

Emotion-dependent modulation of interference processes: an fMRI study

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We studied the effects of experimentally induced emotions on inhibitory control using functional magnetic resonance tomography (fMRI). The Simon task used involves two conditions with different attentional demands and is a well established paradigm for studying inhibitory control. Incompatible trials demand cognitive control for resolving interference. Compatible trials need no inhibitory control. Twelve participants viewed a series of affective pictures inducing positive, negative or neutral affects. Between the picture blocks, participants performed either incompatible or compatible trials. Behavioral and fMRI data revealed an impact of negative emotions only on the processing of incompatible trials. Subjects made more errors and showed less activation of brain areas associated with task performance. There was no effect of positive emotions neither on compatible nor incompatible trials. The results first showed that especially the processing of negative emotions is resource competing and secondly that the competition concerns only the controlled route of cognitive processing.

Key words: interference processes, inhibitory control, Simon paradigm, emotional context, fMRI

INTRODUCTION

Both cognitive processes and affective states function as control systems influencing and regulating ongoing and future behavior (Carver and Schreier 1990, Kosslyn and Koenig 1992, Braver and Cohen 2000, Sommer et al. 2006). Several behavioral (e.g. Erthal et al. 2005) and neurobiological studies (e.g. Simpson et al. 2000, 2001a,b, Gray and Braver 2002, Gray et al. 2002, Meinhardt and Perkun 2003) investigated the dynamic interaction between affective and cognitive processes. However, the impact of emotional responding on cognitive processing is not yet well understood (Blair et al. 2007).

Researchers investigating the behavioral and neurobiological effects of emotions on cognitive processes postulated different types of emotional impact. Cognitive resource models propose a main effect of emotions on cognitive processes. Ellis and Ashbrook

(1988) assumed that emotions may increase the information processing load and drain attentional resources that otherwise might be devoted to task performance. But to what extent emotional stimuli consume attention is still under debate. Based on the results of behavioral (Ohman et al. 2001, Richards and Blanchette 2004) and neurocognitive studies (Vuilleumier et al. 2001, Meinhardt and Pekrun 2003, Phelps et al. 2006). Vuilleumier (2005) suggested that emotional information is processed prioritized especially under conditions where attentional resources are limited. However, Pessoa and colleagues (2001) found the opposite result. In a spatial attention task he found no effects of simultaneously presented emotional stimuli on task performance. Pessoa (2005) assumed that only when sufficient attentional resources are available emotional stimuli are processed independently of the focus of attention. In contrast to the main effect models some researchers postulated an interaction of cognition and emotion. Gray (2001) suggested that approach and withdrawal emotional states can enhance or impair cognitive performance depending on the particular emotion and cognitive process involved. According to

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this hypothesis Heller and Nitschke (1998) found that positive emotions tend to facilitate performance on tasks that depend more on the left prefrontal cortex (PFC), whereas negative emotions tend to facilitate performance on tasks depending on right PFC. Simpson and coworkers (2001a,b) demonstrated that the degree of activity reduction in emotion processing brain areas depends on a combined effect of the task's attentional demands and accompanying performance anxiety.

In sum, results of studies investigating the impact of emotions on cognitive processes are inconsistent. These inconsistencies can be attributed to different research strategies. Some studies did not investigate the impact of an emotional state on cognitive processes, but rather the influence of processing emotional stimuli. In these studies affective and non-affective stimuli were presented simultaneously (Pessoa et al. 2002, Vuilleumier 2005) or they used a short presentation of an emotional stimuli as a distractor (Blair et al. 2007). Other studies investigated the impact of emotion-related personality traits (e.g. test anxiety), or pathological states (e.g. depression) on cognitive tasks (Simpson et al. 2001b). Only a small number of studies evaluated the impact of either explicitly induced emotions or an emotional context. These studies particularly investigated the influence of emotions on memory processes (Maratos et al. 2001, Gray et al. 2002, Erk et al. 2003, Medford et al. 2005). Only the EEG study of Meinhardt and Pekrun (2003) investigated the impact of experimentally induced positive and negative emotions on the performance of an oddball paradigm and found that not only negative but also positive emotions compete with task processing resources. Studies investigating the interactions between emotion processing and such important cognitive functions like executive functions are lacking.

