subject-specific MT ROIs were defined by spheres of radius 6 mm around the peak-activation voxel in the left and the right motion-related MT+ complex. Average activation in these two spheres was then used for individual ROI analyses.

MT ROI analyses were carried out in the trial-to-trial adaptation model earlier used to identify behavior-related conflict adaptation in the ACC. The moving flanker stimuli presented during the experiment were shown to reliably activate MT ($F(1,19) = 99.6$, $p < .001$, $MSE = 16.3$). However, paralleling the unreliable effect of humor on the behavioral compatibility effect, there was no effect of humor on distracter activation as measured in MT ($F(1,19) = 0.002$). This corroborates our conclusion that the breadth of attention is not reliably modulated by humor. The effects of current-trial compatibility, previous-trial compatibility or (higher-order) interactions were not significant ($Fs(1,19) < 1.7$). This is consistent with earlier findings showing that conflict-adaptation does not involve neural adaptation to task-irrelevant information (Egner & Hirsch, 2005).

Discussion

Altogether, our data demonstrate how pleasure induced by funny cartoons affects conflict processing: pleasure attenuates the rACC response to conflict and cancels out the resulting standard conflict adaptation as observed in behavior and monitoring-related dACC activation under neutral conditions. ACC was found to be functionally connected with hedonic hotspots in the VP and VS. Pleasure-related activation in the VP may have inhibited rACC activation, a region which in the neutral condition predicts subsequent behavioral adaptation. This finding implies that the rACC, presumably involved in the negative emotional evaluation of conflict (Bush et al., 2000; Taylor et al., 2006), drives subsequent cognitive control.

This suggestion is corroborated by recent observations from lesion studies showing that conflict-driven activation and behavioral adjustment crucially depends on intact VP and rACC (di Pellegrino, Ciaramelli, & Ladavas, 2007; Ullsperger & von Cramon, 2006). Subsequent adaptations in control were shown to be registered by the dACC, a region well-known for its role in the cognitive monitoring of conflict (Botvinick et al., 2001). Feedback signals for future behavioral optimization processed in the dACC appeared to be conveyed through the VS to become integrated with hedonic state information.

The functional network identified in this study converges with well-known cortico-basal ganglia anatomical connections, looping between ACC and VS through the VP and thalamus (Alexander, Delong, & Strick, 1986). This 'limbic' loop may have played an important role in the affective regulation of conflict-driven behavior observed. Modulation of functional coupling between the basal ganglia (BG) and ACC is probably driven by neuromodulatory input via dopamine and opioid receptors (Holroyd & Coles, 2002; Kringelbach & Berridge, 2009). Conflict-driven motivation and behavioral adjustment may depend on phasic dopamine fluctuations (Holroyd & Coles, 2002; Jocham & Ullsperger, 2009; van Steenbergen et al., 2009). Hedonic liking modulation is probably mediated by tonic opioid input (Barbano & Cador, 2007; Kringelbach & Berridge, 2009). Future research is needed to further understand the neurochemical basis of this BG-ACC network modulation.

This study provides an initial answer to the question why humor and jokes are so central to humanity: they appear to be adaptive means to transiently reduce the impact of cognitive demands on our behavior through activation of the neural reward system. One important goal for future research is to investigate how positive emotions can also promote beneficial neural effects in the long term. Such advances in the cognitive neuroscience of pleasure are necessary to further extend our understanding of how positive emotions can protect and improve our mental and physical health (Garland et al., 2010).

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