The Influence of Emotional Associations on the Neural Correlates of Semantic Priming

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Abstract: Emotions influence our everyday life in several ways. With the present study, we wanted to examine the impact of emotional information on neural correlates of semantic priming, a well-established technique to investigate semantic processing. Stimuli were presented with a short SOA of 200 ms as subjects performed a lexical decision task during fMRI measurement. Seven experimental conditions were compared: positive/negative/neutral related, positive/negative/neutral unrelated, nonwords (all words were nouns). Behavioral data revealed a valence specific semantic priming effect (i.e., unrelated > related) only for neutral and positive related word pairs. On a neural level, the comparison of emotional over neutral relations showed activation in left anterior medial frontal cortex, superior frontal gyrus, and posterior cingulate. Interactions for the different relations were located in left anterior part of the medial frontal cortex, cingulate regions, and right hippocampus (positive > neutral + negative) and left posterior part of medial frontal cortex (negative > neutral + positive). The results showed that emotional information have an influence on semantic association processes. While positive and neutral information seem to share a semantic network, negative relations might induce compensatory mechanisms that inhibit the spread of activation between related concepts. The neural correlates highlighted a distributed neural network, primarily involving attention, memory and emotion related processing areas in medial fronto-parietal cortices. The differentiation between anterior (positive) and posterior part (negative) of the medial frontal cortex was linked to the type of affective manipulation with more cognitive demands being involved in the automatic processing of negative information. *Hum Brain Mapp* 33:676–694, 2012. © 2011 Wiley Periodicals, Inc.

Key words: fMRI; automatic processing; lexical decision; semantic associations; emotional associations

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INTRODUCTION

In a continuous flow of information, we have to focus, select, store, and retrieve relevant information. Amazingly, we are able to access that knowledge within a few milliseconds indicating efficient organization. One principle of organization is the connection between concepts within a semantic network. In this network, associations play an important role. Associations can be defined as “externally related items that interact within events and space” [e.g., car – garage; Lin and Murphy, 2001]. Hence, they do not share any perceptual similarity but rather a functional relationship. An established tool to investigate the processing of semantic associations is semantic priming. Here, a prime (e.g., car) is presented to the subject, followed by a target that could be related (e.g., garage) or unrelated (e.g., bottle) to the prime. A common finding is that related concepts result in faster reaction times than unrelated ones. The cause might be a spread of activation between related concepts within the semantic network [Neely, 1991].

The neural correlates of semantic priming and semantic processing are summarized in a recent review of Binder et al. [2009] who investigated brain regions that contribute specifically to the semantic component of word recognition. They found moderate left-hemispheric lateralization and a network of parietal, temporal, and prefrontal association regions. This neural semantic network contains areas related to concept retrieval and integration (e.g., temporal and angular gyri), semantic processing and executive function of semantic processing (e.g., frontal gyri), and episodic and visuospatial memory functions (e.g., posterior cingulate and precuneus). Moreover, several influences on the semantic system and processing were investigated, e.g. different prime-target relations [associative vs. categorical; e.g., Kalenine et al., 2009; Sachs et al., 2008; Sass et al., 2009b; Warrington and Shallice, 1984], different presentation modalities [visual vs. auditory; e.g. Bright et al., 2004; Kircher et al., 2009; Sass et al., 2009a; Vandenberghe et al., 1996], and different semantic distances [direct vs. indirect; e.g., Kuperberg et al., 2008; McNamara and Altarriba, 1988; Sass et al., 2009a; Spitzer et al., 1993]. Beside these different impacts on semantic processing, the context of items also has an influence. For example, Rossell and Nobre [2004] analyzed the influence of affect on semantic priming. In their study, they showed that there was a priming effect for positive and neutral stimuli but no effect (fearful stimuli) and inhibition for negative information (sad stimuli), respectively. They concluded that positive and neutral stimuli may share a similar semantic network. In contrast, negative information might induce (compensatory) mechanisms that inhibit the spread of negatively valenced associations. Alternatively, the sad affect might reduce the optimization of word-processing so that additional effort or time to process the target stimulus is needed. These suggestions are in line with one theory of emotional processing claiming that there is an