The aims of the present study were threefold: First, we wanted to explore the effects of induced emotions on cognitive processes in healthy people. Until now most studies investigated the impact of affective-related pathological states on cognitive processes, but little is known about the interaction between affective states and cognitive processes in healthy persons. Second, we wanted to investigate differential effects of positive and negative emotions. Most studies investigating emotional impact on cognitive processes compared neutral with negative emotions (Maratos et al. 2001, Medford et al. 2005). These emotions differ in their arousal level and therefore it is possible that an impact

is associated with arousal rather than with emotion processing. Third, the study should help to highlight the effects of emotions on cognitive processes associated with inhibitory control. Inhibition refers to the ability to actively suppress a response, interrupt an activated response, delay a response, and avoid interference. This essential regulatory executive function allows an individual to successfully negotiate their environment. Clinical research showed that the inhibitory control is reduced in patients with anxiety disorders, high impulsivity or obsessive-compulsive disorders (Gehring et al. 2000, Pailing et al. 2002). But until now the impact of emotional states on inhibition in healthy people remains unclear.

One well-established paradigm for studying inhibitory control is the Simon task. In a Simon task visual stimuli are presented on the left or on the right side of a screen. Subjects have to select their spatially defined responses (e.g. a left or right key) on the basis of a non-spatial stimuli feature (e.g. shape). The Simon effect represents the very robust finding that responses where the stimulus location and the response location correspond (compatible trials) are generally faster than responses where the location of the stimulus and the response key do not correspond (incompatible trials; for an overview see Lu and Proctor 1995). In the Simon paradigm, active cognitive control of visual selective attention is needed to resolve conflict between the target features (e.g. shape) and the potent salient distractor (e.g. side of the stimulus presentation) that strongly competes with the target (Lavie 2005). The activation of the corresponding response by the spatial stimulus code is often explained by the dual-route model (e.g. De Jong et al. 1994, Eimer et al. 1995, Kornblum et al. 1990). According to this model, a stimulus automatically activates its spatially corresponding response through an automatic route. Contrarily, the relevant stimulus dimension activates the correct response on the basis of task instruction through a non-automatic, controlled route. Therefore the Simon paradigm involved two conditions with different attentional demands.

We used fMRI to assess brain activity during the performance of a Simon task after emotion induction with pictures. With the Simon paradigm and the induction of positive, negative and neutral emotions we were able to test both differential effects of emotions on tasks with different attentional demands and the effects of different emotions on inhibition processes. We sup-

posed that especially the negative emotions – respectively their cognitive consequences – were task competing for the processing of the Simon task. Because of their higher cognitive demands, the processing of the incompatible trials should have been affected by the competition of resources. We expected no effects of emotions on compatible trials. We assumed higher error rates and longer reaction times for incompatible trials in an emotional negative context. Because behavioral effects like reaction time and error rate would not be statistically reliable in a small sample, we assessed additional 38 participants tested with the same design but without fMRI scanning (total 50 participants). For the imaging data we focused on which brain areas the interaction of emotion and cognition would occur. According to the assumptions of Gray and colleagues (2002) we expected the impact of emotions on task processing to be modulated by cognitive demand and the interaction between emotional and cognitive processing to be primarily relevant in brain areas associated with interference processes, such as the anterior cingulate and the dorsolateral prefrontal cortex (Peterson et al. 2002, Fan et al. 2003). In these brain areas we expected less activation for the negative condition in contrast to the neutral and positive condition during processing of incompatible trials.

METHODS

Subjects

In the fMRI study twelve male, right-handed, healthy volunteers (mean age 29.1 years, range 22–37 years) gave written informed consent and participated in the study according to the guidelines of the local Ethics Committee. All subjects were free of serious head injury, psychiatric, neurological, or substance-abuse problems or history of other medical problems or treatment relevant to the cerebral metabolism and blood flow.

In the additional behavioral study 38 right-handed, healthy volunteers participated (20 male and 18 female; mean age 28 years, range 20–43 years). For these subjects the same exclusion criteria were valid.

Task

Stimuli were presented using a video-beamer on a screen, which could be seen *via* a mirror fixed on the

head coil of the MRI. At the beginning of each Simon task trial, a yellow fixation cross was presented at the center of the black screen for 500 ms. Then in yellow an 'X' or an 'O' appeared for max. 1 000 ms on the left or right side of the black screen. The subjects were instructed to respond as fast as possible with their middle finger of the right hand to the X and with their index finger of the right hand to the O, regardless of the side in which the stimulus appeared. In the compatible trials, the X appeared on the right side and the O on the left side. In the incompatible trials the X appeared on the left side and the O on the right side.

Affective stimuli

For the emotion induction, eighty-four pictures were selected from the International Affective Pictures System¹ (IAPS; CSEA-NIMH). The positive set contained twenty-eight pictures of pleasant stimuli (e.g., romantic couples, babies, animals). The second set contained twenty-eight neutral pictures (e.g., household objects, nature scenes). The third set contained twenty-eight unpleasant pictures (e.g., mutilations, disgusting animals). Self-report ratings of valence and arousal from the technical report of the IAPS (Lang et al. 1995) determined the selection of pictures and designation to categories.

