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Emotion Speeds up Conflict Resolution: A New Role for the Ventral Anterior Cingulate Cortex?

Philipp Kanske[1,2] and Sonja A. Kotz[1]

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Neurocognition of Rhythm in Communication Group, Leipzig 04103, Germany and [2]Department of Cognitive and Clinical Neuroscience, Central Institute of Mental Health, 68159 Mannheim, Germany

Address correspondence to Philipp Kanske, Department of Cognitive and Clinical Neuroscience, Central Institute of Mental Health, Square J5, 68159 Mannheim, Germany. Email: kanske@cbs.mpg.de.

It has been hypothesized that processing of conflict is facilitated by emotion. Emotional stimuli signal significance in a situation. Thus, when an emotional stimulus is task relevant, more resources may be devoted to conflict processing to reduce the time that an organism is unable to act. In the present electroencephalography and functional magnetic resonance imaging (fMRI) studies, we employed a conflict task and manipulated the emotional content and prosody of auditory target stimuli. In line with our hypothesis, reaction times revealed faster conflict resolution for emotional stimuli. Early stages of event-related potential conflict processing were modulated by emotion as indexed in an enhanced frontocentral negativity at 420 ms. FMRI yielded conflict activation in the dorsal anterior cingulate cortex (dACC), a crucial part of the executive control network. The right ventral ACC (vACC) was activated for conflict processing in emotional stimuli, suggesting that it is additionally activated for conflict processing in emotional stimuli. The amygdala was also activated by emotion. Furthermore, emotion increased functional connectivity between the vACC and activity in the amygdala and the dACC. The results support the hypothesis that emotion speeds up conflict processing and suggest a new role for the vACC in processing conflict in particularly significant situations signaled by emotion.

Keywords: affect, EEG, executive control, fMRI, speech

Introduction

Detecting and solving conflict between opposing information is one of the key functions of the dorsal anterior cingulate cortex (dACC; Fan et al. 2003; Botvinick et al. 2004; Weissman et al. 2005; Aarts et al. 2008). In contrast, the ventral portion of the ACC (vACC) responds to conflict between different emotions (Etkin et al. 2006; for a review on ACC function, see also Bush et al. 2000). However, it is unclear how the 2 parts of the ACC engage in the interaction of emotion and conflict processing, that is, when nonemotional conflict is processed in an emotional context. As emotions signal the particular significance of a situation (Scherer 1994), more resources may be allocated to conflict processing when target stimuli are emotional to reduce the time in which an organism is unable to act (Norman and Shallice 1986; Pessoa 2009). We hypothesize that the vACC, in addition to the dACC, is recruited for conflict processing in an emotional context. Not only is the vACC interconnected with the dACC but it also receives input from the amygdala (Vogt et al. 1992; Stein et al. 2007), a structure in the medial temporal lobe that is specialized for rapid detection of emotion (Zald 2003; Sergerie et al. 2008). The vACC may thus integrate emotion and conflict information (Etkin et al. 2006) and prioritize the processing of conflict in an emotional context.

The design we applied tests this hypothesis in an auditory version of the Simon task (see Fig. 1), which creates conflict through incongruent stimulus–response mappings (Simon and Small 1969). Participants performed a gender voice decision task on voices presented to either the right or the left ear. They responded via a left or right hand button press, resulting in congruent and incongruent presentation and response sides. Negative and neutral word utterances created an emotional or neutral context and allowed the investigation of an interaction of emotion and conflict processing.

In addition to functional magnetic resonance imaging (fMRI), we also explored the time course of emotion and conflict processing using event-related potentials (ERPs). Previous results of different conflict tasks showed an enhanced frontocentral negativity for incongruent compared with congruent stimuli, whose exact timing depends on the specific conflict tasks used (~200 to 450 ms; Liotti et al. 2000; van Veen and Carter 2002). The Simon task is less explored but also elicits a negativity (Carriero et al. 2007). Despite the timing differences, source analyses of the reported negativities point to the same region: the ACC (Folstein and Van Petten 2008). We therefore predict that differential engagement of the vACC and dACC for conflict processing in an emotional and neutral context also results in differences in the conflict negativity. As the amygdala already responds to emotional words and prosody within 100 ms poststimulus onset (Sander et al. 2005; Landis 2006), it may rapidly engage the vACC yielding an impact of emotion on the first conflict-sensitive ERP.

In summary, by means of an auditory conflict task, we aim to test the influence of emotion on conflict processing and the role of the vACC, the critical input of the amygdala to the vACC, and an early ERP conflict negativity in processing nonemotional conflict in emotional target stimuli.

Materials and Methods

Rating and Stimuli

All experiments conformed to the policies and principles contained in the Federal Policy for the Protection of Human Subjects (US Office of Science and Technology Policy) and in the Declaration of Helsinki.

