Impaired Conflict Adaptation in an Emotional Task Context following Rostral Anterior Cingulate Cortex Lesions in Humans

Martin E. Maier and Giuseppe di Pellegrino

Abstract

Recent brain imaging studies have implicated the rostral ACC (rACC) in the resolution of conflict between competing response tendencies in emotional task contexts, but not in neutral task contexts. This study tested the hypothesis that the rACC is necessary for such context-specific conflict adaptation. To this end, a group of patients with lesions of the rACC, a group of brain-damaged controls and a group of normal controls classified the emotional expression (emotional task context) or the gender (neutral task context) of faces while ignoring congruent and incongruent words written across the faces. In all three groups, performance was worse with incongruent as compared with congruent stimuli in both task contexts. In the two control groups, this congruency effect was reduced following incongruent trials in both task contexts. By contrast, the rACC group displayed such conflict adaptation only in the neutral, but not in the emotional, task context. These results show that the rACC is necessary for conflict adaptation in emotional but not in neutral task contexts and suggest that the regulation of behavior is context specific.

INTRODUCTION

When performing a task in a complex and dynamic environment, one needs to attend to those stimuli that are needed to solve the task. However, it can be beneficial to process also task-irrelevant environmental stimuli, because they can facilitate performance if they are in line with current goals. By contrast, if task-irrelevant stimuli interfere with current goals, they should be ignored, as their processing can yield performance decrements or even errors. Thus, for an efficient goal-directed performance, it is crucial to have certain internal mechanisms at one’s disposal to make sure that those stimuli that are in line with current goals determine behavior. Such mechanisms are often referred to as cognitive control processes (e.g., Miller & Cohen, 2001; Schneider & Shiffrin, 1977).

Cognitive control processes can be examined in conflict paradigms, which use ambiguous stimuli to evoke conflict between goal-congruent and goal-incongruent responses. For instance, in the Stroop task (Stroop, 1935), participants are required to name the ink color of color words. Ink color and color word can either correspond (congruent stimuli; e.g., the word “red” written in red ink) or not (incongruent stimuli; e.g., the word “red” written in green ink). Because word reading occurs involuntarily, it interferes with color naming, which leads to higher RTs and higher error rates on incongruent trials as compared with congruent trials (see, MacLeod, 1991, for a review). It has been found that this congruency effect is reduced on trials preceded by incongruent trials as compared with trials preceded by congruent trials (Egner & Hirsch, 2005; Kerns et al., 2004).

A prominent theory relates such sequential trial-to-trial modulations of the congruency effect to the detection of response conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001; but see Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey, 2003). According to this theory, an internal conflict monitor continuously monitors for the occurrence of response conflict, which arises due to simultaneous activation of two or more responses. For instance, on an incongruent trial of the color-naming Stroop task, color naming activates the correct response and word reading activates a wrong response. The conflict monitor detects the resulting response conflict and generates a conflict signal. The presence of response conflict implies that attention to task-relevant stimulus features needs to be enhanced to reduce the conflict. Thus, on the basis of the conflict signal, other brain systems can implement behavioral adjustments, which then lead to the observed reduction of the congruency effect on the following trial.

Functional neuroimaging studies have shown that activity in the dorsal ACC (dACC), which is located in the medial pFC, is enhanced in the presence of response conflict (Ullsperger & von Cramon, 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). This is in accordance with the idea that the dACC corresponds to the internal conflict monitor and that enhanced activity in this region functions...
as the conflict signal. Activity in the lateral pFC (LPFC) is enhanced during conflict adaptation, suggesting that this area is involved in implementing behavioral adjustments by increasing selective attention to task-relevant stimulus features on subsequent trials (e.g., Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000). Such enhanced LPFC activation can then lead to an increase of activity in task-relevant sensory processing areas (Egner & Hirsch, 2005) to a decrease of activity in task-irrelevant sensory processing areas (King, Korb, von Cramon, & Ullsperger, 2010) or to both (Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011).