associative network of memory and emotion where emotional states can be represented as nodes in a semantic network [Bower, 1981], i.e., spreading activation between connected nodes could be the cause for asymmetric effects of positive and negative information [Isen, 1987]. In other words, the asymmetry occurs due to different organization of emotional material in memory and, therefore, positive information might be better elaborated and interconnected [Ashby et al., 1999; Isen, 1985]. Thereby, it was proposed that the influence of emotional nodes is restricted to the retrieval of episodic memory events [Macleod, 1987]. Nevertheless, other studies revealed that there were facilitative effects of mood induction on lexical decisions [Haenze and Hesse, 1993; Hesse and Spies, 1996], weaker or no effects of affective information in comparison to semantic information [Kemp-Wheeler and Hill, 1992; Matthews and Southall, 1991; Siegle et al., 2002], greater priming effects for negative emotional information [Matthews et al., 1995; Windmann et al., 2002], or greater effect for positive emotional information [Rossell et al., 2000]. To conclude, the existing behavioral studies revealed heterogeneous results but they also showed that emotional valence does have a specific influence on semantic processing.

On a neural level, distinct areas of activation for emotional processing were found [for a review see Phillips et al., 2003]. For example, orbitofrontal and inferior frontal regions might represent explicit memory contents of emotion, automatic evaluation of emotional valence, retrieval of positive contextual information and retrieval of memories that have been associated with positive emotional context [Cunningham et al., 2004; Damasio, 1996; Dolcos et al., 2004b; Maratos et al., 2001; Rolls, 2000; Smith et al., 2004]. The posterior cingulate seems to be related to the evaluation of an external stimulus with emotional salience and episodic memory retrieval [Cato et al., 2004; Maddock, 1999; Maddock et al., 2003b; Maratos et al., 2001]. In interaction with the hippocampus this region is especially connected to emotional memory retrieval [Dolcos et al., 2004a; Smith et al., 2004]. The more anterior region of the cingulate cortex represents several functions like autonomic control, memory retrieval, conflict monitoring, modulation of emotional behavior, cognitive induction of emotional response, i.e., this region might be connected to the mediation of different emotional processes [Ashby et al., 1999; Barch et al., 1997; Devinsky et al., 1995; Drevets et al., 2008; Phan et al., 2004; Wager et al., 2003]. The impact of emotion on lexical decision was investigated by Kuchinke et al. [2005]. In their study, emotional stimuli were associated with increased activity in medial orbital frontal and bilateral inferior frontal cortices. Positive stimuli induced activation in bilateral middle temporal and superior frontal gyri while negative information resulted in activation of the right inferior frontal gyrus. Overall, emotional information seem to recruit a large bilateral fronto-temporo-parietal network depending on the kind of task and emotional content.

However, only a few neuroimaging studies investigated the influence of emotions on semantic processing [e.g., Kahlaoui et al., 2007; Kuchinke et al., 2005, 2006]. Therefore, the aim of the current study was to investigate the neural correlates of emotional associations on semantic priming using fMRI. By using a lexical decision task, the focus of processing is on the non-emotional aspects (i.e., lexical decision) of the stimuli and not on emotional meaning. Hence, the question arises how the implicit processing of emotions influence semantic processing. Thereby, we wanted to combine earlier knowledge of associative and emotional processing. This combination leads to specific requirements: (1) Castner et al. [2007] showed that only a short stimulus onset asynchrony (SOA) results in a significant affective priming effect [De Houwer et al., 1998; Fazio, 2001; Fazio et al., 1986; Hermans et al., 1994, 2001; Klauer et al., 1997, 2003], i.e., the automatic activation of emotional associations occurs at a prelexical stage of processing. Furthermore, to avoid strategic influence or expectancy on priming-specific patterns of semantic processing, it is necessary to use a short SOA [Grossman et al., 2006]. (2) The construction of an unrelated emotional condition is easily confounded by the semantic relationship between items, i.e., Rossell and Nobre [2004] mentioned that the reassignment of primes and targets within one affective category could still result in semantically related word pairs (e.g., cry – weep, sob – wail). Therefore, they combined stimuli that were not part of the same affective category with each other (e.g., happy primes could be combined with a neutral or a fear/sad target). They defined their unrelated condition based on the emotional category of the target but this resulted in a variation of emotional valence of the prime, i.e., positive unrelated could start with a negative or neutral word, negative unrelated could begin with a neutral or positive prime. However, as Bower [1981] suggested that emotional information are differentially organized within the associative network, a positive prime might have a different influence on the processing of a target than a negative prime. Hence, for the current study, we decided to use a different type of construction by combining items from the positive condition only with items from the negative condition to have a clear distinction between neutral and emotional information and to control for emotional information of the prime and the target. Therefore, 50% of the unrelated items started with a positive prime (positive unrelated) and 50% with a negative prime (negative unrelated). The assumption was that if there is a specific influence of the negative affect on the spread of activation as Rossell and Nobre [2004] suggested and if there is a different organization of emotional material [Bower, 1981], there should be a difference between both unrelated conditions on behavioral as well as on neural level. Altogether, the novelty of our design compared to existing studies lies in the use of short SOA addressing automatic lexico-semantic processing and the combination of semantic and emotional associations. The main research ques-