Participants (32; 16 females, mean age 23.3, standard deviation [SD] 2.8) rated 1000 selected German nouns for emotional valence (negative–neutral–positive), arousal (low arousing–high arousing), and concreteness (concrete–abstract) on a 9-point scale. Based on these ratings, 40 negative and 40 neutral words were selected. The word groups differed significantly in valence and arousal but were controlled for concreteness (Kanske and Kotz 2007), word frequency according to the Wortschatz Lexikon of the University of Leipzig (http://wortschatz.uni-leipzig.de/), and word length in number of letters and

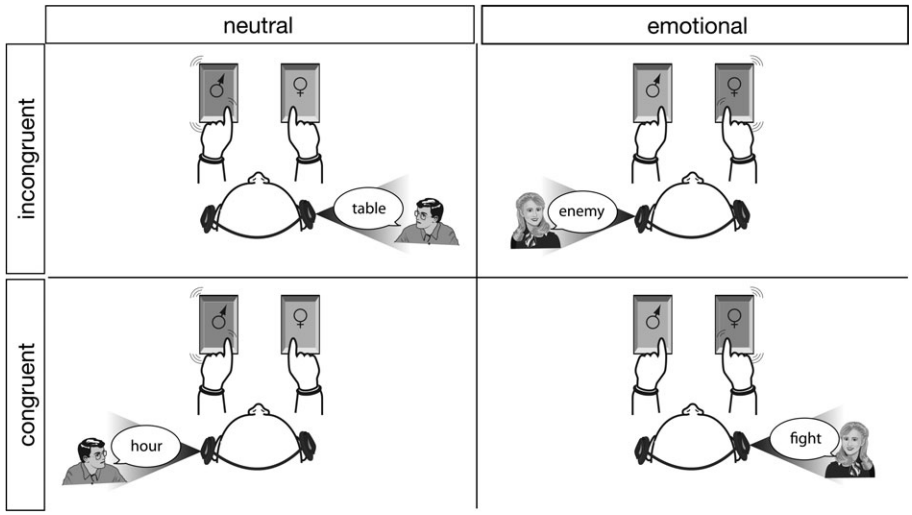


Figure 1. Schematic of the modified Simon task. Participants identified the gender of a voice that was presented to the right or left ear. Responses were given with the right or left hand, yielding congruent and incongruent presentation and response sides. Emotional and neutral words were presented in the corresponding emotional prosody.

syllables (see Table 1). Four auditory recordings of each of these words were spoken by 2 professional actors (male and female) with the emotional expression corresponding to the emotional valence of the words. An additional group of 30 participants (16 females, mean age 24.2, SD 3.1) rated the valence and arousal vocally expressed in these 320 stimuli. One of the recordings of each word from each speaker was then selected, yielding 80 negative and 80 neutral stimuli. These words differed significantly in valence and arousal, but not in duration. All stimuli were normalized to an intensity of 75 dB sound pressure level.

Electroencephalography Experiment

Participants

Twenty-six native speakers of German participated in the experiment. Data from 3 participants were excluded because of increased electroencephalography (EEG) artifacts. The remaining 23 (10 females) participants had a mean age of 25.1 years (SD 2.6). All participants reported normal hearing and were right handed according to the Edinburgh Handedness Inventory (Oldfield 1971), with a mean laterality quotient of 97.6 (SD 5.3).

Task and Procedure

Participants performed a gender voice decision task (see Fig. 1). Words spoken by a male and a female voice were presented either to the left or to the right ear (not binaurally). Participants responded with a left or right hand button press. Mapping of responses to left and right response keys was counterbalanced across participants. Half of the trials were congruent (same stimulus presentation and response hand side) and the other half incongruent. Each stimulus (each word spoken by a male and a female speaker) was presented in the congruent and in the incongruent condition yielding a total of 320 trials. Each trial lasted 6000 ms. The stimulus onset in a trial was jittered (0–2000 ms) to avoid temporal orienting and, in the fMRI experiment, to allow sampling at multiple time points along the blood oxygen level–dependent (BOLD) signal curve. Stimulus presentation duration was 600 ms on average (see Table 1). Maximum response time after stimulus onset was 2000 ms. During the ERP experiment, participants were seated in a comfortable chair in a sound-attenuated electrically shielded room and wore headphones (Sennheiser HD 202). Stimuli were presented with Presentation 12.0 (Neurobehavioral Systems).

EEG Measurement

Ag–AgCl electrodes were used to record the EEG from 64 scalp positions according to the international 10–20 system (Jasper 1958; American Electroencephalographic Society 1991). Vertical eye movements were registered with 2 electrodes positioned above and below the right eye. The horizontal electrooculograms were recorded with lateral electrodes from both eyes. The ground electrode was located on the sternum. Data were referenced to the left mastoid while the right mastoid was passively recorded. Impedances were below 5 kΩ for all recordings. Refa amplifiers and Xrefa recording software were used. The sampling rate was 500 Hz. An anti-alias low-pass filter was applied online with 135 Hz. Further filtering was only applied for graphical display (14 Hz low-pass filter). Data were rereferenced off-line to the average of both mastoids.

Table 1
Descriptives of the word material

	Negative	Neutral
Example word	Tod (death)	Phase (phase)
Rated visual valence	2.4 (0.4)	5.0 (0.1)
Rated visual arousal	6.8 (0.5)	2.3 (0.3)
Rated auditory valence	2.3 (0.2)	5.0 (0.1)
Rated auditory arousal	7.4 (0.3)	2.4 (0.2)
Rated concreteness	6.3 (1.5)	6.0 (1.3)
Word frequency	11.0 (1.9)	11.3 (1.9)
Number of letters	5.5 (1.1)	5.9 (1.1)
Number of syllables	1.7 (0.5)	1.8 (0.4)
Duration	0.6 (0.1)	0.6 (0.1)
Mean pitch	280.8 (58.4)	159.7 (22.7)

Note: Valence, arousal, and concreteness ratings for the selected word groups. The material was also controlled for word frequency, number of letters and syllables, and duration (in seconds).