To control the effectiveness of the emotion induction after each run, the participants rated the emotions they had experienced during the task on eleven unipolar items from a paper and pencil questionnaire. The items were: arousal, joy, contentment, happiness, cheeriness, good temper, fear, adversity, anger, boredom and sadness. Participants rated the felt intensity of each emotion (not at all = 1, very strong = 9). The effectiveness of the emotion induction of the particular run was measured by averaging the scores for the positive affect items (joy, contentment, happiness, cheerfulness and good temper) and for the negative affect items (fear, adversity, anger, boredom and sadness). An internal reliability analysis of the affect scales was performed by averaging items' score across all runs. For analyzing the effects of the emotion induction in each run the

¹ positive set: 1440, 1460, 1710, 1750, 2040, 2070, 2260, 2311, 2550, 2660, 4002, 4220, 4235, 4520, 4608, 4611, 4658, 4660, 4680, 5260, 5600, 5623, 5626, 5700, 5830, 5900, 5910, 5982; neutral set: 1390, 1450, 5520, 5535, 5593, 5711, 5750, 7000, 7002, 7004, 7009, 7010, 7034, 7037, 7039, 7041, 7050, 7080, 7090, 7140, 7150, 7161, 7175, 7190, 7205, 7230, 7950, 1390; negative set: 1050, 1111, 1201, 1220, 1932, 2205, 2683, 2710, 2730, 2750, 2800, 2900, 3000, 3010, 3015, 3053, 3060, 3120, 3130, 3150, 6212, 6230, 6370, 9040, 9050, 9301, 9405, 9560

scores of the negative and positive affect scales were subjected to a within-subjects repeated measures analyses of variance (ANOVA) with the two factors 'Emotion Condition' (pleasant run, unpleasant run) and 'Affect Scale' (negative, positive).

To evaluate the individual assessment of pictures, affective picture ratings were made after scanning. All 84 pictures were shown in random order. Immediately after each picture, the participants judged the affective valence (very unpleasant = 1, very pleasant = 9) and arousal (not at all = 1, very strong = 9) on rating scales. For valence and arousal, separate data analyses were performed using within-subjects repeated measures analyses of variance (ANOVA).

For all behavioral data to compensate for the non-sphericity of data, the significance level of all ANOVA effects was adjusted by the Huynh-Feldt method. Reported *P* values reflect this correction. A significance level of $P < 0.05$ was used in all behavioral analyses. Effects involving variables with more than two levels were followed up by planned *t*-test comparisons when appropriate.

Procedure

Three runs with 100 volumes each were made. Every run included pictures of one valence (negative, positive or neutral). At the beginning of every run the participants viewed 8 affective pictures 3 000 ms each. After the last picture disappeared, a fixation cross was presented for 2 000 ms and then the Simon-paradigm began. The Simon task was separated into six blocks. Every block consisted of 24 trials and lasted between 22–26 s. Three blocks consisted of only compatible trials, and three blocks of incompatible (80%) and few randomly presented compatible (20%) trials. The blocks were presented randomly. Between each Simon block affective picture blocks were presented for 12 s to refresh the emotion induction. Every picture block consisted of four affective pictures. Every picture was presented for 3 000 ms. At the end of each picture block a fixation cross was presented for 2 000 ms. To control for order effects, the presentation order of the three emotion conditions was counterbalanced.

Image acquisition

Blood oxygenation level-dependent fMRI (BOLD) was acquired with a 1.5 Tesla Siemens Symphony

system, (Siemens, Erlangen, Germany) using a gradient echo planar imaging (EPI) sequence. The automated Siemens shim procedure was applied to minimize possible magnetic field inhomogeneities. To prevent head motion, foam pads were placed inside the head coil.

A T2*-weighted echo planar imaging (EPI) sequence (100 measurements; TR = 2 092.0 ms; TE = 60 ms; $\alpha = 90^\circ$ in plane matrix 64×64 ; FoV = 240 mm; slice-thickness = 5.0; distance factor 0.2; pixel size = $3.75 \text{ mm} \times 3.75 \text{ mm}$) was applied with a stack of 20 contiguous slices (5 mm thickness each) aligned to the AC-PC-plane. The EPI sequence began at the cerebral vertex and encompassed the entire cerebrum and the majority of the cerebellum. The time period for the acquisition of the 20 slices was 2 s. In each run a total of 100 images was acquired for each subject, with the first four images being discarded in later data processing. For anatomical correlation, a high-resolution T1-weighted scan was acquired before the fMRI experiment (TR = 11.1 ms, TE = 4.3 ms, matrix 256^3 , isotropic voxel size 1 mm^3).

