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Neural Systems Supporting the Control of Affective and Cognitive Conflicts

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Abstract

Although many studies have examined the neural bases of controlling cognitive responses, the neural systems for controlling conflicts between competing affective responses remain unclear. To address the neural correlates of affective conflict and their relationship to cognitive conflict, the present study collected whole-brain fMRI data during two versions of the Eriksen flanker task. For these tasks, participants indicated either the valence (affective task) or the semantic category (cognitive task) of a central target word while ignoring flanking words that mapped onto either the same (congruent) or a different (incongruent) response as the target. Overall, contrasts of incongruent > congruent trials showed that bilateral dorsal ACC, posterior medial frontal cortex, and dorsolateral pFC were active during both kinds of conflict, whereas rostral medial pFC and left ventrolateral pFC were differentially active during affective or cognitive conflict, respectively. Individual difference analyses showed that separate regions of rostral cingulate/ventromedial pFC and left ventrolateral pFC were positively correlated with the magnitude of response time interference. Taken together, the findings that controlling affective and cognitive conflicts depends upon both common and distinct systems have important implications for understanding the organization of control systems in general and their potential dysfunction in clinical disorders.

INTRODUCTION

From reading a book on a noisy train to finding the best word to express a thought, we rely everyday on the ability to attend to and respond to some stimuli while ignoring others. In the past decade, cognitive neuroscience research has taken great strides toward understanding the neural bases of this ability. Across imaging, electro-physiological, and lesion studies, dorsal regions of the cingulate and the pFCs have been shown to be essential for monitoring conflicts between and selecting among competing perceptual or semantic inputs and their associated responses (Ullsperger & von Cramon, 2004; Botvinick, Braver, Barch, Carter, & Cohen, 2001; Milham et al., 2001; Miller & Cohen, 2001; van Veen, Cohen, Botvinick,

Stenger, & Carter, 2001; Carter et al., 1998). Importantly, this work has provided a foundation for translational work on clinical disorders, such as schizophrenia, that has helped clarify the mechanisms by which breakdowns in cognitive control may contribute to dysfunctional behavior (Ochsner, 2008; Kerns et al., 2005; MacDonald et al., 2005).

Comparatively less attention has been paid, however, to the neural systems important for controlling how one attends to and responds to affectively charged stimuli (Ochsner & Gross, 2005, 2008). This is surprising, given that behavioral studies have shown that deficits in this ability characterize numerous clinical disorders, ranging from chronic pain to anxiety, panic, and posttraumatic stress disorder (PTSD; Vythilingam et al., 2007; Wilson & MacLeod, 2003; Eccleston & Crombez, 1999). In recognition of these facts, a growing number of functional imaging studies have begun to investigate the neural mechanisms supporting the ability to control attention to affective inputs. The majority of these studies have asked participants to engage in a primary cognitive task or judgment while resisting interference from task-irrelevant affective information. Although their results have been somewhat mixed, they generally have been consistent with either one of two hypotheses.

The first is that rostral medial regions may play a special role in controlling attention to emotional information, in part because of their interconnections with subcortical structures involved in emotional responding (Ongur, Ferry, & Price, 2003; Ongur & Price, 2000). Consistent with this hypothesis, some studies have found activity in rostral cingulate (rCC) and medial prefrontal (mPFC) cortices when participants make simple judgments about neutral target stimuli or neutral stimulus dimensions (such as color) while ignoring affective stimuli or affective stimulus dimensions (Bishop, Duncan, Brett, & Lawrence, 2004; Compton et al., 2003; Shin et al., 2001; Bush, Luu, & Posner, 2000; Whalen et al., 1998). Interpreting the meaning of this activity is complicated, however, by the fact many of these studies failed to show behavioral evidence that the affective distracters interfered or conflicted with performance of the primary cognitive task. This raises the possibility that rCC activation reflects the extent to which affective stimulus properties are monitored or attended (hence reach awareness) rather than control over cognition–emotion response conflicts per se, an interpretation that is consistent with findings of rCC/mPFC activation when participants explicitly attend to and judge their emotional states (Ochsner et al., 2004; Phan et al., 2003; Gusnard, Akbudak, Shulman, & Raichle, 2001; Lane, Fink, Chau, & Dolan, 1997).

The second hypothesis is that screening out affective distracters may depend upon domain general systems important for controlling conflicts between various kinds of stimuli, regardless of their type. These regions include the dorsal anterior cingulate cortex (dACC) and the posterior medial frontal cortex (pmPFC) thought to be involved in monitoring response conflicts, and the dorsolateral pFC (dlPFC) implicated in goal maintenance and response control (Botvinick et al., 2001; MacDonald, Cohen, Stenger, & Carter, 2000). Consistent with this hypothesis, two studies have found dACC and dlPFC activity in paradigms showing behavioral evidence that the presentation of an affective word or image may interfere with cognitive judgments of a subsequently presented stimulus (Blair et al., 2007; Luo et al., 2007).

As important as the aforementioned studies have been for understanding conflicts between cognition and emotion, it is notable that none of them directly investigated conflicts *within* the emotional domain, that is, the ability to control competition between different kinds of affective responses. This ability may be important whenever situations engender conflicts among or between different kinds of positive and negative emotional responses—an ability that may pose particular problems for clinical disorders, such as borderline personality disorder, anxiety, and PTSD, that are characterized by emotional instability and affect dysregulation (Vythilingam et al., 2007; Constans, McCloskey, Vasterling, Brailey, & Mathews, 2004; Lang, Davis, & Öhman, 2000; Linehan et al., 1999).

To date, only three studies have investigated this issue. All found behavioral evidence of response conflict using a variant of the Stroop task in which participants paid attention to facial expressions and ignored emotion words printed across them that were either incongruent or congruent with the expressions (Egner, Etkin, Gale, & Hirsch, 2007; Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; Haas, Omura, Constable, & Canli, 2006). Imaging results were mixed, however. Although the incongruent versus congruent contrast activated dACC in all studies, only two reported an additional dIPFC activity and an inverse relationship between rCC and amygdala during conflict (Egner et al., 2007; Etkin et al., 2006). One of these articles compared their affective distracter task to a variant in which the distracter words were nonaffective gender labels that either were or were not consistent with the gender of the attended face (Egner et al., 2007). Both affective and nonaffective distracters produced dIPFC activity, but only the affective distracters recruited rCC.