Interestingly, recent functional neuroimaging studies suggest that it is not always the LPFC, which implements behavioral adjustments. Rather, different neural systems might be responsible for conflict adaptation in different task contexts. Egner, Etkin, Gale, and Hirsch (2008) used a modified version of the Stroop task, in which participants were required to classify faces either with respect to their emotional expression (happy vs. fearful) or with respect to their gender (female vs. male). In the emotional task context, the words “happy” or “fear” were written across the faces, whereas in the neutral task context, the words “male” or “female” were written across the faces. The words could either correspond with the information conveyed by the face (congruent stimuli) or not (incongruent stimuli). In both the emotional and the neutral task contexts, strong congruency effects were observed at the behavioral level, suggesting that the automatic reading of task-irrelevant words interfered with the classification of the face stimuli creating response conflict. Moreover, in both task contexts, conflict adaptation effects were observed. Activity in the dACC was enhanced in the presence of high response conflict in both task contexts. However, during conflict adaptation, the rostral ACC (rACC) located ventrally in the medial pFC was more strongly activated in the emotional context (see also Etkin, Egner, Peraza, Kandel, & Hirsch, 2006), whereas the LPFC was more strongly activated in the neutral context (Egner et al., 2008). These results suggest that whereas conflict detection is supported by the rACC regardless of the task context, dissociable systems are engaged in the implementation of conflict adaptation depending on whether the task context is neutral or emotional.

There are at least two reasons to suggest that the rACC is involved in implementing behavioral adjustments in emotional task contexts. First, from a neuroanatomical perspective, the rACC seems to be a good candidate for subserving this function. Because of its tight interconnectivity with limbic areas such as the amygdala, the OFC, and the insula (Öngür & Price, 2000; Devinsky, Morrell, & Vogt, 1995) and due to its strong activation in “emotional” as opposed to “cognitive” task contexts (Bush, Luu, & Posner, 2000), it was proposed that the rACC mediates primarily affective (e.g., Bishop, Duncan, Brett, & Lawrence, 2004; Paus, 2001; Bush et al., 2000) and regulative functions (e.g., Vogt, Finch, & Olson, 1992). Second, there is evidence for the notion that conflict adaptation is highly context specific. For instance, conflict adaptation does not generalize across tasks, which evoke different types of conflict (Funes, Lupianez, & Humphreys, 2010; Egner, Delano, & Hirsch, 2007). Therefore, conflict adaptation appears to be implemented in multiple context-specific conflict control loops, which may also have distinct anatomical basis (see, Egner, 2008, for a review).

One way to test the hypothesis that the rACC implements conflict adaptation in emotional task contexts is to investigate patients with focal lesions of this brain area. Unfortunately, the results reported by the few existing studies on conflict adaptation in patients with ACC damage are equivocal. In one study, four patients with extensive lesions of the medial pFC including the rACC showed entirely intact conflict adaptation in the classic color-naming Stroop task, which suggests that this brain region is not necessary for conflict adaptation (Fellows & Farah, 2005). Since it is reasonable to assume that the classic Stroop task represents a neutral task context, this finding is in line with the hypothesis that the rACC implements conflict adaptation in emotional task contexts only. However, contrary to this hypothesis, conflict adaptation was completely absent in another study, where a neutral task context was used with a group of eight patients with lesions of the rACC (di Pellegrino, Ciaramelli, & Ladavas, 2007). However, the latter study used a Simon task (Simon, 1969), where response conflict is induced by the task-irrelevant but response-incompatible stimulus position. Because Simon and Stroop tasks are known to evoke different types of conflict (Kornblum, 1994), and given the context specificity of conflict adaptation across these types of conflict (Funes et al., 2010; Egner et al., 2007), it is possible that differences in the tasks are responsible for the above discrepant results.

Thus, to test whether the rACC is necessary for conflict adaptation in emotional task contexts, this study examined conflict adaptation in patients with focal lesions of the rACC in the Stroop task. The modified Stroop task from the Egner et al. (2008) study was used (see Figure 1) to realize an emotional and a neutral task context. If patients with rACC lesions show preserved conflict adaptation in both the emotional and the neutral task contexts, this would imply that the rACC plays no critical role for conflict adaptation in the Stroop task, neither in neutral nor in emotional task contexts. By contrast, if patients with rACC lesions show a selective impairment of conflict adaptation in the emotional task context, this would imply that the rACC is necessary for conflict adaptation in emotional task contexts as suggested by recent imaging work (Egner et al., 2008; Etkin et al., 2006) and would provide supportive evidence for context specificity in conflict adaptation. Finally, although unlikely in the light of a previous study on conflict adaptation in patients with ACC lesions using the Stroop task (Fellows & Farah, 2005), it is also possible that rACC lesions impair conflict adaptation in both the emotional and the neutral task contexts. This result would
imply that the rACC is generally necessary for conflict adaptation.