fMRI data analysis

The fMRI data processing was performed using Brain Voyager 4.6 (BrainInnovation, Maastricht, The Netherlands; www.braininnovation.com). Prior to statistical analysis, the time series of the functional images were aligned for each slice in order to minimize the signal changes related to small motions of the subject during acquisition. Temporal filtering of functional time series included removal of the linear drifts of the signal with respect to time from each voxel's time-course and removing frequency components below 3 cycles within the time series. After these pre-processing steps, each complete functional time series was co-registered to the three-dimensional anatomical volume and normalized into Talairach space. A separate general linear model (GLM) with the two regressors 'compatible trials' and 'incompatible trials' was defined for each participant and each emotion condition (Friston et al. 1995). Each regressor was convolved with the standard gamma model of the hemodynamic response function. Then a GLM with the two factors 'Emotion' (negative, positive, neutral) and 'Compatibility' (incompatible, compatible) for the group was computed. The GLM was corrected for temporal autocorrelation using a first-order autoregressive model. The

resulting statistical map was thresholded to display only those voxels where the statistic reached a corrected P value less than 0.001.

First, we analyzed the effects of incompatibility without emotional influence by contrasting incompatible trials *versus* compatible trials in the neutral condition. Second, we analyzed the effects of the emotion induction on task performance. Brain areas with a significant ‘Emotion \times Compatibility’ interaction were identified as integration sensitive brain areas and defined as regions of interest (ROIs). For these ROIs, a t -statistic was computed. The resulting map of the t -statistic was thresholded to display only those voxels whose t -statistic reached a P value less than 0.001.

RESULTS

Behavioral data

Emotion induction

Internal reliability analysis for the averaged items showed that scale reliability was quite satisfactory. Reliabilities of the averaged positive and the averaged negative affect indices were $\alpha = 0.90$ and 0.83 . It must be mentioned that these relatively high reliability indices for the two scores might have been caused by the high homogeneity of the included five items.

The within-subject repeated measures ANOVA with the two factors ‘Emotion Condition’ (pleasant, unpleasant) and ‘Affect Scale’ (positive, negative) revealed a significant main effect for ‘Emotion Condition’ ($F_{1,11}=14.53$, $P<0.01$) and ‘Affect Scale’ ($F_{1,11}=24.7$, $P<0.001$) and a significant interaction between ‘Emotion Condition \times Affect Scale’ ($F_{1,11}=144.7$, $P<0.001$, $\varepsilon=1.00$) (see Fig. 1). Planned contrasts showed that the ratings were concordant with the emotional categories. Ratings for positive affect were highest for the pleasant condition ($M = 6.5$, $SD = 1.4$) and much lower for the unpleasant condition ($M = 1.9$, $SD = 0.7$; $t_{11}=11.3$, $P<0.001$). Contrarily, ratings of negative affect were higher for the unpleasant condition ($M = 3.4$, $SD = 1.7$) and much lower for the positive condition ($M = 1.3$, $SD = 0.5$; $t_{11}=-4.6$, $P<0.01$).

In addition we analyzed the ratings for the arousal item. Compared to the neutral condition ($M = 3.0$, $SD = 2.2$), subjects reported significantly higher arousal ratings for the pleasant ($M = 5.7$, $SD = 1.6$; $t_{11}=3.6$,

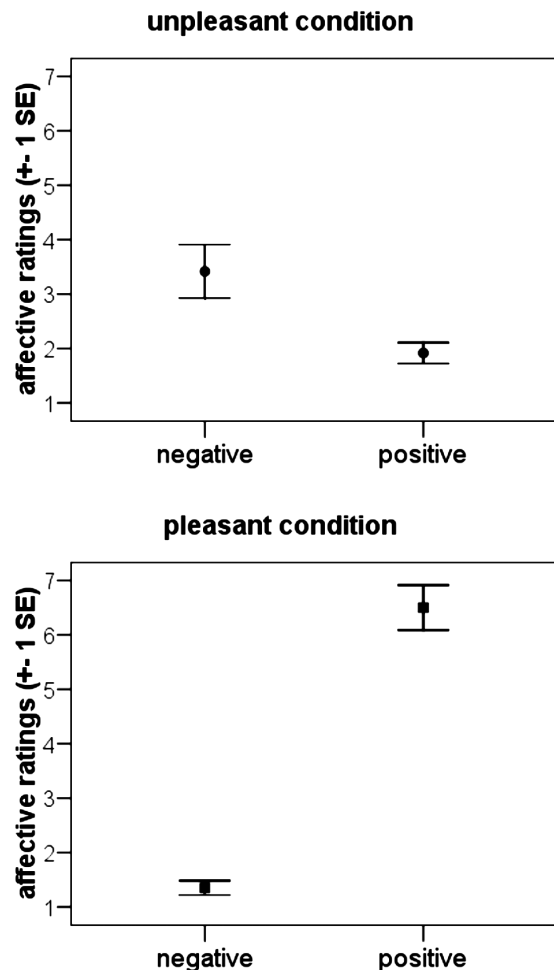


Fig. 1. Affective ratings of the emotion conditions. (Top) Ratings for the unpleasant condition show that participants indicated significantly more negative affect than positive affect. (Bottom) Contrarily, in the pleasant condition, ratings for the positive affect were significantly higher than for the negative affect.