Whatever the reasons for the differences in results of these studies turn out to be, the fact that the stimuli used in this type of task differ in terms of both valence and stimulus type raises the possibility that these activations reflected not only the need to control affective conflicts but also processes specifically related to the types of stimuli used. For example, face stimuli are among the most reliable activators of the amygdala, which could explain its activation here (Phan, Wager, Taylor, & Liberzon, 2002). In addition, these tasks could involve cross-domain conflicts between competing verbal/ semantic and pictorial representations. These conflicts (e.g., seeing a fearful face with the word HAPPY printed over it) may have heightened ambiguity about the meaning of the depicted facial expressions, which itself may be a source of conflict and cingulate (Botvinick et al., 2001) as well as amygdala (Whalen, 1998) activation.

Taken together, extant work suggests that the neural systems important for controlling processing conflicts created by affective information may depend upon dorsal cingulate and lateral prefrontal systems implicated in domain general cognitive control, upon rostral medial systems implicated in attention to emotion, or some combination of both. These conclusions are tentative, however, because the factors determining if and when each type of system may come into play are not yet clear. Some variability may have to do with the different processing demands of the diverse paradigms employed across studies as well as the lack of behavioral evidence of conflict in some studies. Perhaps most salient, however, is the fact that few studies have examined the neural systems for controlling conflict between competing affective responses, and that none have directly compared them to the systems

important for controlling cognitive conflicts. As a consequence, important questions about the nature of affective conflict and its relationship to cognitive conflict remain.

To help clarify these issues, the goal of the present study was to provide the first direct test of whether the control of affective and cognitive (i.e., nonaffective) conflicts depends upon common or distinct neural systems. To achieve this goal, we developed two versions of the Eriksen flanker task in which participants attended to and judged a target word while ignoring distracting flanker words presented above and below the target. In the *affective* version of the task, differences in valence between target and flanker words created response conflict. In the *cognitive* version of the task, differences in semantic category membership between affectively neutral target and flanker words (kinds of metal or fruit) created response conflict. In contrast to the methods used in prior work, a key feature of this paradigm was that for each task variant, the target and the distracter stimuli differed in terms of either their affective valence or their semantic category membership but never both at once and never in terms of their representational format (see Figure 1). The aim here was to isolate processes related to within-domain conflicts that were affective or nonaffective and could not be attributed to the differences in the valence or stimulus type between targets and distracters that have been present in prior work.

Using these tasks, we sought to test two hypotheses about the relationship between affective and cognitive conflicts. First, motivated by prior work, we hypothesized that monitoring of both types of conflict may be mediated by prefrontal and cingulate regions whose activation during conflicts between many types of cognitive and perceptual responses (e.g., Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Botvinick et al., 2001; Ullsperger & von Cramon, 2001; van Veen et al., 2001; Carter et al., 1998) suggests they may play a general role in mediating affective response conflicts as well (Haas et al., 2006; Botvinick, Cohen, & Carter, 2004; Eisenberger & Lieberman, 2004; Hazeltine, Bunge, Scanlon, & Gabrieli, 2003). Second, we hypothesized that whereas affective conflict might differentially depend upon rostral medial regions associated with awareness and selection of affective responses (Etkin et al., 2006; Bishop et al., 2004; Cato et al., 2004; Ochsner et al., 2004), the kind of semantic or meaning-based cognitive conflict studied here might differentially depend upon lateral prefrontal systems implicated in selecting goal-relevant representations from semantic memory (Badre & Wagner, 2007; Thompson-Schill, 2003).

Two kinds of analyses were used to address these hypotheses. First, we identified regions more active on incongruent than on congruent trials for each task and then compared them to determine whether the control of affective and cognitive conflicts depends upon common or distinct patterns of activity. Second, for each task, across participants we correlated conflict-related brain activity with our behavioral index of response conflict—the magnitude of response time slowing on incongruent as compared with congruent trials. This was done in recognition of the fact that group-averaged contrasts only identify regions active in all participants and consequently may fail to detect regions predictive of task performance that are active only in those individuals who perform poorly or well.

METHODS

Participants

Sixteen right-handed participants (9 women; mean age = 21.22 years) were recruited, gave informed consent in compliance with Stanford University human subjects regulation, and were paid \$60 for completion of this study. All were screened for any medications or psychological/ neurological conditions that might influence the measurement of CBF.

Behavioral Paradigm

As graphically illustrated in Figure 1, participants completed two modified versions of the Eriksen flanker task that assessed affective and cognitive conflicts, respectively. On the “affective flanker” task, participants indicated whether a central “target” word was positive or negative while ignoring flanking stimuli of either the same (congruent trials) or the opposite valence (incongruent trials) that appeared above and below the central target word for the duration of the presentation. On the “cognitive flanker” task, participants indicated whether a central “target” word was a metal or a fruit while ignoring stimuli from either the same (congruent) or a different (incongruent) semantic category that flanked the central “target” word above and below it.

During each trial, the target and the flanking words remained on the screen for 2 sec followed by a 2-sec fixation cross, for a total trial length of 4 sec. Using a four-button response box, participants used their dominant right hand to indicate the affective or the cognitive category of the central target word by pushing the response button assigned to each category and were instructed to respond as quickly as possible without sacrificing accuracy. Response times were recorded for each trial. From top to bottom, the central target and the flanking stimuli subtended approximately 4.0 vertical degrees of visual angle in the center of the participants’ field of vision.

Because the primary goal of this study was to identify regions involved in monitoring affective and/or cognitive conflict, we did not design the flanker tasks to systematically examine the effects of prior trial interference that may influence the amount of conflict resolution required on the current trial (Etkin et al., 2006; Carter et al., 1998). Instead, we sought to avoid conflict adaptation effects attributable to repetition of trial types (Mayr, Awh, & Laurey, 2003) by intermixing congruent and incongruent trials with filler trials of no theoretical interest (where an affective or semantic target was flanked by XXXXXs). For each task, participants completed two blocks of 168 total trials. Each block was comprised of equal numbers ($n = 52$) of congruent, incongruent, and filler trials that were randomly inter-mixed with the 12 fixation trials that involved presentation of a fixation cross rather than a word stimulus.

Across tasks, words were matched for mean length (5.53 letters), number of syllables (1.81), and mean frequency (stimulus words averaged 0.00002% of the written or spoken words in the British National Corpus norms). A separate pilot norming study ($n = 11$) collected ratings of valence (1 = *negative*, 9 = *positive*) and arousal (1 = *not arousing*, 9 = *highly arousing*) for all stimuli. These ratings confirmed (a) that positive and negative words differed in valence (positive = 8.16, negative = 1.75; $p < .05$) but were equated in arousal

(arousal: positive = 6.74, negative = 6.75, $p = ns$), and (b) that these affective words were more valenced and more arousing (all $p < .05$) than were the fruit and the metal words used on the cognitive task, which were selected to be of comparatively neutral valence (fruit = 6.30, metal = 4.65) and lower arousal (fruit = 3.52, metal = 2.51).