tions addressed (1) the neural networks involved in the processing of neutral and emotional information—do they rely on the same set of brain areas or engage different components? and (2) the neural networks involved in the processing of positive and negative emotions—do these networks overlap?

We predicted that neutral and positive associations would lead to a semantic priming effect whereas the negative condition might induce only a small or even an inhibitory priming effect [Rossell and Nobre, 2004]. Regarding the comparison between both positive and negative unrelated conditions, we would suggest that if there was an inhibition of word recognition [Rossell and Nobre, 2004], slower reaction times should be seen for targets that are preceded by a negative prime. In contrast, if negative information induces compensatory mechanisms, no reaction time differences should be seen for negative primes.

On a neural level, we expected differences between the three conditions, i.e., emotional valence might increase the intensity of the “emotional” neural correlates in comparison the neutral ones. According to earlier studies on emotional word recognition, we hypothesize to find enhanced medial and lateral frontal activation for emotional over neutral stimuli [Crosson et al., 1999, 2002; Kuchinke et al., 2005] with positive stimuli inducing activation in fronto-temporal regions and negative information in fronto-temporal regions and posterior cingulate [Canli et al., 2004; Kuchinke et al., 2005; Mickley and Kensinger, 2008]. Moreover, as the focus of the current study is on non-emotional aspects (i.e., lexical) of the stimuli and we were interested in emotional influence across the whole brain rather than on specific regions, we did not expect activation of the amygdala in line with earlier work on semantic processing [Kuchinke et al., 2005; Liu et al., 2010; Luo et al., 2004]. The amygdala is involved during reading of emotional words per se [e.g., Herbert et al., 2009] but it is suggested that attention on the emotional stimulus is needed to elicit signal changes in this region. Hence, the amygdala is “critical in automatically evaluating an affective stimulus, but other areas like inferior frontal or orbitofrontal gyrus may also subserve these automatic processes” [Kuchinke et al., 2005]. This is supported by the model of Kensinger and Corkin [2004] who suggested that there might be a distinction between arousal-dependent amygdalar-hippocampal and a valence-dependent prefrontal cortex-hippocampal network. Since semantic priming and lexical decision are based on valence rather than on arousal, no amygdala activation might be seen [Cunningham et al., 2004]. Further support for the “missing” amygdala activation arises from (1) the assumption that emotional words might have a lower emotional arousal than faces that induce amygdala signal changes and (2) the assumption that attention on the emotional dimension is needed for amygdala involvement. In contrast, during semantic priming the focus is on non-emotional aspects leading to no involvement of the amygdala [Liu et al., 2010; Luo et al., 2004].

MATERIALS AND METHODS

Participants

Sixteen healthy age-matched participants (8 male, 8 female) with an average age of 24.88 years ($S.D. = 2.06$) were recruited from the staff of the RWTH University Hospital Aachen. They were paid a fee for participation. All participants were native German speakers, had normal or corrected-to-normal vision and were right-handed according to the Edinburgh Inventory of Handedness [Oldfield, 1971]. They were matched according to age, sex and educational level. Participants were excluded if they had been diagnosed with a past or present psychiatric, neurological, or medical disease. The study was approved by the local ethics committee and all participants gave informed consent to participate in the study.