$P<0.01$) and unpleasant ($M = 5.5$, $SD = 1.9$; $t_{11}= 3.3$, $P<0.01$) condition. There was no difference in arousal between the two affect conditions.

Affective picture ratings

Subjective ratings of valence and arousal of the presented pictures were separately averaged for each participant and the positive, neutral and negative picture set. On valence ratings, the within-subject repeated measures ANOVA revealed a significant effect for ‘Picture Set’ ($F_{2,22}=275.2$, $P<0.001$, $\varepsilon=0.93$). Average valence ratings were significantly higher for the posi-

tive ($M = 6.56$, $SD = 0.49$), than for the neutral picture set ($M = 5.42$, $SD = 0.60$, $t_{11}=6.02$, $P < 0.001$), and higher for the neutral than for the negative set ($M = 2.66$, $SD = 0.50$, $t_{11}=20.45$, $P < 0.001$). On arousal ratings, ANOVA also revealed a significant effect for ‘Picture Set’ ($F_{2,22}=17.12$, $P < 0.001$, $\epsilon=0.69$). Both the positive ($M = 4.75$, $SD = 1.33$) and negative ($M = 5.39$, $SD = 1.83$) picture sets had significantly higher arousal ratings than the neutral set ($M = 2.31$, $SD = 1.41$, $t_{11}=5.06$, $P < 0.001$, and $t_{11}=4.29$, $P < 0.001$).

Simon-Paradigm

Reaction times were only analyzed for the correct answers. We found no effects of the emotion induction on reaction time for the 12 participants of the fMRI study (‘Compatibility \times Emotion’ interaction $F_{2,18}=0.87$, n.s.). But there was a significant main effect for ‘Compatibility’ ($F_{1,11}=103.4$, $P < 0.001$, $\epsilon=1.0$). Reaction times for incompatible trials ($M = 494.6$ ms, $SD = 67.4$) were significantly longer than for compatible trials ($M = 408.1$, $SD = 65.4$; $t_{11}=10.2$, $P < 0.001$). Because behavioral effects are not statistically reliable in a small sample, we also reported the behavioral effects of an additional 38 participants tested in a similar design without fMRI scanning. For this larger sample we found no main effect ‘Emotion’ ($F_{2,74}=1.1$, n.s.), but a main effect ‘Compatibility’ ($F_{1,37}=141.9$, $P < 0.001$, $\epsilon=1.0$) with significantly longer reaction times for incompatible trials ($M = 515.2$, $SD = 84.9$) compared to compatible trials ($M = 421.2$, $SD = 74.5$; $t_{40}=12.2$, $P < 0.001$). Additionally, there was a trend for the ‘Compatibility \times Emotion’ interaction ($F_{2,74}=2.8$, $P=0.08$, $\epsilon=0.843$).

For the error rate, the 12 participants of the fMRI study showed a significant main effect ‘Compatibility’ ($F_{1,11}=19.5$, $P < 0.01$, $\epsilon=1.0$) with significantly more errors in the incompatible condition ($M = 7.6$, $SD = 5.8$) than in the compatible condition ($M = 0.6$, $SD = 0.8$, $t_{11}=4.4$, $P < 0.01$). Additionally, we found main effect ‘Emotion’ ($F_{2,22}=3.8$, $P=0.05$, $\epsilon=0.8$), but no interaction. Figure 2 shows that negative emotions lead to more errors, in contrast to positive and neutral emotions in the incompatible condition. The analysis of the error rates for the 38 participants of the behavioral study showed two significant main effects ‘Compatibility’ ($F_{1,74}=54.29$, $P < 0.0001$, $\epsilon=1.0$) and ‘Emotion’ ($F_{2,74}=3.6$, $P < 0.05$, $\epsilon=1.0$), and a significant interaction ($F_{2,74}=4.1$, $P < 0.05$). In agreement with the literature, error rates for incompatible trials were significantly higher

($M = 8.1$, $SD = 6.5$) than for compatible trials ($M = 0.8$, $SD = 1.1$, $t_{37}=7.4$, $P < 0.001$). Figure 2 shows that in contrast to the positive and neutral emotions, negative emotions lead to significantly more errors in the incompatible condition (negative vs. neutral, $t_{37}=2.1$, $P < 0.01$; negative vs. positive, $t_{37}=1.9$, $P < 0.05$). Planned post-hoc tests revealed no effect of the emotional context on the error rates of the compatible trials.