METHODS

Participants

Three groups of subjects participated in the study: (a) a group of patients with focal lesions centered on the rACC and the adjoining ventromedial pFC (rACC group, \( n = 9 \), mean age = 55.4 years, \( SE = 3.21 \) years, \( n = 1 \) woman); (b) a brain-damaged control group of patients with focal lesions outside the rACC and the adjoining ventromedial pFC (BDC group, \( n = 8 \), mean age = 50.9 years, \( SE = 3.42 \) years, \( n = 1 \) woman); and (c) a normal control group of healthy subjects (NC group, \( n = 9 \), mean age = 59.0 years, \( SE = 3.63 \) years, \( n = 1 \) woman).

Brain-damaged patients were recruited from the Centre for Studies and Research in Cognitive Neuroscience in Cesena, Italy. They were selected on the basis of lesion location by inspection of CT or structural MRI scans. At the time of testing, all patients were more than a year post onset, were not taking psychoactive drugs, and were free of any other diagnosis likely to affect cognitive control processes such as significant psychiatric disease, alcohol misuse, or a history of cerebrovascular disease. All participants gave informed consent to participate in the study according to the Declaration of Helsinki (International Committee of Medical Journal Editors, 1991) and the Ethical Committee of the Department of Psychology, University of Bologna.

Table 1 shows demographic and clinical data, as well as the Mini-Mental Status Examination score (MMSE; Folstein, Robins, & Helzer, 1983). The rACC group did not differ significantly from the NC group and the BDC group with respect to the reported demographic data, all \( ps \geq .593 \). The MMSE score was lower in the rACC group than the NC group, \( t(16) = 3.57, p = .007, \eta_p^2 = 0.61 \), but did not differ significantly between the rACC group and the BDC group, \( t(15) = 0.030, p = .867, \eta_p^2 < 0.01 \).

For each patient, lesion extent and location were documented by using the most recent clinical CT or MRI scan. Lesions were traced on the T1-weighted template MRI scan from the Montreal Neurological Institute provided with the MRIcro software (Rorden & Brett, 2000). This scan is normalized to Talairach space and has become a popular template for normalization in functional brain imaging. Superimposing each patient’s lesion onto the standard brain allowed us to estimate the total brain lesion volume in cubic centimeters (cc). For the overlays of individual brain lesions, the same MRIcro software was used. Figure 2 shows the extent and overlap of the brain lesions in the rACC group. In this group, lesions were restricted to the rostral portion of the medial surface of the frontal lobe and were either the result of ruptured aneurysms of the anterior communicating artery (\( n = 8 \)) or ischemic stroke (\( n = 1 \)). The Brodmann’s areas with most extensive damage were areas 10, 11, 24, 25, and 32, with region of maximal overlap occurring in the rostral portion of Brodmann’s area 32 (i.e., the rostral portion of ACC), where all cases had lesions. Three patients in the rACC group had unilateral lesions (\( n = 1 \) left, \( n = 2 \) right), and six patients had bilateral lesions.

Table 1. Demographic, Clinical, and Lesion Data of Brain-Damaged Control Patients (BDC Group) and of Patients with Focal Lesions of the Rostral Anterior Cingulate Cortex (rACC Group) and Demographic and Clinical Data of Normal Control Participants (NC Group)