Stimuli and Design

The related word pairs consisted of a prime and an associatively related target. The associative relation was defined by a functional relationship between prime and target, i.e., items are externally related occurring within scenes or events [Lin and Murphy, 2001]. For the different related conditions, we combined (1) two positive nouns, (2) two negative nouns, or (3) two neutral nouns. The unrelated conditions were constructed by combining two neutral words that had no relations (neutral unrelated) or by combining two emotional words whereby 50% of the words started with a positive word or a negative word. During fMRI data acquisition, for the lexical decision task a verbal prime was presented to the participants (e.g., cup), followed by a visually presented string of letters (target) in the center of the screen with a 60 Hz refresh rate. Participants had to decide whether this string of letters was a real word (e.g., can) or not (e.g., fubber) by pressing one of two buttons. Seven experimental conditions were used: (1) 30 positively related word pairs, e.g., heaven – angel, (2) 30 negatively related word pairs, e.g., conflict – aggression, (3) 30 neutrally related word pairs, e.g., can – cup, (4) 30 positive unrelated word pairs starting with a positive prime, e.g., present – arrogance, (5) 30 negative unrelated stimuli starting with a negative prime, e.g., grave – luck, (6) 30 unrelated word pairs, e.g., question – mortar, and (7) 60 nonwords, e.g., flower – bresch.

To ensure that the word pairs had a strong relationship a pretest was conducted. Twenty volunteers not participating in the actual fMRI study were asked to rate 400 word pairs on different scales. First, they were asked to rate word pairs regarding their contextual relatedness and their interaction in time and space on a scale from 1 (=unrelated) to 7 (=highly related). Second, emotional valence was rated on a scale from –3 (=highly negative) to 3 (=highly positive) with 0 referring to a neutral valence, 1–3 referring to a positive and –1––3 referring to a negative valence [Rossell and Nobre, 2004]. Subjects were instructed to rate both

words together. Words selected had to be values of 5 or higher on the relatedness scale and above 1 or below –1 on the emotional valence scale, i.e., the neutral word pairs should have a valence between –1 and 1. The unrelated targets had to be scored 2 or less in the same test. The selected word pairs had a relatedness score over 6.42 (positive: $M_{\text{Rating}} = 6.49$, $S.D. = 0.37$; negative: $M_{\text{Rating}} = 6.42$, $S.D. = 0.34$; neutral: $M_{\text{Rating}} = 6.57$, $S.D. = 0.22$; $F(2,58) = 1.70$, $P = 0.19$) and below 1.55 (positive: $M_{\text{Rating}} = 1.54$, $S.D. = 0.08$; negative: $M_{\text{Rating}} = 1.44$, $S.D. = 0.07$; neutral: $M_{\text{Rating}} = 1.31$, $S.D. = 0.08$; $F(2,58) = 2.66$, $P = 0.08$), respectively. The emotional valence rating revealed significant differences between all related conditions ($P < 0.001$) with negative word pairs being rated below –2.45, positive word pairs above 2.31 and neutral word pairs with 0.32. The unrelated word pairs were rated between –0.27 and 0.1 on the emotional valence scale. In addition, the valence of the emotionally positive or negative stimuli was matched according to the Berlin Affective Word List [BAWL; Vo et al., 2006]. The results revealed that there are significant differences between positive primes/targets/word pairs and negative primes/targets/word pairs (all $P < 0.001$). Nonwords were pronounceable German words that were constructed by changing one or two consonants in real target words. The selected stimuli (i.e., primes, targets and word pairs) were matched within and between conditions (i.e., positive, negative and neutral). The criteria for all matches were lexical frequency [CELEX database; Baayen et al., 1993; see Table I for examples of stimuli used in the experiment], word length, syllables and concreteness [Wilson, 1988]. The results revealed no significant differences between the pairs ($P > 0.07$) except for concreteness ($P < 0.001$). The reason was that the target words in each condition were more abstract than the primes. But as this was true for each condition, concreteness should not have a systematic influence on results. Additionally, the positive and negative stimuli were compared according to their arousal based on the Affective Norms for English Words [ANEW; Bradley and Lang, 1999]. Arousal refers to the intensity of a stimulus and ranges from dull to arousing [Heilman, 1997]. The results revealed no differences between positive and negative information ($P > 0.20$).