Data Analysis

EEG data were analyzed with the software package EEP (ERP Evaluation Package EEP 3.2, Max Planck Institute for Human Cognitive and Brain Sciences). Epochs of 1000 ms after stimulus onset were computed with an additional 200 ms prestimulus baseline. All trials were visually inspected for artifacts. An automatic rejection of trials exceeding an amplitude shift of 30 μV for the 2 eye channels and 40 μV for CZ and PZ within a sliding time window of 200 ms was applied. Trials were averaged for each condition, participant, and for each condition across participants (grand average). After visual inspection of the grand averages and a time line analysis with 50 ms time windows, a time window between 420 and 550 ms was chosen for quantification of the conflict negativity. Channels were grouped into 4 regions of interest with 11 electrodes each (left anterior: FP1, AF3, AF7, F3, F5, F7, F9, FC3, FC5, FT7, and FT9; right anterior: FP2, AF4, AF8, F4, F6, F8, F10, FC4, FC6, FT8, and FT10; left posterior: CP3, CP5, TP7, TP9, P3, P5, P7, P9, PO3, PO7, and O1; right posterior: CP4, CP6, TP8, TP10, P4, P6,P8, P10, PO4, PO8, and O2). Repeated-measures analyses of variance (ANOVAs)

including the within-factors congruency (congruent and incongruent) and emotion (negative and neutral) were computed for the behavioral data. In addition, the analysis of the EEG data included the factors region (anterior and posterior) and hemisphere (left and right). Significant main effects and interactions were followed up by simple effects analyses and pairwise comparisons. Only critical experimental interactions were followed up and are reported. As a measure of effect size, ω^2 (Kirk 1995) is reported when effects are compared.

fMRI Experiment

Participants

Twenty-two volunteers (10 females) participated in the experiment. Mean age was 24.7 years (SD 2.7). All participants were native speakers of German, reported normal hearing, and were right handed according to the Edinburgh Handedness Inventory (Oldfield 1971) with a mean laterality quotient of 98.0 (SD 4.3).

Task and Procedure

The task was the same as in the ERP experiment. Twenty null events (6 s each and no stimulus presentation) were added and randomly interspersed in the experimental trials to allow for baseline contrasts.

fMRI Recording

MRI data were collected at 3.0 T using a Bruker 30/100 Medspec system (Bruker Medizintechnik GmbH). A standard birdcage head coil was used. The experiment consisted of 2 separate but consecutive sessions. In the first session, high-resolution whole-head 3D Modified Driven Equilibrium Fourier Transform (MDEFT) brain scans (128 sagittal slices, 1.5 mm thickness, field of view [FOV] 25:0 × 25:0 × 19:2 cm, data matrix of 256 × 256 voxels) were acquired to improve localization (Ugurbil et al. 1993). The second session started with the collection of scout spin echo sagittal scans to define the anterior and posterior commissures on a midline sagittal section. For each participant, structural and functional (echo planar) images were obtained from 22 axial slices parallel to the plane intersecting the anterior and posterior commissures (AC–PC plane). The whole range of slices covered almost the entire brain. For functional imaging, a gradient echo echo planar image (EPI) sequence was used with a time echo of 30 ms, a flip angle of 90°, a time repetition of 2000 ms, and an acquisition bandwidth of 100 kHz. The matrix acquired was 64 × 64 with an FOV of 19.2 cm, resulting in an in-plane resolution of 3 × 3 mm. The slice thickness was 4 mm with an interslice gap of 1 mm. To align the functional EPIs to 3D-MDEFT images, conventional T_1-weighted MDEFT and T_1-weighted EPIs were obtained in-plane with the T_2^* EPIs as reference.

Data Analysis

The data processing was performed using the software package LIPSIA (Lohmann et al. 2001). Functional data were corrected for motion using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one scan, a cubic spline interpolation was applied. A temporal high-pass filter with a cutoff frequency of 1/100 Hz was used for baseline correction of the signal, as well as a spatial Gaussian filter with 4.24-mm full-width at half-maximum (FWHM). To align the functional data slices with a 3D stereotactic coordinate reference system, a rigid linear registration with 6 degrees of freedom (3 rotational and 3 translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT (Ugurbil et al. 1993; Norris 2000) and EPI-T_1 slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set was acquired for each participant during a previous scanning session. The MDEFT volume data set with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space (Talairach and Tournoux 1988). The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation so that the resulting functional slices were aligned with the stereotactic coordinate system. This linear normalization process was improved by a subsequent additional nonlinear normalization.

The statistical evaluation was based on a least squares estimation using the general linear model for serially autocorrelated observations (Friston 1994; Friston, Holmes, Poline, et al. 1995; Friston, Holmes, Worsley, et al. 1995; Worsley and Friston 1995). The design matrix was generated with a synthetic hemodynamic response function (Josephs et al. 1997; Friston et al. 1998) and its first derivative. The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4-s FWHM to deal with the temporal autocorrelation (Worsley and Friston 1995). In the following, contrast images (i.e., estimates of the raw score differences between specified conditions) were generated for each participant. As noted previously, each individual functional data set was aligned with the standard stereotactic reference space, so that a group analysis based on the contrast images could be performed. Contrasts between the different conditions were calculated using the t statistic. Subsequently, t values were transformed into Z scores. A multiple comparisons correction was done using Monte-Carlo simulations. This procedure generates voxels at a rate equal to the significance criterion specified, proportional to the total number of voxels in the data set, and calculates a cluster size that corresponds to the true false-positive rate for these conditions. Using 1000 iterations, a false-positive cluster probability of $P < 0.05$ was achieved with a minimum cluster size of 216 mm^3 at a threshold of $P < 0.001$ (uncorrected) for individual voxels. In the next step, this synthetically determined statistical threshold was applied to all voxels in the real data. The advantages of combining a voxel-based threshold with a minimum cluster size have been described elsewhere (Forman et al. 1995). As we had strong hypotheses regarding the amygdala, we used a lower threshold to analyze amygdala activations in the negative–neutral words contrast to a critical Z score of greater than 2.33 ($P < 0.01$) and a volume threshold of greater than 108 mm^3 (4 measured voxels). For similar approaches, see, for example, Nomura et al. (2004), Etkin et al. (2006), Dougal et al. (2007). To further validate the results, we conducted time line statistics, averaging BOLD signal change (in %) from 3 to 8 s poststimulus onset for all voxels in the activated vACC and dACC and amygdala clusters.