<table>
<thead>
<tr>
<th>Group</th>
<th>Age (years)</th>
<th>Education (years)</th>
<th>Lesion Volume (cc)</th>
<th>MMSE Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>NC</td>
<td>59.0 (( SE = 3.63 ))</td>
<td>10.2 (( SE = 2.16 ))</td>
<td>--</td>
<td>29.6 (( SE = 0.85 ))</td>
</tr>
<tr>
<td>BDC</td>
<td>50.9 (( SE = 3.21 ))</td>
<td>11.4 (( SE = 2.03 ))</td>
<td>47.7 cc (( SE = 4.91 ) cc)</td>
<td>26.8 (( SE = 1.22 ))</td>
</tr>
<tr>
<td>rACC</td>
<td>55.4 (( SE = 3.14 ))</td>
<td>10.4 (( SE = 1.55 ))</td>
<td>48.1 cc (( SE = 4.90 ) cc)</td>
<td>26.8 (( SE = 1.56 ))</td>
</tr>
</tbody>
</table>
In the BDC group, lesions mostly involved the cerebral cortex outside the frontal lobes ($n = 7$). These lesions included the occipital lobe ($n = 3$), the temporal lobe ($n = 2$), insula and putamen ($n = 1$), or the parieto-temporo-occipital junction ($n = 1$). The lateral parieto-temporal lesion of one patient extended to the lateral portion of the right frontal lobe. Lesions of patients in the BDC group were the result of ischemic ($n = 4$) or hemorrhagic ($n = 3$) stroke or aneurism ($n = 1$). None of the BDC patients had lesions in areas 10, 11, 24, 25, or 32, that is, the ACC and adjoining ventromedial pFC.

In the BDC group, seven patients had unilateral ($n = 6$ left, $n = 1$ right) lesions, and one patient had a bilateral lesion. There was no significant difference in lesion volume between rACC patients (48.1 cc, $SE = 4.90$ cc) and BDC patients (47.7 cc, $SE = 4.91$ cc), $t(15) = 1.01$, $p = .345$, $\eta^2_p = 0.13$.

Apparatus

Stimuli were presented on the 12-in. color monitor of an IBM-compatible notebook and responses were registered via the integrated keyboard.

Stimuli

Gray-scale photographs of 10 male and 10 female faces in front view showing either a happy or a fearful expression were taken from the KDEF picture library (Lundqvist & Litton, 1998). Each face stimulus was combined with each of the Italian words uomo (English: man), donna (English: woman), gioia (English: happiness), and paura (English: fear) written in red letters across it such that the word could either correspond with the expression or the gender of the face (congruent stimuli) or not correspond (incongruent stimuli; see Figure 1). This resulted in a total of 160 stimuli. All stimuli were presented on a black background and were resized to a visual angle of 8.23$^\circ$ height and 9.83$^\circ$ width at a viewing distance of 50 cm. The words subtended 1.14$^\circ$ vertically and 5.61$^\circ$ ($donna$), 4.81$^\circ$ ($uomo$), 4.35$^\circ$ ($gioia$), and 5.38$^\circ$ ($paura$).

Procedure

On each trial, a white fixation cross was presented in the center of the screen. After 1000 msec, the face stimulus replaced the fixation cross and remained on the screen until the participant responded. After the response, the screen turned black for 2000 msec until the next trial started. To create a neutral task context, face stimuli with the words uomo or donna written across them were used and participants were instructed to classify the stimuli with respect to the gender of the faces (male, female) while ignoring the words. To create an emotional task context, face stimuli with the words gioia or paura written across them were used, and participants were instructed to classify the stimuli with respect to the emotional expression of the faces (happy, fearful) while ignoring the words. Participants were instructed to respond as quickly and as accurately as possible by pressing the left Alt key with their left index finger and the right Alt key with their right index finger. Two participants in the BDC group responded with the middle and index fingers of their left hand by pressing the S and X keys, respectively, because they had right hemiparesis due to their left-sided brain lesions. Otherwise, the stimulus—response mapping was completely counterbalanced across participants within each group. Trials were presented in blocks of 80 trials (one for each stimulus in each task) in random order. For each task context, one practice block and three test blocks were
presented resulting in a total of 240 test trials per task. Half of the participants in each group started with the emotional task context, and the other half started with the neutral task context. The whole experiment lasted for approximately 1 hr. For participants who had difficulty concentrating on the task for the duration of the entire experiment, task contexts were presented on successive days (n = 6 in the rACC group and n = 2 in the BDC group). One half of these participants completed the emotional task context first, and the other half completed the neutral task context first.