MRI Data Acquisition

Whole-brain imaging data were collected on a 3T GE Scanner (GE Signa LX Horizon Echospeed Scanner). Twenty-eight 4-mm axial slices were acquired using a T2*-sensitive gradient-echo spiral-in/out pulse sequence (30 msec TE, 2000 msec TR, two interleaves, 608 flip angle, 24 cm field of view, 64×64 data acquisition matrix) following high-order shimming (Glover & Law, 2001; Glover, 1999). Anatomical scans were acquired for each participant using T2-weighted flow-compensated spin-echo scans (2000 msec TR, 85 msec TE). Stimulus presentation and response time collection were controlled by an Apple computer running the experimental presentation program Psyscope. Stimuli were back projected onto a screen attached to a custom-built head coil. Participants made their responses by pressing one of two buttons on a four-button box with the index and middle fingers of their dominant right hand. Head motion was limited by a bite bar attached to the head coil and by foam padding around participants' heads. Participants completed a short training session before being placed in the scanner to ensure that activation effects were due neither to task novelty nor to incomplete understanding of the task.

Data Analysis

Preprocessing and basic statistical analyses were conducted using SPM2 (Wellcome Department of Cognitive Neurology). Slice time correction, realignment (motion correction), and normalization were performed on the functional images, after which the anatomical images were coregistered to the mean functional image. The anatomical images were then normalized and smoothed to a standard template brain, and the normalized functional images were interpolated to $2 \times 2 \times 2$ -mm voxels and smoothed with a Gaussian filter (6 mm at full-width half-maximum).

Individual participants' data were modeled as fixed effects using the general linear model, with blood flow responses to each trial type modeled as events producing a canonical hemodynamic response at the onset of each 4-sec trial. Contrast images for each participant summarizing differences between trial types were used to create SPM{T} maps for the group using a random-effects model. Statistical maps for group contrasts were thresholded at $p < .001$ uncorrected for multiple comparisons with an extent threshold of five voxels. Maxima are reported in ICBM152 coordinates as in SPM2.

To examine sources of individual variability in conflict-related activations, we used robust regression analyses (Wager, Keller, Lacey, & Jonides, 2005) to correlate individual differences in response time interference with brain activity during either affective or cognitive conflict. Robust regression is useful for examining questions about individual differences because it down-weights potential outliers that could exert undue leverage on results. The goal of these analyses was to identify regions that were correlated with performance to a greater extent during one task as compared with the other. To accomplish

this goal, we used custom Matlab scripts (courtesy Tor Wager) to correlate conflict-related response time differences (i.e., the incongruent – congruent RT difference) with activity in the incongruent–congruent contrast for both the affective and the cognitive flanker tasks. We then used the method of Steiger (1980) to identify regions more significantly correlated (at $p < .05$) with conflict-related brain activity during one task as compared with the other. These regressions were conducted only within mPFC and IPFC regions and cingulate regions previously implicated in cognitive control (Botvinick et al., 2001; Miller & Cohen, 2001) attention to emotion and emotion regulation (Olsson & Ochsner, 2008; Ochsner & Gross, 2005; Bishop et al., 2004; Ochsner et al., 2004; Lane et al., 1998; Lane, Ahern, Schwartz, & Kaszniak, 1997), which included Brodmann’s areas 8, 9, 10, 23, 24, 25, 32, and 44–47. This was done using an mPFC mask constructed and defined by the coordinates of the mPFC regions enumerated above as given by the Talairach atlas and transformed into MNI space. Resulting activation clusters falling within the structural mask were treated as functional ROIs from which beta values from peak voxels data were extracted to illustrate relationships between brain activity and task performance.

RESULTS

Behavioral Results

Accuracy was at or above 98% for all trial types. Hence, all analyses were conducted on response times for correct trials. A repeated measures ANOVA with type of task (Cognitive or Affective), type of trial (Incongruent or Congruent), and type of target stimulus (Negative or Fruit, or Positive or Metal) as within-participant factors was computed on response times. The only significant effect was for type of trial, $F(1, 15) = 23.72$, $p < .001$, with response times slower on incongruent ($M = 708.33$ msec) than on congruent ($M = 682.90$ msec) trials for both tasks. The interaction of task and type of trial was not significant ($p > .1$). Planned comparisons verified that each task showed significant incongruent (I) > congruent (C) response time differences (cognitive: I > C, RTs = 714.22 vs. 680.32, $F(1, 15) = 29.35$, $p < .001$; affective: I > C, RTs = 702.44 vs. 685.48, $F(1, 15) = 7.34$, $p < .02$). These data are shown in Figure 2.

Imaging Results

Because behavioral data indicated that there were no significant effects of stimulus target type, imaging analyses focused on effects of trial type, task type, and their interaction.

Regions Involved in Both Cognitive and Affective Conflicts—To identify regions involved in controlling conflicts between competing affective and competing cognitive responses, we first computed contrasts of incongruent > congruent (I > C) trials for the affective and cognitive flanker tasks. These contrasts showed activation in bilateral dACC, pmPFC and dlPFC, left precuneus, and superior parietal cortex during cognitive conflict (Table 1) and activation of bilateral dACC and pmPFC, right dlPFC, and right precuneus during affective conflict (Table 2). The method of Kampe, Frith, and Frith (2003; see also Ochsner et al., 2004) was then used to identify regions active during conflict for both the affective and the cognitive tasks. The I > C contrast for the affective flanker task computed at a threshold of $p < .01$ was used to generate a mask image for computing the I > C contrast

for the cognitive flanker task, which was then thresholded at $p < .01$. Using the Fisher method of combined probability, the resulting contrast image reflects a joint probability of $< .001$ that a given region would be activated in both tasks (Ochsner et al., 2004; Kampe et al., 2003). This analysis indicated that dACC, pmPFC, and dlPFC were activated bilaterally for the I > C contrast in both tasks (Table 3, Figure 3). To verify that these regions were equivalently active during conflict in both tasks, we extracted parameter estimates for conflict-related (i.e., I–C) activity from each commonly active dACC, MFC, and dlPFC cluster and used planned t tests to compare activity for each task in each of these ROIs. As can be seen from the illustrative graphs in Figure 3, no significant effects were observed: Conflict-related activity in each region was statistically equivalent for each task (all p values $> .50$). Finally, it should be noted that we used correlation analyses (described in the next section) to look for regions whose magnitude of conflict-related activity correlated with the magnitude of response conflict in both tasks.