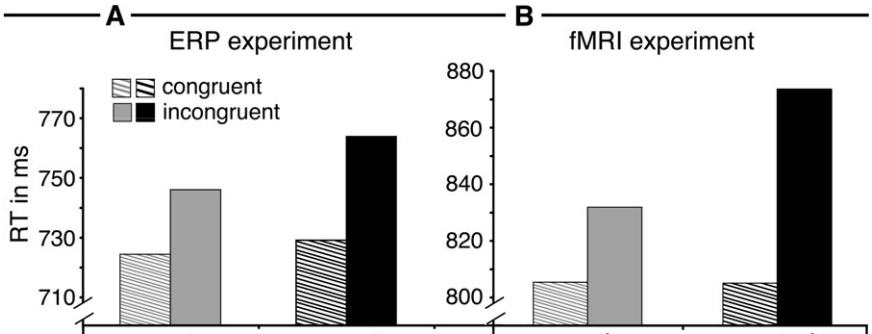
To assess functional connectivity between the activated clusters, a correlational analysis was applied (see Obleser et al. 2007). Time courses (percent signal change) for each trial were extracted with LIPSIA for all voxels in the observed clusters in the amygdala, the vACC, and the dACC for each participant. Subsequently, the time courses were averaged across participants yielding condition- and cluster-specific time courses with 80 sampling points (1 per trial) in each condition. Pearson's correlation coefficients were then analyzed between the brain regions separately for incongruent emotional and neutral conditions. Thus, we related variations in percent signal change in one condition in one region to that in another region. If this correlation is significant in one condition, but not in another condition, it can be assumed that the 2 regions are functionally coupled, that is, their BOLD response changes covary for one specific condition. Note that this method controls for simple main effects as 2 regions may be found equally activated in a condition but do not show covariation in percent signal change.

Results

ERP Experiment

Behavioral Data

Response accuracy was 99.7% (SD 0.6; reaction time mean = 740.8 ms, SD 129.6). There were no significant differences in accuracy rates. RTs were shorter for congruent compared with incongruent trials (see Fig. 2; $F_{1,22} = 17.6$, $P < 0.001$). Emotion did not have a significant main effect on RTs, but the interaction of emotion and conflict was significant ($F_{1,22} = 4.8$, $P < 0.05$). Follow-up analyses revealed that the conflict effect was smaller for negative compared with neutral trials ($F_{1,22} = 8.6$, $P < 0.01$, $\omega^2 = 0.14$ vs. $F_{1,22} = 22.4$, $P < 0.0001$, $\omega^2 = 0.32$). This effect was driven by reduced RTs in negative



	ERP experiment			fMRI experiment		
	congruent	incongruent	conflict	congruent	incongruent	conflict
negative	724.3 (139.2)	745.9 (136.9)	21.6	805.2 (153.5)	831.6 (181.6)	26.4
neutral	729.1 (120.7)	763.8 (125.8)	34.7	804.9 (185.9)	873.4 (174.8)	68.4

Figure 2. Mean RTs and SDs (in parentheses) in the ERP and fMRI experiment. The conflict effects refer to the difference of incongruent–congruent RTs.

incongruent trials that marginally differed from neutral incongruent trials ($F_{1,22}$ = 3.1, P < 0.10). There was no difference between negative and neutral congruent trials ($F_{1,22}$ = 0.6, P > 0.40).

ERP Data

A negative deflection starting around 420 ms, with a larger amplitude for incongruent than congruent trials, was observed at frontal and central sites. Figure 3*A* shows the waveforms for incongruent and congruent trials. The ERPs of incongruent negative and neutral, as well as congruent negative and neutral trials, are displayed in Figure 3*B*. Repeated-measures analyses of mean amplitudes between 420 and 550 ms yielded a significant main effect of conflict ($F_{1,22}$ = 5.0, P < 0.05). The conflict negativity was only significant over anterior sites (anterior: $F_{1,22}$ = 5.5, P < 0.05; posterior: $F_{1,22}$ = 2.4, P > 0.10). There was also an interaction of emotion, conflict, and region ($F_{1,22}$ = 4.1, P < 0.05). The interaction of emotion and conflict was only significant at anterior and not at posterior electrode sites ($F_{1,22}$ = 4.7, P < 0.05 vs. $F_{1,22}$ = 2.4, P > 0.10). At the anterior sites, conflict was significant for emotional, but not for neutral trials ($F_{1,22}$ = 13.1, P < 0.01 vs. $F_{1,22}$ = 0.1, P > 0.70). There was no conflict negativity for negative or neutral trials over posterior electrodes ($F_{1,22}$ = 2.6, P > 0.10; $F_{1,22}$ = 1.1, P > 0.30).