Data Analyses

Dependent variables were error rates and RT of correct responses, defined as the time between stimulus onset and the subsequent key press. To control for outliers, trials with an RT of more than 2.5 standard deviations above or below the condition mean were excluded (NC group: 2.85%, BDC group: 2.82%, rACC group: 2.85%). Because errors usually lead to posterior slowing (Rabbitt, 1966) and other strategic adjustments on subsequent trials (e.g., Maier, Yeung, & Steinhauser, 2011), which may distort sequential modulations of the congruency effect, trials following errors were also excluded (NC group: 2.46%, BDC group: 2.52%, rACC group: 2.82%).

It has been argued that sequential modulations of the congruency effect could also arise due to repetition priming effects in the absence of cognitive control (e.g., Hommel et al., 2004; Mayr et al., 2003; but see Ullsperger, Bylsma, & Botvinick, 2005). In our experiment, exact stimulus repetitions never occurred, thus precluding selective priming of congruent trials preceded by congruent trials and incongruent trials preceded by incongruent trials by exact stimulus repetitions. Furthermore, we excluded all direct repetitions of the same face with varying word distractors, thus controlling for partial repetition effects due to target repetitions (cf. Egner et al., 2008).

To investigate whether the congruency effect on the current trial was modulated by the congruency on the previous trial, error rates and RT of correct responses were submitted to four-way ANOVAs with repeated measurement with the between-subject variable group (NC, BDC, rACC) and the within-subject variables task (neutral, emotional), previous trial congruency (congruent, incongruent), and current trial congruency (congruent, incongruent). If the four-way ANOVA revealed an interaction with the variable group, we also conducted three-way ANOVAs with the within-subject variables task (neutral, emotional), previous trial congruency (congruent, incongruent), and current trial congruency (congruent, incongruent) for each group separately to examine sequential modulations of the congruency effect within each group. Where necessary, multiple comparisons were performed by using the Newman–Keuls test. Frequency data were arcsine transformed (Winer, Brown, & Michels, 1991). Where applicable, the standard error (SE) was adjusted for repeated measures designs by removing between-subject variance within each experimental group (Morey, 2008; Cousineau, 2005).

RESULTS

Error Data

The error data are presented in Table 2. The four-way ANOVA on the error rates revealed a main effect of current trial congruency, F(1, 23) = 5.26, p = .031, ηp² = 0.19, denoting that the error rate was slightly higher on incongruent trials (3.20%, SE = 0.34%) than on congruent trials (2.07%, SE = 0.39%). No further effects reached significance (all ps > .087).

RT Data

The RT data are depicted in Figure 3. The four-way ANOVA on RT revealed a main effect of group, F(2, 23) = 6.22, p = .007, ηp² = 0.35. Mean RT was slower in the rACC group (1044 msec, SE = 30.9 msec) than in the NC group (694 msec, SE = 13.0 msec), F(1, 16) = 19.6, p < .001, ηp² = 0.55. By contrast, no significant differences in mean RT were found between the rACC group and the BDC group, F(1, 15) = 2.18, p = .167, ηp² = 0.12, and between the HC group and the BDC group, F(1, 15) = 2.69, p = .106, ηp² = 0.17. The ANOVA also revealed main effects of task, F(1, 23) = 26.1, p < .001, ηp² = 0.53, and current trial congruency, F(1, 23) = 36.6, p < .001, ηp² = 0.61, indicating that mean RT was faster in the neutral task (974 msec, SE = 20.2 msec) than in the emotional task (942 msec, SE = 30.9 msec) and faster for congruent (829 msec, SE = 24.3 msec) than for incongruent stimuli (907 msec, SE = 29.1 msec).

Furthermore, the ANOVA revealed a two-way interaction of previous trial congruency, and current trial congruency, F(1, 23) = 31.4, p < .001, ηp² = 0.58, indicating that the congruency effect was modulated by the congruency on the previous trial. The congruency effect calculated as the difference between the mean RT for incongruent trials and the mean RT for congruent trials was smaller following incongruent trials (55.5 msec, SE = 12.7 msec) than following congruent trials (102 msec, SE = 11.0 msec).