fMRI Procedure

A rapid event-related fMRI (erfMRI) design was used to present related, unrelated, and nonword trials [Amaro and Barker, 2006; Gold et al., 2006; Kircher et al., 2009; Sass et al., 2009a,b; Whitney et al., 2009]. The idea behind the design was that the presentation of trials from the same condition in a sequence leads to a better sampling of the HRF curve and hence to a better signal. Therefore, small blocks of stimuli from the same condition were constructed with a small intertrial-interval (ITI) of 1.5–2.5 seconds between trials ($M_{\text{ITIsmall}} = 2$ s). In addition, longer ITIs (jittered 3–5 s; $M_{\text{ITIlong}} = 4$ s) were placed randomly

TABLE I. Examples of the stimuli used in the experiment

Related conditions		Unrelated condition			
Neutral (English translation)	Positive (English translation)	Negative (English translation)	Neutral (English translation)	Positive (English translation)	Negative (English translation)
Landkarte – Geographie (map – geography)	Himmel – Engel (heaven – angel)	Konflikt – Aggression (conflict – aggression)	Konzert – Wasser (concert – water)	Sonne – Terror (sun – terror)	Grab – Glück (grave – luck)
Kette – Amulett (necklace – charm)	Urlaub – Erholung (holiday – rest)	Folter – Gewalt (torture – force)	Sohle – Unterricht (sole – education)	Frieden – Anklage (peace – accusation)	Gestank – Aussicht (malodor – outlook)
Zeitung – Nachrichten (newspaper – news)	Heimat – Familie (home – family)	Pistole – Munition (gun – ammunition)	Kasse – Biologie (till – biology)	Erfolg – Streitmacht (success – force)	Krankheit – Triumph (disease – triumph)
Planet – Weltall (planet – space)	Medaille – Sieger (medal – winner)	Friedhof – Urne (graveyard – urn)	Feder – Umsatz (feather – revenue)	Komödie – Verbrechen (comedy – crime)	Armut – Sommer (poverty – summer)
					Bus – Reinsa (bus – reinsa)
					Insel – Banibri (island – banibri)
					Drohung – Brozwant (threat – brozwant)
					Plakat – Tami (poster – tami)

between the small blocks so that the overlapping HRFs are deconvolved [see Sass et al., 2009a for a detailed description of the design]. Participants obtained no information about the construction and arrangement of stimuli and conditions. Three pseudo-randomized versions of the experiment were counterbalanced across the participants to avoid a systematic effect of condition order. The stimuli display was controlled using a Presentation script file (Version 11.0 software package Neurobehavioral Systems, <http://www.neurobs.com/>) projected through MR-compatible video goggles (VisuaStim XGA, Resonance Technology, Inc., <http://www.mri-video.com/>).

Each trial began with an attention cue “+” (500 ms) and the prime (200 ms). The following target was shown for duration of 1,000 ms (see Fig. 1). After the target, a hash sign appeared that was shown for the jittered range of 1.5 to 2.5 s (small jitter; $M_{IT\text{small}} = 2$ s) or 3 to 5 s (long jitter; $M_{IT\text{long}} = 4$ s). Participants were instructed to press one of two buttons as fast and correct as possible depending on the kind of target word (real word, right button or nonword, left button). Pressing was done with the index or middle finger of the left hand to avoid motor-related activation in the left hemisphere.

Data Acquisition

The scanning was performed on a 3T TRIO MR scanner (Siemens Medical Systems, Erlangen, Germany) using standard gradients and a circular polarized phased-array head coil. For each subject, we acquired three series of functional volumes of T2*-weighted axial EPI-scans including five initial dummy scans parallel to the AC/PC line with the following parameters: number of slices (NS), 34; slice thickness (ST), 3.5 mm; interslice gap (IG), 0.30 mm; matrix size (MS), 64×64 ; field of view (FOV), 240×240 mm²; echo time (TE), 30 ms; repetition time (TR), 2 s. For anatomical localization, we acquired high resolution images with a T1-weighted 3D FFE sequence [TR = 1,900 ms; TE = 2.52 ms; NS = 176 (sagittal); FOV = 256×256 mm²; voxel size = $1 \times 1 \times 2$ mm³].

Behavioral Data Analysis

Reaction time was measured from the moment the target was presented until the participant made a correct response. Data were entered into repeated measures ANOVA with emotion (positive, negative, neutral) and relation (related, unrelated) as independent variables. Planned paired *t*-tests were conducted to examine the source of any interactions between relatedness.

fMRI Data Analysis

Image processing and statistical analyses were performed using statistical parametric mapping software (SPM5, www.fil.ion.ucl.ac.uk) implemented in MATLAB

Figure 1.