Regions Differentially Involved in Cognitive or Affective Conflict—To identify regions differentially involved in affective as compared with cognitive conflict, we computed an interaction contrast by subtracting the I > C contrast for the cognitive flanker task from the I > C contrast for the affective flanker task [Affective (I > C) – Cognitive (I > C)]. Affective conflict did not selectively activate any regions at $p < .001$. However, given a prior interest in the role of medial frontal cortex in affective conflict, we relaxed the threshold to $p < .005$ in this region only and found that affective conflict did selectively recruit a region of right rostral mPFC. By contrast, cognitive conflict [Cognitive (I > C) – Affective (I > C)] did not differentially activate any medial frontal regions. Instead, it selectively recruited left ventrolateral pFC (vlPFC) and left parietal cortex (Table 4, Figure 4). To verify this selectivity in frontal regions, we extracted parameter estimates for conflict-related (i.e., I–C) activity from the functionally defined medial and lateral frontal ROIs and entered them into an ANOVA with type of task (Affective and Cognitive) and ROI (mPFC and vlPFC) as factors. We found a significant interaction, $F(1, 15) = 49.41, p < .001$, and no other significant effects, as illustrated in Figure 4.

As described in the Methods section, we then performed a second analysis that contrasted the strength of correlation between brain activity and performance for each flanker task. This analysis was intended to complement the group-averaged contrasts presented above and involved two steps used previously (Zaki, Ochsner, Hanelin, Wager, & Mackey, 2007) that were described in the Methods section. First, we used robust regression analyses to perform a search within a prefrontal mask for regions significantly correlated with performance in one task or the other at $p < .01$. For this analysis, response time interference (RT for incongruent trials – RT for congruent trials) was correlated with measures of activation in the I > C contrast for both the affective and the cognitive flanker tasks. A liberal threshold was chosen for this step so as to minimize chances of false-negative findings at the next step. Second, we used the method of Steiger (1980) for comparing dependent correlations to determine which of these regions was significantly more correlated with performance in one task as compared with the other. Thus, all regions identified in this analysis must show a correlation with performance at $p < .01$ for one task, and that correlation must also be greater than that shown in the other task at $p < .05$ (Steiger, 1980). This analysis revealed

that activation of different regions predicted increases in RT interference during performance of each task: Right rostral/subgenual cingulate cortex correlated with interference for the affective flanker task, whereas a region of left ventral pFC correlated with interference for the cognitive flanker task (Table 4, Figure 5).

DISCUSSION

The goal of the present article was to identify common and distinct neural systems underlying the control of affective and cognitive conflicts. Toward that end, we devised affective and cognitive variants of the Eriksen flanker task that produced statistically equivalent levels of conflict-related response time slowing. Contrast analyses of functional imaging data revealed two key findings. First, conflict on both tasks was associated with activity in bilateral regions of dACC, pmPFC, and dlPFC. Second, affective and cognitive conflicts differentially recruited rostral mPFC and left vlPFC, respectively. Correlational analyses dovetailed with these findings by demonstrating that the magnitude of behavioral response conflict predicted greater conflict-related activity in rCC and mPFC for the affective task and greater conflict-related activity in left vlPFC for the cognitive task. Taken together, these data provide the first evidence for common and distinct neural systems for controlling conflicts between competing affective or competing cognitive responses.

The finding that both types of conflict activated overlapping regions of pmPFC and dlPFC is consistent with the view that these regions comprise a domain-general system for higher-level behavioral control (Botvinick et al., 2001; Miller & Cohen, 2001). That being said, how best to characterize the functions of these regions remains a topic of debate. Dorsal ACC and related pmPFC regions like those activated here have been described as important for conflict monitoring, expectancy violation, error detection, and response selection (van Veen & Carter, 2006; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger & von Cramon, 2004; Botvinick et al., 2001; Milham et al., 2001). Although the present study was not designed to discriminate among these alternatives, we favor the general view that posterior regions on the medial wall of the frontal lobe are important for signaling the need for a change in control processes, which may be motivated by the detection of processing conflicts, expectancy violations, and stimuli that may be salient to current goals (Davis et al., 2005; Eisenberger & Lieberman, 2004; Botvinick et al., 2001; Ochsner et al., 2001).

On this view, lateral prefrontal systems—like those activated here—are important for the implementation of control processes that accomplish tasks goals (Botvinick et al., 2001). These processes could include the maintenance of the goals themselves, which is essential for performance of both the affective and the cognitive flanker tasks (MacDonald et al., 2000). Given the verbal nature of the tasks employed here, they might also include processes involved in the controlled retrieval of information from semantic memory, as suggested by work associating these processes with regions of mid-vlPFC near those activated here (Badre & Wagner, 2007). This account would suggest that the site of common prefrontal activation reflects increased retrieval demands on incongruent as compared with congruent trials, as participants focus on retrieving semantic information about target but not flanker stimuli in both tasks. In future work, it will be important to disentangle these alternative possibilities. Whichever interpretation turns out to be correct, it is noteworthy that our data are consistent

with prior work employing flanker tasks, only some of which employed verbal stimuli, that have shown conflict-related activity in similar regions of dACC/pMFC and/or lateral pFC (Hazeltine et al., 2003; Ullsperger & von Cramon, 2001; van Veen et al., 2001; Hazeltine, Poldrack, & Gabrieli, 2000).

The finding that distinct neural systems were activated during affective and cognitive conflicts joins prior work showing that there may be material-specific effects associated with the stimulus features responsible for processing conflict (Hazeltine et al., 2003). At the broadest remove, the present findings fit with emerging views of the relative processing specializations of medial and lateral prefrontal systems. On these views, medial regions may serve to integrate information about internal mental and visceral states—which are essential components of affective responses—whereas lateral regions may play a greater role in the maintenance and the manipulation of nonaffective information (Lieberman, 2007).