fMRI Experiment

Behavioral Data

The results resemble those of the ERP experiment. Overall accuracy was slightly lower, at 93.0% (SD 3.8). However, there were no significant differences between conditions. Mean RTs were 828.8 ms (SD 172.9). The ANOVA yielded a significant main effect of conflict ($F_{1,21}$ = 63.7, P < 0.0001). Congruent trials were responded to faster than incongruent trials (see Fig. 2). There was an interaction of conflict and emotion ($F_{1,21}$ = 4.92, P < 0.05). Follow-up analyses revealed a reduced conflict effect for emotionally negative compared with neutral trials ($F_{1,21}$ = 4.4, P < 0.05, ω^2 = 0.07 vs. $F_{1,21}$ = 52.0, P < 0.0001, ω^2 = 0.54). Comparable to the ERP experiment, the effect was driven by reduced RTs in the emotional incongruent condition compared with the neutral incongruent trials ($F_{1,21}$ = 9.1, P < 0.01), while the difference between negative and neutral was not significant in the congruent condition ($F_{1,21}$ = 0.0, P > 0.90).

fMRI Data

Regional brain activations. The left and right dACC showed enhanced activation for incongruent compared with congruent trials, as well as the right superior temporal gyrus and paracentral lobule (see Fig. 4 and Table 2). Furthermore, activation in the right vACC was found for conflict in emotional trials. As an additional validation of these results, a time line statistic was conducted for the vACC and dACC, averaging BOLD signal change (in percentage) from 3 to 8 s poststimulus onset for all voxels in the clusters. For the dorsal regions of the ACC, there was a main effect of conflict (right: $F_{1,21}$ = 28.9, P < 0.0001; left: $F_{1,21}$ = 38.6, P < 0.0001) but no effect of emotion or an interaction. For the vACC, a main effect of conflict was found ($F_{1,21}$ = 8.6, P < 0.01), as well as an interaction of emotion and conflict ($F_{1,21}$ = 5.7, P < 0.05), confirming enhanced activation of the vACC for negative incongruent ($F_{1,21}$ = 8.0, P < 0.01) but not neutral incongruent trials ($F_{1,21}$ = 0.2, P > 0.60) compared with congruent trials, respectively. The amygdala was bilaterally activated for negative as compared with neutral words, as was the right superior temporal gyrus. The time line statistic for the amygdala yielded a significant effect of emotion (right: $F_{1,21}$ = 4.4, P < 0.05; left: $F_{1,21}$ = 4.3, P < 0.05) but no effect of conflict or an interaction.

To also control for potential effects of the reaction time (RT) differences between conditions, we repeated the analysis including RTs for each trial as a regressor in the design matrices. The results of this analysis did not differ from the previous analysis.

Functional connectivity. As described above, the dACC and amygdala showed main effects of conflict and emotion, respectively, but no interaction. However, the time line statistics in the vACC yielded an interaction of emotion and conflict in this region. We therefore compared functional connectivity between the vACC and the amygdala and the dACC in both emotional and neutral incongruent trials. Interestingly, functional connectivity between these regions was modulated by emotion such that the activation in the right