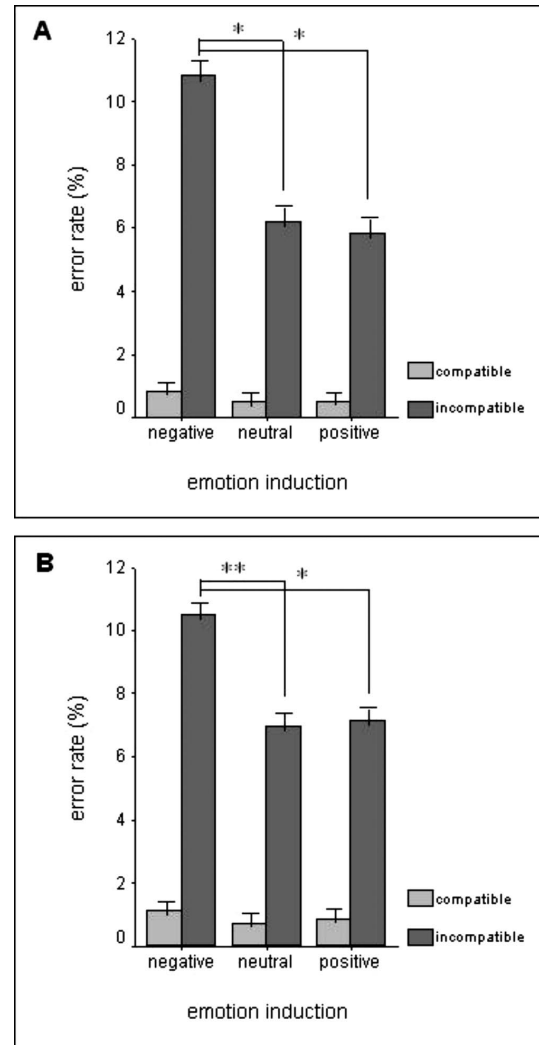


Fig. 2. Error rate of the Simon Paradigm: (A) results of the 12 participants of the fMRI study; (B) results of the participants of the behavioral study ($n=38$). Error rates were significantly higher for incompatible trials (dark grey) than for compatible trials (light grey). Emotion induction only influences the incompatible trials. In contrast to the positive and neutral emotional context in the negative emotional context, subjects made significantly more errors for incompatible trials (* $P < 0.05$; ** $P < 0.01$).

fMRI-data

In the neutral condition, incompatible trials in contrast to compatible trials show more activation in the left precentral frontal gyrus (BA 6; $x=-33$, $y=-16$, $z=60$), the right middle frontal gyrus (BA 9, $x=30$, $y=31$, $z=37$), the middle cingulate gyrus (BA 24; $x=-8$, $y=2$, $z=49$), the bilateral temporal gyrus (BA 37; right: $x=46$, $y=-59$, $z=0$; left: $x=-35$, $y=-62$, $z=-9$), the right insula (BA 13; $x=35$, $y=9$, $z=10$), the bilateral thalamus (right: $x=6$, $y=21$, $z=10$; left: $x=-15$, $y=-17$, $z=15$), the bilateral inferior parietal gyrus (BA 40; right: $x=46$, $y=-35$, $z=35$, left: $x=-33$, $y=-55$, $z=35$), as well as the right parietal gyrus (BA 7: $x=16$, $y=-68$, $z=41$).

The analysis of the influence of pleasant and unpleasant emotions on interference processes revealed several areas sensitive to the 'Emotion \times Compatibility' interaction, including the left superior frontal gyrus (BA9; $F_{2,22}=6.44$, $P<0.05$), the right inferior frontal gyrus (BA9; $F_{2,22}=6.55$, $P<0.01$), the right middle frontal gyrus (BA 10; $F_{2,22}=5.14$, $P<0.05$) and the left cingulate cortex (BA24; $F_{2,22}=5.61$, $P<0.05$). These regions show no main effect for 'Compatibility' or 'Emotion' (Table I).

Post-hoc tests of the 'Emotion \times Compatibility' interaction revealed an influence of the emotion induction only for incompatible trials (Fig. 3). Negative emotions in contrast to neutral emotions led to significantly less activation in right BA10 ($t_{11}=2.46$, $P<0.05$), right inferior BA9 ($t_{11}=2.87$, $P<0.05$), left superior BA 9 ($t_{11}=-2.7$, $P<0.05$) and cingulate cortex ($t_{11}=-2.36$, $P<0.05$). There were no differences between the neutral and positive conditions.

DISCUSSION

The present study explored the influence of experimentally induced emotions on interference processes. Using fMRI we investigated the neural correlates of the influence of emotions on the inhibitory control of prepotent or dominant responses and the process of resolving interference.