In this context it is important to note that there are two ways in which the conflict induced by the affective flanker task may differ from that in the cognitive flanker task. On one hand, affective conflict involved stimuli that differed in their valence to a greater extent and were of higher arousal than the stimuli that elicited cognitive conflict. Given this, it makes sense that the rostral mPFC region selectively active during affective conflict is quite similar to regions whose activity may covary with the judged arousal or valence of affective responses (Gilbert et al., 2006; Ochsner et al., 2004; Phan et al., 2004; Lane, Fink, et al., 1997). On the other hand, it could be argued that the affective and the cognitive flanker tasks both asked participants to semantically categorize target stimuli, albeit in different ways. Here it is interesting to note that the rostral mPFC identified here also has been activated by tasks that require participants to generate category exemplars for affectively charged as compared with neutral semantic categories (Cato et al., 2004; Crosson et al., 2002). These views are not mutually exclusive, however, and it is possible that the ability to semantically categorize affective information is what underlies the association of mPFC with judgments of experienced valence and arousal (Ochsner et al., 2004).

Either way, the present findings fit with prior research implicating rostral medial regions in cognitive–affective conflicts (Bishop et al., 2004; Whalen et al., 1998) and affective–affective conflicts (Egner et al., 2007; Etkin et al., 2006) but goes beyond these studies in two ways. First, it confirms that activity in mPFC is related to behavioral conflict per se, which has not been shown in some prior studies (Bishop et al., 2004; Whalen et al., 1998). Second, it shows that this conflict-related activity can be based on the affective properties of stimuli and is not dependent on cross-talk between different representational channels related to facial, verbal, visual–spatial, or affective as compared with nonaffective processing (in prior work, targets and distracters differed in valence as well as type—faces vs. words, faces vs. houses, number vs. identity of words).

Whereas the affective flanker task drew more heavily on mPFC systems important for selecting among competing affective representations, the cognitive flanker task drew more heavily on left lateral pFC systems that may be associated in general with selecting stimuli based on their semantic category membership (Badre & Wagner, 2007). As noted above, common activity across flanker tasks was observed in bilateral vlPFC, and we also observed

additional activity in left pFC in a region anterior and ventral to the common focus. It has been suggested that recruitment of left inferior vIPFC regions may be important for selecting among semantic representation after they have been retrieved by mid-vIPFC regions (Badre & Wagner, 2007). As applied to the present data, this view suggests that selecting based on semantic category membership in the cognitive flanker task taxes this postretrieval process more heavily than does the affective flanker task, which in turn depends on a similar process mediated in mPFC. Although consistent with the present data, future work will be necessary to more directly test this interpretation.

Another key feature of the present results was the finding that correlational analyses both supported and extended the contrast analyses described above. In general, correlations between measures of task performance and neural activity may identify brain regions more or less active in good or poor performers that are not revealed in group-averaged contrasts. Here we found that conflict-related response time increases and brain activity were positively correlated in different regions for each flanker task: Behavioral evidence of conflict predicted greater activity in rCC and ventromedial pFC for the affective flanker and greater activity in left vIPFC for the cognitive flanker task. The fact that these correlations were positive suggests that as flankers caused more interference across subjects, additional activity in these regions was required to focus on and select the appropriate target response.

The fact that these regions were close to, but distinct from, the medial and the lateral regions identified in contrasts as selective for affective or cognitive conflict could be interpreted in two ways. One interpretation is that the systems identified in the contrasts reveal systems that are consistently necessary for selecting among competing affective and cognitive responses and that the correlational analyses indicate that greater recruitment of essentially similar processes is required in individuals who experience greater response conflict. This interpretation may fit the region showing a performance–activity correlation for the cognitive flanker task, which may fall within the portion of left vIPFC most sensitive to selecting among competing semantic representations (cf. Badre & Wagner, 2007). An alternative interpretation is that correlational analyses reveal not that more of the same kind of processing is needed, but that additional kinds of processes come into play as selection becomes particularly difficult. This interpretation may fit the region showing a performance–activity correlation for the affective flanker task, which fell within a portion of ventral mPFC previously associated with self-referential processing and the so-called “default state” present during uninstructed baseline conditions (Gillihan & Farah, 2005; Gusnard et al., 2001). Although speculative, this may suggest that affective conflict is difficult to the extent that it has personal meaning or elicits personal associations, which makes sense given that computing the affective significance of a stimulus by definition is about its relevance to one's personal goals, wants, and needs (Lazarus, 1991).

One caveat for the present findings is we did not use task manipulations, such as conflict adaptation (Egner et al., 2007; Etkin et al., 2006; Carter et al., 2000), or various means of parametrically manipulating response selection demands (Badre, Poldrack, Pare-Blagoev, Inslar, & Wagner, 2005; Durston et al., 2003) that might allow the dissociation of different types of control processes associated with goal maintenance, conflict monitoring, or response selection per se. Here, the emphasis was on taking a first step toward, showing that

extinguish affective responses, which has been shown in normals to be associated with the structural integrity and the functional activation of ventral mPFC regions (Milad, Rauch, Pitman, & Quirk, 2006; Quirk & Beer, 2006; Rauch, Shin, & Phelps, 2006; Milad et al., 2005; Phelps, Delgado, Nearing, & LeDoux, 2004). The present results suggest a slightly different interpretation of these data. Namely, that the ability to select task-appropriate affective responses, which is associated with this region, may manifest itself in a variety of ways in both normal and abnormal populations. On this view, extinction is a specific example of needing to select a context-appropriate affective response, and failures to recruit ventral mPFC to support selection of appropriate responses may contribute to a variety of affective disorders, including PTSD. Future work examining cognitive and affective conflicts in clinical populations will be essential for addressing these possibilities.

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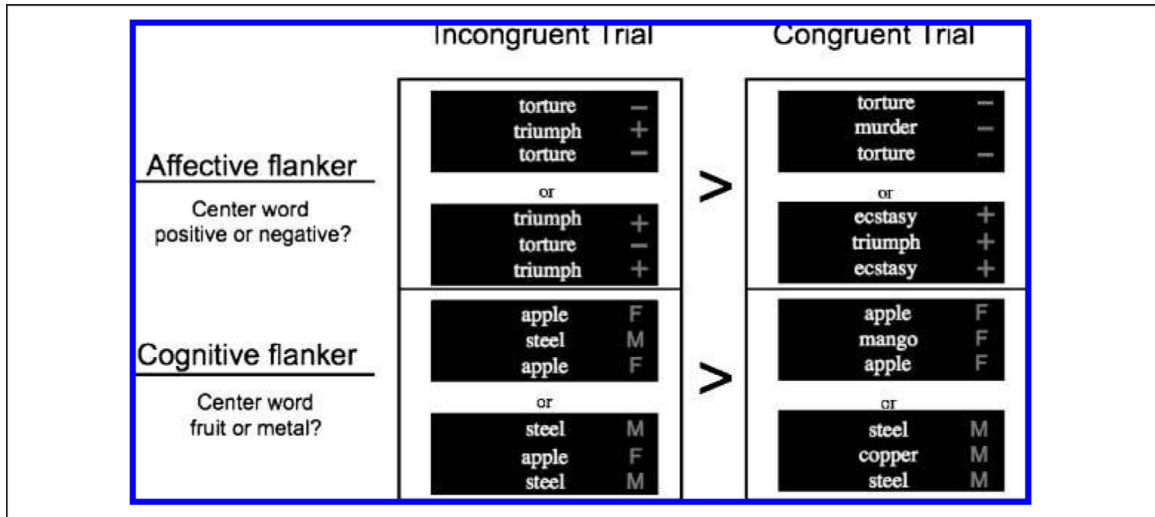