Most importantly, however, the ANOVA also revealed a four-way interaction of group, task, previous trial congruency, and current trial congruency, F(2, 23) = 4.18, p = .028, ηp² = 0.27.1 The ANOVAs for each group separately revealed that robust two-way interactions of previous trial congruency and current trial congruency were present in the NC group, F(1, 8) = 22.5, p < .001, ηp² = 0.74, as well as in the BDC group, F(1, 7) = 16.0, p = .005, ηp² = 0.70. These interactions denote that the congruency effect was reliably modulated by the congruency on the previous trial in the NC group as well as in the BDC group. Accordingly, the NC group and the BDC group showed
significant two-way interactions of current trial congruency and previous trial congruency both in the neutral task ($F(1, 8) = 33.0, p < .001, \eta^2_p = 0.81,$ and $F(1, 7) = 13.0, p = .009, \eta^2_p = 0.65,$ respectively) and in the emotional task ($F(1, 8) = 9.31, p = .016, \eta^2_p = 0.54,$ and $F(1, 7) = 6.36, p = .040, \eta^2_p = 0.48,$ respectively). Neither the NC group nor the BDC group displayed a three-way interaction of task, previous trial congruency, and current trial congruency ($F(1, 8) = 0.01 p = .999, \eta^2_p < 0.01,$ and $F(1, 7) = 0.94, p = .364, \eta^2_p = 0.12,$ respectively). Thus, in neither of the control groups had the variable task an effect on the modulation of the congruency effect by the congruency on the previous trial.

By contrast, in the rACC group, besides a significant two-way interaction of previous trial congruency and current trial congruency, $F(1, 8) = 5.74, p = .043, \eta^2_p = 0.85,$
also a significant three-way interaction of task, previous trial congruency, and current trial congruency was found, $F(1, 8) = 9.75, p = .014, \eta^2_p = .91$. This effect denoted that mean RT for rACC patients displayed a significant two-way interaction of previous trial congruency and current trial congruency in the neutral task, $F(1, 8) = 7.22, p = .028, \eta^2_p = 0.43$, but no such interaction in the emotional task, $F(1, 8) = 1.99, p = .196, \eta^2_p = 0.19$. Thus, although the rACC group showed a smaller congruency effect following incongruent trials than following congruent trials in the neutral task (previous congruent: 137 msec, $SE = 7.64$ msec; previous incongruent: 63.4 msec, $SE = 7.38$ msec, $p = .002$), no such modulation of the congruency effect was observed in the emotional task (previous congruent: 138 msec, $SE = 9.15$ msec; previous incongruent: 124 msec, $SE = 5.28$ msec, $p = .561$).

**DISCUSSION**

This study tested the hypothesis that the rACC located in the ventromedial pFC is necessary for conflict adaptation in an emotional task context. To this end, we compared sequential modulations of the congruency effect in a modified Stroop task between a group of patients with focal lesions of the rACC (rACC group), a group of normal controls (NC group), and a group of brain-damaged control patients (BDC group). Participants were asked to classify faces either with respect to their gender (neutral task context) or with respect to their emotional expressions (emotional task context) while ignoring congruent or incongruent distractor words written with bold red letters across the faces.

In both the neutral and the emotional task contexts, performance was worse with incongruent stimuli, as compared with congruent stimuli in all three groups of participants, as evidenced by longer RT and higher error rates. This congruency effect was comparable between groups, which suggests that the ability to override the word reading response in favor of the face classification response was not impaired by brain lesions. Importantly, the congruency effect in the RT was subject to sequential modulations by the congruency on the previous trial. Both the NC group and the BDC group displayed a reduction of the congruency effect following incongruent trials in both task contexts. However, in accordance with our hypothesis, the rACC group showed a reduction of the congruency effect following incongruent trials in the neutral task context only, but equally strong congruency effects following congruent and incongruent trials in the emotional task context.