Behavioral data

Self-ratings showed that our emotion induction procedure was done successfully. Participants felt emotionally affected as a consequence of viewing pleasant and unpleasant IAPS pictures. Unfortunately, it was not possible to measure the participant's affective state online. Therefore we measured the effects of the emotion induction by using rating scales. Immediately after each run participants rated the emotions they had experienced during the task on a questionnaire. Although we could show that the participants felt emotionally affected, critically, it is possible that the participant's affective state fluctuated during the whole run.

Subjects' reaction times confirmed the well-known interference effect of the Simon paradigm. Independent of the induced emotion, reaction times for incompatible trials were significantly longer than for compatible trials. This result is in accordance with the dual process theory of Schneider and Shiffrin (1977). They postulated that controlled processing is typically slower and more sensitive to capacity limits than automatic processing.

Table I

Areas sensitive to cognition-emotion integration					
Brain region	BA	Center Talairach Coordinates			Size, voxels
		x	y	z	
Right inferior frontal gyrus	9	36	7	29	258
Left superior frontal gyrus	9	-20	40	31	130
Right middle frontal gyrus	10	32	41	17	157
Cingulate gyrus	24	0	2	47	295

Areas sensitive to cognition-emotion integration (confidence range = 4.4–8.0; minimal cluster size = 60). The effect was corrected for serial correlation ($P(\text{corrected})<0.001$). X, Y, Z are coordinates according to the Talairach system (BA = Brodman's area).

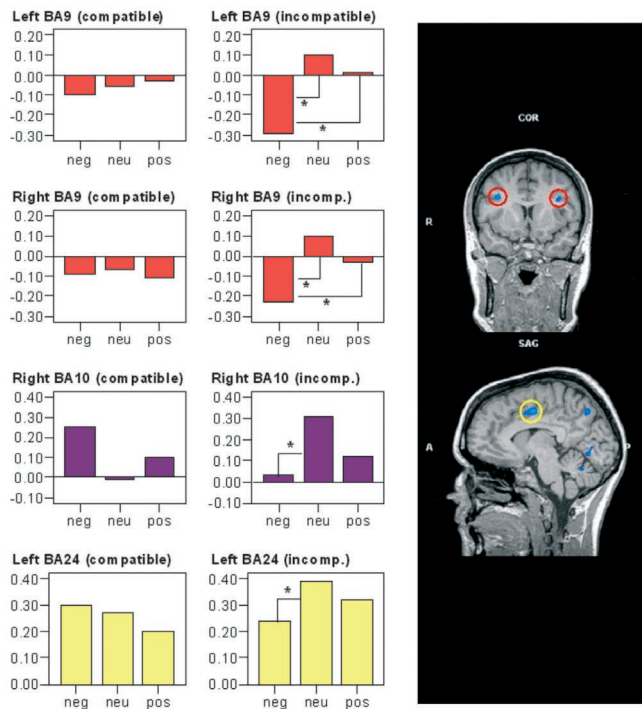


Fig. 3. (Left) Percent signal change in the brain areas showing a significant “Compatibility \times Emotion” interaction. For compatible trials there was no significant influence of the emotional context on the hemodynamic response. For incompatible trials we found less activation during the negative emotional context in contrast to the neutral and positive context ($P < 0.01$). (Right) Brain areas showing a significant interaction effect [(red) left inferior frontal gyrus (BA9); (purple) right middle frontal gyrus (BA10); (yellow) cingulate cortex (BA24)].

In the present study we found an impact of emotions on error rates only for incompatible trials but not for compatible trials. After negative emotion induction, participants made more errors in incompatible trials compared to compatible trials. Resolving interference in a Simon task requires the inhibitory control of prepotent motor responses in a controlled information processing mode. The present results showed first, that the interference process is sensitive for conditions limiting cognitive capacity; second, that particularly the processing of negative emotions is resource competing; and third, that the resource competition concerns only the processing of controlled inhibition and not cognitive processes *per se*. This result cannot be explained by an unspecific arousal effect. The subjective arousal ratings did not differ between the positive and negative emotional conditions.

fMRI data

In the neutral condition, incompatible trials in contrast to compatible trials activate the precentral and middle frontal gyrus, the cingulate gyrus, the temporal and parietal gyrus, the thalamus, the insula and the basal ganglia. This neural activation pattern is in line with previous fMRI studies that investigated interference processes (Peterson et al. 2002, Fan et al. 2003, Sylvester et al. 2003). Although we used a block-design we suggest that we were able to replicate the Simon effect.