Figure 1. Diagrammatic representation of the two main trial types used in the affective (top) and cognitive (bottom) flanker tasks. Each black square shows example stimuli that could be present on screen during a given incongruent or congruent trial. During the affective flanker task, target stimuli differ in valence from the flanking stimuli that appear above and below it. During the cognitive flanker task, target and flanker stimuli differ not in valence but in their semantic category. The main comparisons of interest are response time, and brain activation increases on incongruent as compared with congruent trials, as illustrated by the “>” symbols separating the panels representing each trial type. The +/- and M/F symbols shown to the right of each sample screen are not shown during performance of the actual task and are included here to clearly illustrate the differences between target and flanker stimuli in each task.

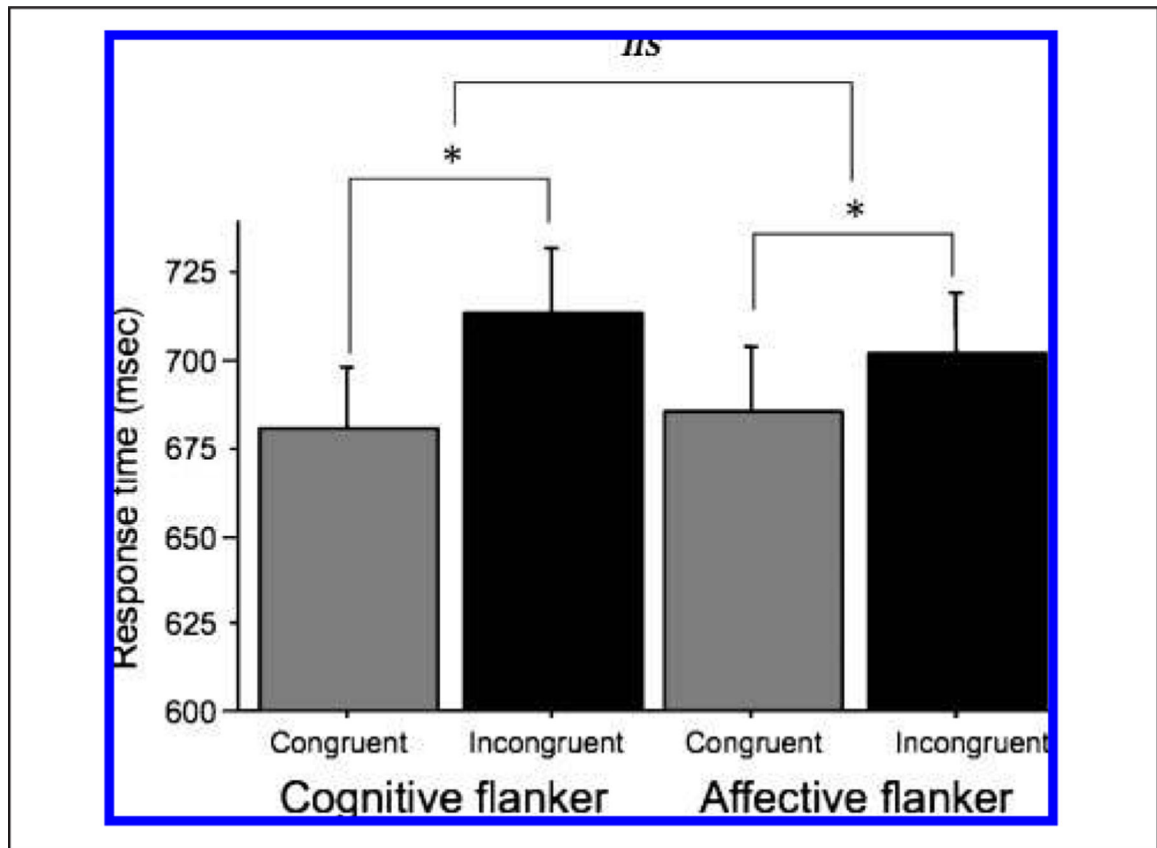


Figure 2.

Graph showing response times for congruent and incongruent trials for both the affective and the cognitive flanker tasks. As can be seen here, response times are significantly and equivalently slower on incongruent trials for both tasks. Inc = incongruent; Con = congruent. *Effect of incongruence significant for each task at $p < .05$; *ns* = nonsignificant interaction effect.