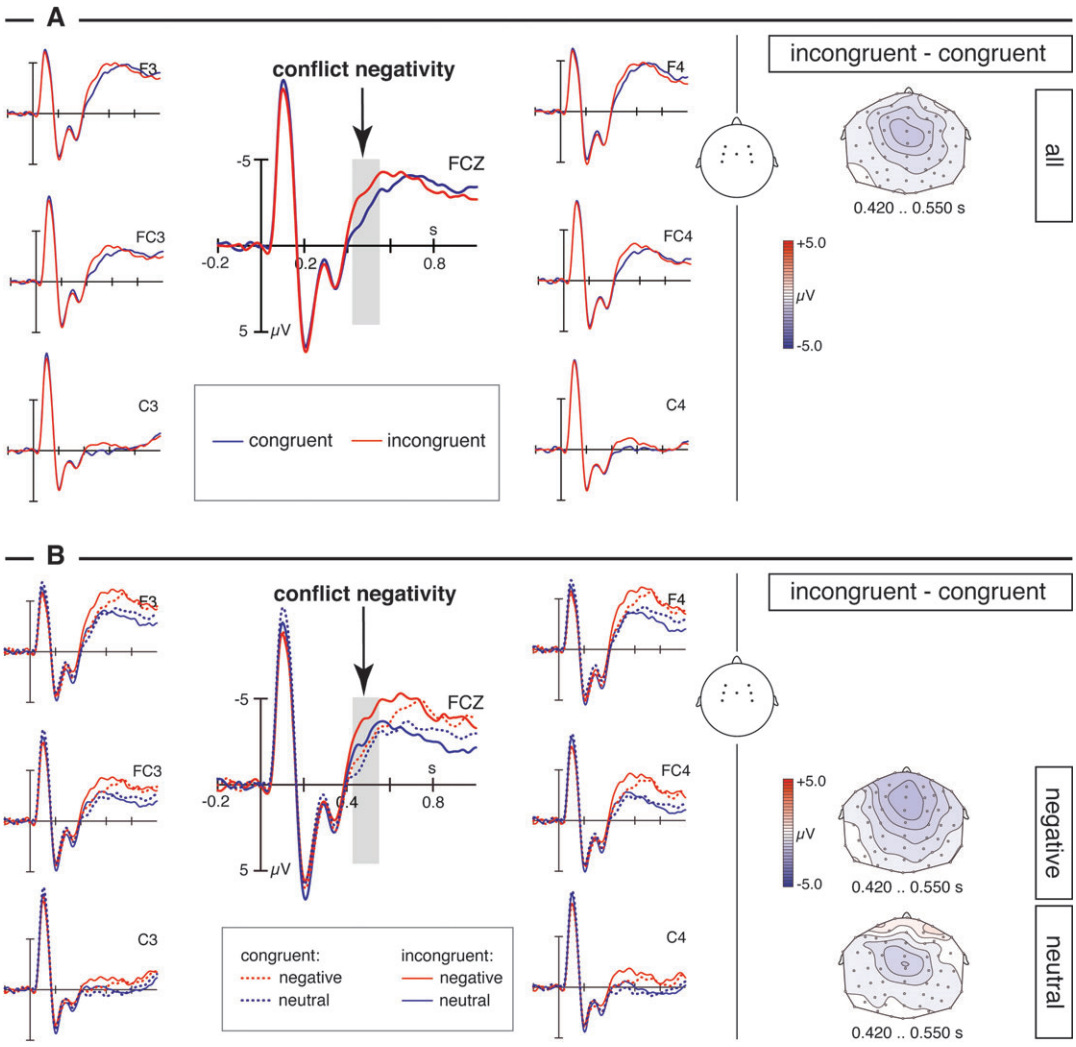


Figure 3. ERPs at selected electrodes for the conflict main effect (*A*) and for each condition separately (*B*). The corresponding difference maps are displayed on the right hand side.

vACC was significantly correlated with the right amygdala ($r = 0.25$, $P < 0.05$) and dACC activation ($r = 0.37$, $P < 0.01$) in incongruent emotional but not in incongruent neutral trials ($r = -0.15$ and $r = -0.05$, $P > 0.10$, respectively; see Fig. 5). As a further control for the positive correlations, we also computed correlations between the amygdala and the dACC, which yielded no significant effects (all $P > 0.60$).

Relation of reaction times and vACC activation. A last step of analysis was taken to further assess whether activity in the vACC is related to faster behavioral conflict resolution in emotional trials. We correlated individual RT conflict scores (incongruent–congruent) with vACC activity in incongruent compared with congruent trials. In emotional trials, increased vACC activity was significantly correlated with reduced RT conflict ($r = -0.60$, $P < 0.01$). There was no significant correlation in neutral trials ($r = 0.20$, $P > 0.35$).

Discussion

The current experiments aimed to investigate the impact of emotion on conflict processing and the role of the ACC in mediating this influence.

Our data show conflict-related activity in the dACC and activation of the vACC for processing of conflict in an emotional context. This vACC activation was accompanied by faster behavioral conflict resolution and an amplified ERP conflict negativity. The data show that emotion can modulate conflict processing by recruiting additional resources in the vACC that speed up the processing of conflict. The interaction of emotion and conflict processing is already reflected in the first conflict-sensitive ERP response, suggesting that emotion is signaled rapidly to the ACC. Consistently, functional connectivity between the vACC and the activity in the amygdala was increased in emotional trials.

The current results are in line with theoretical accounts of emotions as "relevance detectors" that prepare the system for action in particularly significant situations. Scherer (1984, 1994) argued that emotions allow for rapid evaluation of stimuli regarding central needs and goals of an organism, preparation of a response tendency, and allocation of motivational force to carry out an action (see also Tomkins 1962; Gray 2004). Thus, emotion may speed up conflict resolution by biasing the key control processes, namely, selection of one of the incompatible activations and commitment of resources to