The influence of negative emotions on interference processes is not only reflected in the behavioral data, but also in the neural correlates. For incompatible trials we found several areas sensitive to the influence of induced negative emotions, including right inferior frontal cortex (BA 9), right middle frontal gyrus (BA 10), left superior frontal gyrus (BA 9) and cingulate cortex (BA 24). Compared to the neutral condition, the negative emotions lead to less activation of these areas during interference processing. This result is consistent with studies showing an emotion associated modulation of activity in areas primarily involved in the processing of the cognitive task (Maratos et al. 2001, Gray et al. 2002). Unlike the study of Maratos and others (2001), the present results reveal that the additional emotion processing did not recruit extra brain areas, e.g. areas known to be activated during emotion processing, but they modulated areas concerned with resolving interference.

For resolving interference, it is supposed that the dorsolateral prefrontal cortex maintains and updates/manipulates the contents of working memory (e.g. the response rule; Goldman-Rakic 1996, Jonides and Smith 1997). In the present study, the dorsolateral prefrontal cortex was sensitive to both emotion and cognitive processing (Fig. 3). According to Gray and coauthors (2002), emotional states are able to enhance or impair cognitive functions, whereby they could adaptively bias the overall control of thought and behavior to meet situational demands effectively. A functional integration of emotion and cognition would allow goal-directed control of behavior depending on the emotional context. Gray and others (2002) suggested that the lateral prefrontal cortex is a candidate area for the integration of emotion and cognition.

The engagement of the anterior cingulate cortex (ACC) in conflict processing, especially the overriding of prepotent responses, is one of the most established

results in cognitive neuroscience (Fan et al. 2003; for an overview see Botvinick et al. 2004). Most results pertain to Stroop task, where relative ACC activation has been observed in association with incompatible trials (Compton et al. 2003), but has also been observed in the Simon task (Peterson et al. 2002). In line with these results, we also found activation of the ACC for incompatible trials in contrast to compatible trials in the neutral condition. Several imaging studies suggested that dorsal ACC and areas of the lateral prefrontal cortex operate together during tasks that involve a high level of mental effort (Dehaene et al. 1998, Bush et al. 2000). This idea is consistent with our results showing increased activation of ACC and dorsolateral frontal areas bilaterally during incompatible trials. Additionally, the ACC activation and also the dorsolateral prefrontal activation was affected by emotion manipulation. This differential activation effect was not found in the rostral anterior cingulate division of the ACC, which is associated with emotion-related tasks, but in the more dorsal anterior cingulate division, which is associated with cognitively demanding tasks (Bush et al. 2000). The division of the ACC in a more cognitive and a more affective part based upon studies using emotional stimuli (e.g. emotional counting Stroop; Whalen et al. 1998). The results of our study suggest that the processing of negative emotions also influences the cognitive division of the ACC during a cognitive task.

In sum, the behavioral and fMRI data provide evidence that experimentally induced emotions influence the processing of an important regulatory cognitive function such as inhibitory control. After negative emotion induction, participants made more errors in incompatible trials compared to compatible trials. Additionally, negative emotions induced less activation in brain areas which are involved in inhibitory control. Notwithstanding, the positive emotion induction showed no effects neither on compatible trials nor on incompatible trials.

Some limitations of our study must be noted. First, we used a block design. Block designs in which individual events are clustered into periods of activation alternated with control periods have the advantage of nearly optimal detection power, but poor detection efficiency (Liu and Frank 2004). Although we were not interested in studying the neural mechanisms of interference processes, future studies evaluating the effects of emotions on conflict task should use event-related

fMRI. Nevertheless, we think that our study can make some contributions to neurocognitive aspects of the emotion-cognition interaction. Although we used a block-design, the analysis of the neutral condition revealed activated brain areas which are in line with previous imaging studies on interference processes (Peterson et al. 2002, Fan et al. 2003). Durston and colleagues (2003) examined the influence of preceding context on response competition by using a flanker task. They found that the anterior cingulate, the dorsolateral prefrontal cortex and superior parietal regions showed activity depending on the number of preceding compatible or incompatible trials. The modulation of brain activity in our study is not associated with the number and kind of preceding stimuli. We found a modulation of brain activity depending on the emotional context only in blocks with primarily incompatible trials showing that cognitive and affective processes compete for task processing load. This is especially true in conditions where the attentional resources are limited. Second, we found no interaction between emotion and compatibility on error rates or reaction time for the twelve participants of the fMRI study. However, we suggest that the significant interaction of the greater sample supports the assumption that in the controlled processing mode, negative emotions increase the load and drain resources that otherwise might be devoted to task performance.

CONCLUSIONS

The present results first suggest an impact of negative emotions on interference processes. Second, they suggest that induced negative emotions modulate the controlled processing mode, while the automatic processing mode is not concerned. And finally, they indicate that negative emotions modulate brain areas primarily associated with the processing of the cognitive task. Although the Simon paradigm represents a comparatively easy task with no highly demanding cognitive input, the induced negative emotions modulate the activity of the brain areas involved.

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