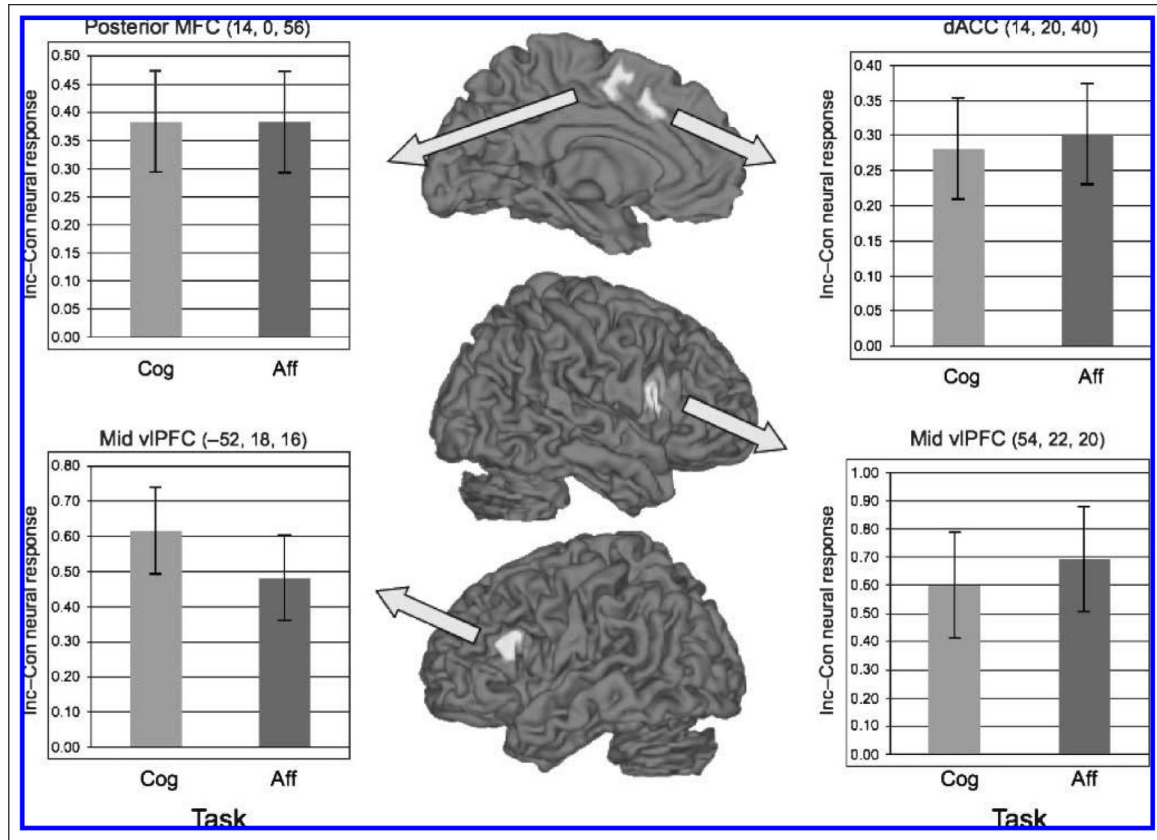


Figure 3.

Regions showing greater conflict-related activity in the incongruent-congruent contrast for both the affective and the cognitive flanker tasks. Graphs at the left and the right show the magnitude of this activity for selected functional ROIs shown in the center panels. As can be seen in these graphs, these regions are equivalently activated (all pairwise p values = ns) during both affective and cognitive conflicts. dACC = dorsal anterior cingulate cortex; MFC = medial frontal cortex; vIPFC = ventrolateral pFC. MNI coordinates for each region are shown in parentheses.

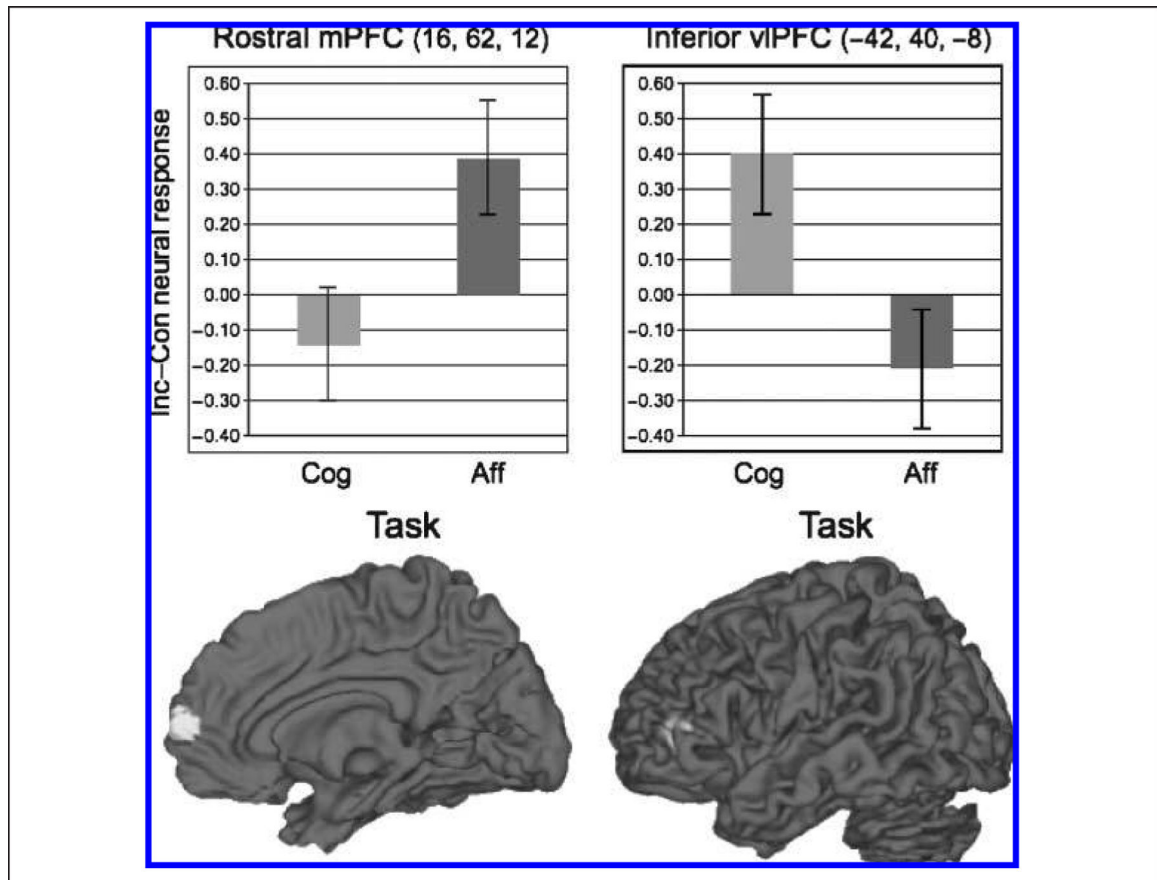


Figure 4. Regions selectively activated for affective (left panel) or cognitive (right panel) conflicts. Comparison of left and right panels makes clear that affective and cognitive conflicts differentially depend upon medial and left lateral prefrontal systems, respectively. mPFC = medial pFC; vIPFC = ventrolateral pFC. MNI coordinates for each region are shown in parentheses.