Schematic display of the semantic priming task. After presenting an attention cue for 500 ms, a prime was presented lasting 200 ms. Then the target appeared, followed by the intertrial interval (ITI). The target was positively, negatively, neutrally related or unrelated to the prime.

7.0 (Mathworks Inc., Sherborn, MA). The first five volumes were discarded for all protocols due to initial recording burst. Participants' fMRI images were realigned to the first functional image in order to correct for head movement. The resliced volumes were normalized to the standard stereotaxic anatomical MNI-space by using the transformation matrix calculated from the first EPI-scan of each participant and the EPI-template. For the normalization, the default SPM5 settings with 16 nonlinear iterations and the standard EPI-template of SPM5 were used. Each normalized image was then smoothed using an 8-mm Gaussian kernel to accommodate differences in anatomy between participants. The time series data were filtered with a high-pass cut-off 1/128 Hz. The first-order autocorrelations of the data were estimated and corrected for.

Following preprocessing, statistical analyses for each individual participant were conducted. The hemodynamic response triggered by the target word in each condition was modeled with a canonical HRF. The model parameters were estimated using restricted maximum likelihood (ReML). Parameter estimates of the HRF regressor for each of the different conditions were calculated from the least mean squares fit of the model to the time series. At the second level, an SPM5 random effects group analysis was performed by entering the parameter estimates for all conditions into a within-subject one-way ANOVA to create a statistical parametric map (SPM). Because we assume that the differences between the processing of semantic relations might be small, we chose to employ Monte-Carlo simulation of the brain volume to establish an appropriate voxel contiguity threshold [Slotnick et al., 2003]. This correction has the advantage of higher sensitivity to smaller effect sizes, while still correcting for multiple comparisons across the whole brain volume. Assuming an individual voxel type I error of $P < 0.0005$ a cluster extent of 8 contiguous resampled voxels was indicated as necessary to correct for multiple voxel comparisons at $P < 0.05$.

First, we examined the semantic priming effect concerning response enhancement (RE) or response suppression (RS). To examine RE, the unrelated condition was subtracted from the related condition (neutral related > neutral unrelated; positive related > positive unrelated; negative related > negative unrelated). The opposite contrast was calculated to obtain RS. To ensure, that the activations (RS) and deactivation (RE) were a result of the differences between the related and unrelated conditions and to assess only those voxels that are activated or deactivated in both conditions, all contrasts were exclusively masked with the nonword condition [e.g., Bright et al., 2004; Devlin et al., 2002; Kircher et al., 2009]. The mask was thresholded at $P < 0.05$ uncorrected. Second, to examine differences between emotional processing regions and the neutral condition, we investigated the interaction between these contrasts by subtracting the neutral from both emotional conditions [(positive related > positive unrelated) and (negative related > negative unrelated) > (neutral related > neutral unrelated)] and vice versa. These contrasts were also masked exclusively with nonword. Third, differences between all conditions were calculated by interaction, e.g., for the questions which regions are activated for positive over neutral and negative the contrast (positive related > positive unrelated) > [(neutral related > neutral unrelated) + (negative related > negative unrelated)] was calculated. This was done for the following comparisons: negative over neutral and positive, neutral over negative and positive. Final, to compare the influence of the emotional valence of the prime, we compared the positive and negative unrelated conditions with each other.

The reported voxel coordinates of activation peaks were from the MNI space (ICBM standard). For the anatomical localization the functional data were referenced to probabilistic cytoarchitectonic maps [Eickhoff et al., 2005].

Figure 2.

Behavioral priming effects. For the semantic priming effect the related condition was subtracted from the unrelated condition. Subjects were faster if the words were positively or neutrally related in comparison to unrelated word pairs whereas there was no difference between negatively related and unrelated words.

RESULTS

Behavioral Data

Accuracy

The percentage of errors was entered into a repeated measure ANOVA with relation (related, unrelated) and emotion (neutral, positive, negative) as independent variables. Results revealed that there was no effect of relation [$F(1, 15) = 1.71, P = 0.21$] but a significant effect of emotion [$F(2, 30) = 3.85, P < 0.05$]. There was no interaction of emotion and relation [$F(2, 30) = 0.79, P = 0.45$]. Mean results were: related positive 4.2% (S.D. = 5.1%), related negative 2.7% (S.D. = 4.1%), related neutral 1.7% (S.D. = 3.2%), unrelated positive 4.9% (S.D. = 4.2%), unrelated negative 1.9% (S.D. = 3.2%) and unrelated neutral 3.3% (S.D. = 5.2%). Incorrect responses were excluded from further analysis (4.4%).