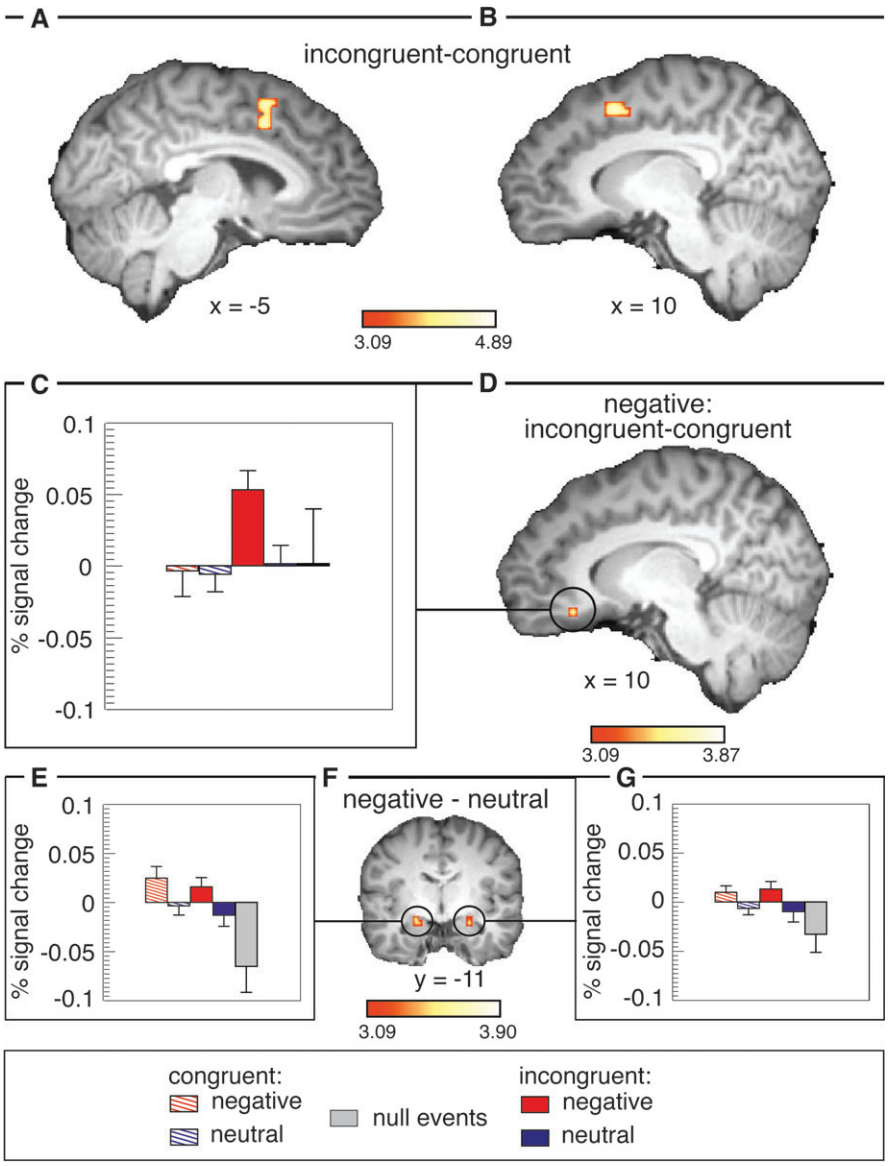


Figure 4. Incongruent–congruent contrast images for the left (*A*) and right (*B*) hemisphere. Activation of the right vACC (*D*) in the same contrast for emotional trials and the corresponding percent signal change (*C*). Negative–neutral contrast image (*F*) and activation of the left (*E*) and right (*G*) amygdala in percent signal change.

that selection (Posner et al. 2007). An emotional target stimulus, such as the words in the present study, will signal relevance and require a rapid response. This information alone did not have behavioral consequences; RTs in the congruent emotional and neutral conditions did not differ. However, in the incongruent condition, in which incompatible response activations competed, emotion biased selection and commitment of resources leading to reduced RTs in incongruent emotional trials. Two conclusions follow from this. First, it is not strengthened sensory representations alone that yield the effect, as this would have affected RTs in the congruent condition as well. Rather, emotional salience is integrated with information on current goals (e.g., to react to voice gender not presentation side) leading to biased selection and commitment of resources and, thus, affecting RTs in the incongruent condition. This does, of course, not negate sensory effects, which we know to be present (Vuilleumier 2005), but means that sensory effects alone cannot explain the present data. Second, an emotional stimulus that is not the target of the present task will not elicit the present data pattern. It will also signal relevance and potentially bias selection and commitment of resources but not in accord with the present goals. Indeed, when emotional stimuli are presented prior to the targets or in the target background, a deterioration in conflict resolution can be found (e.g., Blair et al. 2007; Dennis et al. 2008; Lim et al. 2008). This position is also in line with the recently formulated "dual competition" model (Pessoa 2009). The model predicts enhanced executive control in response to affective signals because of 1) strengthened sensory representations that receive prioritized attention and 2) affective information being directly conveyed to control structures. If an emotional stimulus is task relevant, additional control resources will be devoted to it, thereby enhancing behavioral performance.

The model also assumes that the amygdala and ACC are crucial areas in a neural network mediating these effects (Pessoa 2009). Our data support this assumption, as we report

activation for emotional words in the amygdala. With regard to the ACC, we find an interaction of emotion and conflict in the vACC and a main effect of conflict in the dACC. This suggests that the ACC as a control structure is differentially engaged in the processing of conflict when it receives affective information. While the dACC is processing conflict irrespective of emotion, the vACC is processing conflict only in affective stimuli. Consistently, functional connectivity between the vACC and the amygdala and the dACC is increased in emotional compared with neutral trials. The active involvement of the vACC in conflict processing in emotional trials is further corroborated by the correlation of increased vACC activity with decreased RT interference effects in emotional but not in neutral trials. These data correspond well with the established dorsal cognitive and ventral affective subdivisions of the ACC (for a meta-analysis, see Bush et al. 2000).

Therefore, the current data add to defining a new functional role of the vACC. It has previously been proposed that the vACC resolves conflict among emotional stimuli of different valence, for example, happiness and sadness (see Etkin et al. 2006 who presented words superimposed on faces, e.g., "anger" superimposed on a happy face). Our data extend the role of the vACC to the processing of nonemotional conflict, for example, incongruent stimulus and response sides, when the target stimuli are emotional. This suggests that it is the affective significance that activates the vACC for the processing of either emotional or nonemotional conflict.

Table 2
Peak activations

Contrast	H	*x*	*y*	*z*	Cs	*Z*max	BA
Incongruent–congruent							
dACC	L	−5	9	29		3.80	32
	R	10	11	43	1431	4.02	32
Paracentral lobule	R	22	−43	45	270	3.61	5
Superior temporal gyrus	R	64	−28	9	324	4.89	42
Negative–neutral							
Amygdala	L	22	−9	−12	189	2.40	
	R	−20	−10	−11	180	2.61	
Superior temporal gyrus	R	58	−21	9	243	3.60	42
Negative: incongruent–congruent							
vACC	R	10	33	12	675	3.17	24

Note: Activation clusters for the respective contrasts. H, hemisphere; Cs, cluster size in cubic millimeters; BA, Brodmann area.

The main objective of the ERP study was to see whether the first conflict-related event-related brain response would already be modulated by emotion, suggesting an influence of emotion on early conflict processing stages. Consistent with ERP data from other conflict tasks, we observe a negativity for incongruent versus congruent stimuli (Gehring et al. 1992; Kopp et al. 1996; Liotti et al. 2000; van Veen and Carter 2002). The onset of this ERP response was slightly later than in another EEG study utilizing the Simon task (Carriero et al. 2007). This difference may result from the use of different modalities. Carriero et al. (2007) presented arrows on the right or the left of fixation. The pointing direction that determined the response was either congruent or incongruent with the presentation side. Thus, conflict was present at stimulus onset. However, in the current study, conflict was only present after identification of the correct response hand, which requires identification of the gender of the voice coherent with the original Simon task (Simon and Small 1969). This may have delayed the onset of the negativity, which has also been reported in a later time window for other conflict tasks (N450; West and Alain 1999; Liotti et al. 2000; West and Alain 2000). Importantly, the amplitude of the conflict negativity was modulated by emotion. As the conflict negativity, starting at 420 ms poststimulus, was the first conflict-sensitive event-related response, emotion seems to exert an influence on the earliest stages of conflict processing.