These results demonstrate for the first time that the rACC is necessary for conflict adaptation in both task contexts, although this brain region plays no critical role for conflict adaptation in neutral task contexts. Our findings corroborate recent neuroimaging studies using the same task. In these studies, increased activation of the rACC was found during conflict adaptation in the emotional task context, and this activity predicted down-regulation of activity in the amygdala (Eghner et al., 2008; Etkin et al., 2006). Neither increased rACC activity nor modulations of amygdala activity were found during conflict adaptation in the neutral task context, where increased activation of the LPFC and an up-regulation of activity in the fusiform face area were observed instead (Egner et al., 2008). These results suggest that conflict adaptation is mediated by a system involving the rACC in an emotional task context and by a system involving the LPFC in a neutral task context. Our results show that these systems indeed operate independently of each other: rACC lesions disrupted the conflict adaptation system for emotional task contexts, although they did not interfere with conflict adaptation in the neutral task context. Conversely, a recent study using the same task reported impaired conflict adaptation in the neutral task context and intact conflict adaptation in the emotional task context in healthy aging (Monti, Weintraub, & Eghner, 2010), a condition associated with altered lateral prefrontal function (e.g., Paxton, Barch, Racine, & Braver, 2008). This suggests that the LPFC is involved in conflict adaptation in neutral but not in emotional task contexts.

Thus, our findings support the longstanding notion that the rACC is involved in the processing of emotions (e.g., Bishop et al., 2004; Paus, 2001; Bush et al., 2000). The question emerges as to the exact functional role of the rACC in emotion processing. Although RT was higher in the emotional than in the neutral task context, this effect was comparable between groups suggesting that lesions of the rACC did not interfere with processing of emotional cues per se. Rather, the specific impairment of conflict adaptation in the emotional task context caused by rACC lesions suggests that this brain region is necessary for integrating emotional cues from the environment and using them for the regulation of behavior. This is in accordance with studies implicating the ventromedial pFC in the flexible adaptation to emotional cues in the environment (e.g., Schiller & Delgado, 2010; Schiller, Levy, Niv, LeDoux, & Phelps, 2008) and also more generally in the regulation of social behavior (e.g., Rudebeck, Bannerman, & Rushworth, 2008; Amodio & Frith, 2006) and future-directed decision making (Sellitto, Ciaramelli, & Di Pellegrino, 2010; Bechara, Tranel, & Damasio, 2000), both of which are situations where the integration of either external or internal emotional cues is of fundamental importance.

The fact that patients with rACC lesions displayed intact conflict adaptation effects in the neutral task context in this study suggests that the rACC is not necessary for behavioral adaptation in general. This is in accordance with the results from an earlier study reporting intact conflict adaptation in patients with extensive lesions of the medial pFC including the rACC (Fellows & Farah, 2005). By contrast, it seems to contradict a previous study, which showed impaired conflict adaptation with rACC lesions (di Pellegrino et al., 2007). However, these discrepancies might be due to the different tasks used in these studies. Whereas both this
study and the study by Fellows and Farah (2005) used Stroop tasks, di Pellegrino et al. (2007) used a Simon task, where the task-irrelevant but response-incompatible position of the stimulus produces response conflict (Simon, 1969). The fact that lesions of the rACC interfered with conflict adaptation in the Simon task (di Pellegrino et al., 2007), but not in the Stroop task (Fellows & Farah, 2005, present results) suggests that the rACC is necessary only for the resolution of Simon-type conflict, but not for the resolution of Stroop-type conflict. Indeed, in accordance with this possibility, a recent study found enhanced activity in the rACC during conflict adaptation with Simon-type conflict (Wittfoth, Schardt, Fahle, & Herrmann, 2009).

In support of the notion that different systems are involved in the resolution of different types of conflict, recent studies, which combined Simon-type conflict and Stroop-type conflict observed conflict adaptation only when the type of conflict was repeated, but not when the type of conflict changed from trial to trial (Funes et al., 2010; Egner et al., 2007). This indicates that conflict adaptation is specific for the type of conflict evoked in the Stroop and in the Simon tasks (see Kiesel, Kunde, & Hoffmann, 2006; Wendt, Kluwe, & Peters, 2006, for other examples of conflict-specific conflict adaptation). Thus, converging evidence from neuroimaging (Egner et al., 2008; Etkin et al., 2006), behavioral (Funes et al., 2010; Egner et al., 2007; Kiesel et al., 2006; Wendt et al., 2006), lesion (di Pellegrino et al., 2007; Fellows & Farah, 2005, present results), and aging (Monti et al., 2010) studies suggests that conflict adaptation is specific for the type of conflict evoked by the task at hand. A recent review proposed that multiple conflict control loops mediate conflict adaptation depending on the context of the task (Egner, 2008). This position is in accordance with the available evidence because it allows for the possibility that different neural systems mediate the resolution of different types of conflict in different contexts.