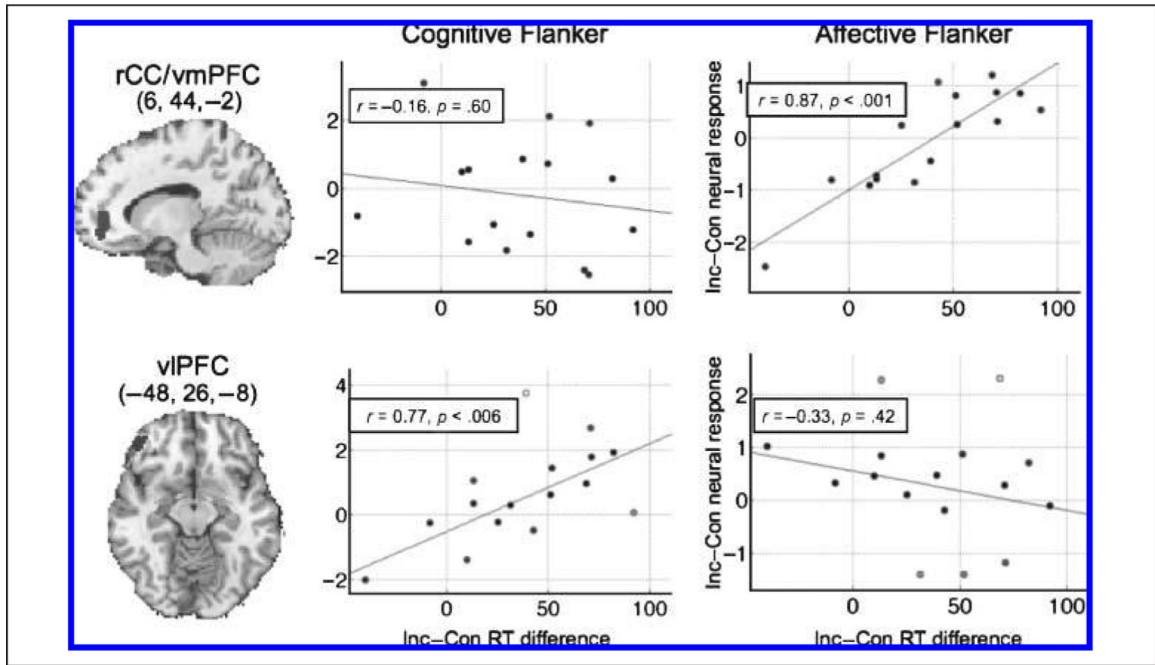


Figure 5.

Regions whose conflict-related activity differentially correlated with the magnitude of response time interference on incongruent as compared with congruent trials during the affective (right panels) or cognitive (left panels) flanker tasks. Each point represents data for a single subject, with gray/partially filled circles representing relative outliers down-weighted by the robust regression algorithm (Wager et al., 2005) used to compute the observed relationships. Top and bottom panels show medial and ventrolateral regions whose activity differentially correlated positively with the magnitude of behavioral response conflict during either each task. These data dovetail with an extend those shown in Figure 4 by showing additional regions of rostral medial and left inferior vIPFC selectively associated with affective as compared with cognitive conflict, respectively. rCC/vmPFC = rostral cingulate/ventromedial pFC; vIPFC = ventrolateral pFC. Inc = incongruent; Con = congruent.

Table 1.

Group Activations for Incongruent > Congruent for Semantic Flanker Task

Region of Activation	Brodmann	Coordinates			Z Score	Volume (mm ³)
		x	y	z		
Middle frontal gyrus	L9	-36	22	28	3.48	56
Middle frontal gyrus	R6	32	-6	44	4.33	1168
Middle frontal gyrus	R6	10	-10	58	4.05	472
Middle frontal gyrus	R9	14	40	30	4.04	88
Inferior frontal gyrus	L45/9	-56	20	24	3.91	720
Insula/inferior frontal gyrus	R13	36	22	16	3.53	40
Precentral/inferior frontal gyri	L6	-38	-6	42	4.36	1072
Precentral gyrus	R6	34	2	28	3.93	560
Precentral gyrus	R6	58	-10	44	3.70	144
Medial frontal gyrus	L32	-16	12	50	3.67	40
Cingulate gyrus	L24/32	-16	14	34	5.18	392
Cingulate gyrus	L32	-8	22	46	4.09	400
Cingulate gyrus	L24	-6	-6	40	3.47	120
Superior parietal lobule	L7	-40	-66	50	3.62	136
Parahippocampal gyrus	L	-38	-26	-16	3.75	56
Precuneus	L39	-32	-66	36	3.39	80

Volumes are in cubic millimeters, where 1 voxel = 8 mm³. Coordinates are in MNI space.

Table 2.
Group Activations for Incongruent > Congruent Trials for Affective Flanker Task

Region of Activation	Brodmann	Coordinates			Z Score	Volume (mm ³)
		x	y	z		
<i>Group Contrast</i>						
Superior frontal gyrus	L6	14	2	58	3.58	184
Middle frontal gyrus	L8	-8	38	44	3.33	144
Middle frontal gyrus	L6/9	-10	30	38	3.18	40
Middle frontal/cingulate gyri	L8/32	-6	16	52	3.93	42
Inferior frontal gyrus/insula	L47/13	-34	16	-8	3.56	48
Inferior frontal gyrus	R45	58	22	20	3.18	40
Cingulate gyrus	L32/24	-4	10	22	3.52	40
Cingulate gyrus	R32/24	16	16	32	3.76	72
Cingulate gyrus	R32	16	20	44	3.51	160
Cingulate gyrus	R23	12	-16	32	3.47	48
Superior temporal gyrus	R38/22	50	14	-8	3.65	72
Precuneus	R7	14	-64	38	3.49	120
Caudate	R	6	2	22	3.38	48

Volumes are in cubic millimeters, where 1 voxel = 8 mm³. Coordinates are in MNI space.

Group Activations Common to Affective (Incongruent > Congruent) and Cognitive (Incongruent > Congruent) Conflicts

Table 3.

Region of Activation	Brodmann	Coordinates			Z Score	Volume (mm ³)
		x	y	z		
Anterior cingulate cortex	R24	26	-20	34	3.81	464
Anterior cingulate cortex	R32	14	18	46	3.37	384
Posterior medial frontal	R6	14	2	58	3.58	640
Posterior medial frontal	L8	-6	16	52	3.93	448
Posterior medial frontal	R6	32	6	28	3.20	96
Inferior frontal gyrus	R45	56	22	20	3.25	416
Inferior frontal gyrus	L44	-52	16	16	3.31	576

Volumes are in cubic millimeters, where 1 voxel = 8 mm³. Coordinates are in MNI space.

Table 4.

Group Activations Specific to Affective or Cognitive Conflict

Region of Activation	Brodmann	Coordinates			Z Score	Volume (mm ³)
		x	y	z		
<i>Affective Conflict</i>						
Rostral mPFC*	BA 9/10	14	62	12	2.80	24
<i>Cognitive Conflict</i>						
vIPFC	L47	-42	40	8	3.67	136
Lateral parietal		-42	-72	46	3.41	96

Volumes are in cubic millimeters, where 1 voxel = 8 mm³. Coordinates are in MNI space.

* $p < .005$.