The direction of this modulation of the conflict negativity is difficult to interpret, as the implications of amplitude modulations are still unclear. Interestingly, we observed larger amplitudes in emotional than neutral trials; thus, increased amplitudes went along with faster behavioral conflict resolution. A couple of studies showed a similar pattern. For example, an increase of the conflict negativity has previously been reported in development when children become faster in solving conflict tasks (Ladouceur et al. 2004, 2007; Rueda et al. 2005). Conversely, the effect decreases in size in aging populations that also show behavioral deficits in conflict resolution (West 2004). However, there are also data showing that younger children exhibit larger and more sustained ERP conflict effects than adults (Rueda et al. 2004). The present data seem to suggest that the conflict negativity occurs in conflicting situations, with larger amplitudes in more efficient behavioral conflict processing, potentially indexing the recruitment of additional resources. However, this needs to be directly tested in future studies.

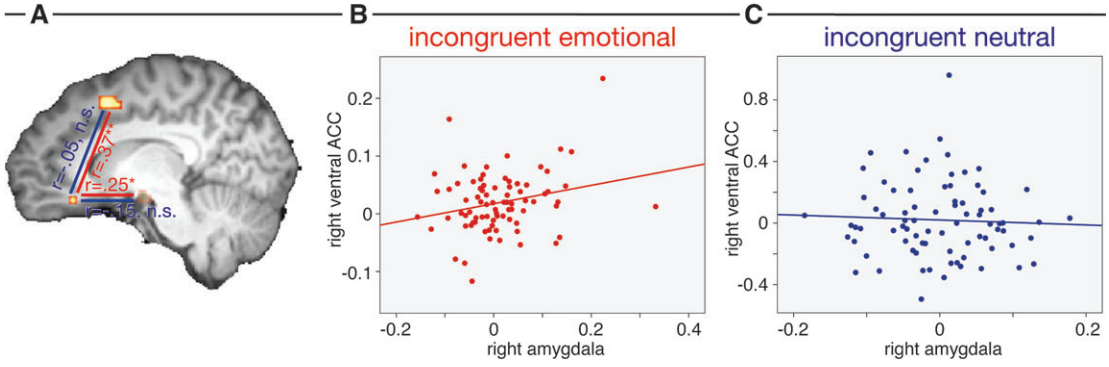


Figure 5. Display of correlation coefficients between right hemisphere brain regions for incongruent emotional (red) and neutral (blue) conditions (*A*). Exemplary scatterplots for the correlations of the right amygdala and vACC are also displayed (*B*, *C*). *$P < 0.05$, **$P < 0.01$, NS, $P > 0.10$

The modulation of the first conflict-related ERP, that is, the first stage of conflict processing, via emotion is also plausible considering the speed of emotion detection in the amygdala and its connections with the vACC. The amygdala is vital for emotion detection from auditory stimuli, as patients with lesion in the amygdala show deteriorated abilities to recognize emotional prosody (Scott et al. 1997; Sprengelmeyer et al. 1999; Sander et al. 2005; Landis 2006). Connections from the amygdala to the vACC have been found in functional imaging and neuroanatomical studies (Vogt et al. 1992; Bush et al. 2000; Stein et al. 2007). Thus, if the modulation of the conflict negativity reflects vACC activation in emotional trials, this would indicate very early engagement of this region for conflict processing through amygdala connections.

While it is difficult to draw conclusions about the neural generators of ERPs, we hypothesized that differential engagement of the vACC and dACC in conflict processing emotional and neutral stimuli will also show in the conflict-related negativity. Regarding the main effect of conflict, the data are in line with previous results relating the conflict negativity to activity in the dACC (van Veen and Carter 2002). The enhancement of the conflict negativity in the emotional context may reflect the additional activation of the vACC. Future studies should elucidate this point by means of source localization of the conflict negativity.

While the dACC was activated bilaterally for conflict, the vACC responded to conflict in an emotional context unilaterally in the right hemisphere. This lateralization effect may result from the prominent emotional prosodic manipulation of the auditory stimuli that impacts the emotional character of the utterance. A right hemispheric dominance for emotional prosody has repeatedly been reported and is also reflected in models of vocal emotional processing (Kotz et al. 2006; Schirmer and Kotz 2006). It also conforms with our finding of increased activation of the right superior temporal gyrus for emotional compared with neutral utterances. It remains open whether the lateralization pattern changes when stimuli of other emotion expression are used.

We found no effects of the experimental conditions on error rates, which is most likely due to the very high accuracy. The relation of the conflict negativity and the error-related negativity has been extensively discussed in recent reports (see, e.g., van Veen and Carter 2002). The present data set allows no conclusions about this relation, as there were not enough errors to investigate the error trials separately.

To conclude, processing of conflict is accelerated in emotional stimuli. Early stages of conflict processing are modulated by emotion as indexed in the enhanced ERP amplitude of the conflict negativity. This enhancement may reflect the recruitment of the vACC for conflict processing in the emotional targets. The amygdala was activated by emotional stimuli and signaled affective significance to the vACC as reflected in the increased functional connectivity in emotional trials. The dACC reacts to conflict as reported in earlier studies with the different versions of conflict tasks.

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