A possible limitation of this study is that the stimuli in the emotional task context are not only emotional but also social in nature. Namely, to successfully regulate behavior based on the emotional expression of another person’s face, it is not only necessary to correctly identify the expressed emotion but also to correctly interpret the meaning of this emotion in a social context. Indeed, patients with lesions to the rACC and the adjoining ventromedial pFC show marked deficits in social interaction (Moretti, Dragone, & Di Pellegrino, 2009; Bechara, Damasio, & Damasio, 2000). Moreover, the rACC is not only implicated in the processing of emotions, but also in situations that require the consideration of social cues in the environment (e.g., Zaki, Henningan, Weber, & Ochsner, 2010; see Anmodio & Frith, 2006, for a review). Hence, it is difficult to discern whether the fact that rACC patients displayed impaired conflict adaptation in the emotional task context of this study stems entirely from a deficit to use emotional cues for regulating behavior or whether a deficit in interpreting social cues in a social context also contributed to the observed results. Thus, it would be interesting for future studies to disentangle social and emotional components of the behavior regulation deficit in patients with lesions of the rACC.

In summary, this study shows that the rACC is necessary for successful conflict adaptation in an emotional task context, but not in a neutral task context, and thus underpins the importance of the rACC for using emotional cues for the regulation of behavior (see also Bishop et al., 2004; Paus, 2001; Bush et al., 2000). Moreover, the results of this study suggest that behavioral regulation is context specific (Funes et al., 2010; Egner, 2008; Etkin et al., 2007, 2008; Etkin et al., 2006; Kiesel et al., 2006; Wendt et al., 2006).

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Reprint requests should be sent to Martin E. Maier, Centro Studi e Ricerche in Neuroscienze Cognitive, Via Riccardo Brusi 20, 47025 Cesena (FC), Italy, or via e-mail: martinernst.maier@unibo.it.

Notes
1. To investigate whether the results were influenced by the fact that a greater portion of patients in the rACC group (six of nine) completed the task contexts on different days than in the BDC group (two of eight) and in the NC group (none), a four-way ANOVA with repeated measurement with the between-subject variables task (neutral, emotional), lesion (di Pellegrino et al., 2007; Fellows & Farah, 2005, present results), and testing day (1 and 2) was performed. The within-subject variables task (congruent, incongruent) and current trial congruency (congruent, incongruent) and previous trial congruency (congruent, incongruent) and current trial congruency (congruent, incongruent) were performed on the RT data of the six rACC patients who completed the task contexts on different days. There was neither a main effect of testing day nor a four-way interaction of testing day, task, previous trial congruency, and current trial congruency (Fs < 0.526). Instead, there was a trend toward a three-way interaction of task, previous trial congruency, and current trial congruency, F(1, 4) = 3.88, p = .120, ηp2 = 0.49, which numerically replicated the overall pattern revealed by the ANOVA on all participants from the rACC group. Thus, it is unlikely that testing day significantly influenced the results.

2. The question emerges as to why this could be the case. In both tasks, conflict effects can be explained by a dual-route model with a fast automatic route, which processes both task-relevant and task-irrelevant stimulus features in parallel and a slower deliberate route where processing of task-irrelevant information is selectively inhibited (e.g., Ridderinkhof, 2002). However, there is evidence that automatic response activation and thus the requirement for selective inhibition of the automatic route is much larger in the Simon task than in the Stroop task (Notebaert & Soetens, 2006). Several functional imaging studies have implicated the rACC in tasks requiring response inhibition such as go/no-go tasks (Menon, Adleman, White, Glover, & Reiss, 2001; Kiehl, Liddle, & Hopfinger, 2000). Thus, a possible explanation for a greater involvement of the rACC in the resolution of Simon-type conflict is that this brain area is more involved whenever active inhibition is required to a...
strong degree and that resolving Simon-type conflict requires more inhibition than resolving Stroop-type conflict.

REFERENCES


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1. Please provide volume number of Bishop et al., 2004.

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