Reaction time

A repeated measure ANOVA was calculated with relation and emotion as independent variables. The results indicated that there was a main effect of relation [$F(1, 15) = 21.25, P < 0.0001$] and emotion [$F(2, 30) = 18.92, P < 0.0001$] as well as a significant interaction between relation and emotion [$F(2, 30) = 9.43, P < 0.001$]. The paired sample t -tests revealed that subjects responded faster in response to related compared to the unrelated condition [neutral: $t(15) = 5.26, P < 0.0001$; positive: $t(15) = 5.24, P < 0.0001$] but only if word pairs were neutral or positive. In contrast, if the unrelated condition starts with a negative prime, there was no difference between the negative unrelated and the

negative related condition [negative: $t(15) = 0.36, P = 0.721$]. A further paired sample t -test comparing both unrelated conditions (starting with positive or negative stimuli) revealed that there was a significant difference between both [$t(15) = 4.32, P < 0.001$], i.e., subjects responded faster if a negative word occurs first. The comparison of the size of the priming effects showed no difference between neutral and positive conditions ($P = 0.437$) but significant differences between the neutral and the negative ($P < 0.003$) and the positive and negative condition ($P < 0.001$; see Fig. 2).

Imaging Data

Priming effects

Positive condition. Subtracting the positive related from the positive unrelated condition [positive unrelated > positive related] revealed activation within the right fusiform gyrus. For the opposite contrast, we found activation in left frontal (anterior rostral superior medial and middle frontal) regions, the posterior cingulate gyrus and the precuneus. In addition, right hemispheric activation was found in the angular gyrus, the cerebellum, inferior temporal, parahippocampal and middle occipital gyri (see Fig. 3).

Negative condition. For the contrast [negative unrelated > negative related] activation was found in the bilateral precuneus. Right-hemispheric activation was located in frontal (superior and middle) and the angular gyrus, as well as the middle cingulate and the hippocampus. Left-lateralized activation was found in the posterior cingulate and the cerebellum. The opposite contrast revealed one

Figure 3.

Correlates of the positive priming effects and parameter estimates. Significant activations for the comparison of positively related and positively unrelated word pairs. Response enhancement (related > unrelated) was found in the left middle frontal gyrus (MFG), posterior cingulate (PCC), and anterior rostral part of the superior medial gyrus (SmedFG). Right-hemispheric activation was located in the angular gyrus

(AngG), inferior temporal gyrus (ITG) and parahippocampal gyrus. Plots of mean parameter estimates with 90% confidence interval showing response amplitude of all regions. Labeling of the y-axis is in arbitrary units. The coordinates are the corresponding MNI coordinates. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

activation cluster in the left posterior rostral superior medial gyrus (see Fig. 4).

Neutral condition. Response suppression [neutral unrelated > neutral related] was found in the left anterior part of the rostral anterior cingulate, the posterior cingulate and the superior frontal gyrus. Right-hemispheric activation was found in the fusiform gyrus and the cuneus (see Fig. 5 and Table II). The opposite contrast revealed no significant area of activation.

Interaction of the Emotional and Neutral Conditions

The contrast [(positive related > positive unrelated) + (negative related > negative unrelated)] > (neutral related > unrelated) revealed significant effects in the left anterior part of the rostral anterior cingulate gyrus (extending through the superior medial gyrus), the posterior cingulate and superior frontal gyrus. Analysis of parameter estimates revealed that the difference in the ACC and the posterior cingulate occurs mainly between the positive and the neutral condition (see Fig. 6 and Table III).

The opposite contrast revealed no significant differences

Interaction Between the Conditions

Comparison of the positive over neutral and negative conditions

The contrast (positive related > positive unrelated) > [(neutral related > neutral unrelated) + (negative related

> negative unrelated)] showed significant effects in the left cingulate gyrus (anterior, middle, posterior), the superior medial gyrus and the calcarine gyrus. Right-hemispheric signal changes were found in the hippocampus and the superior and inferior parietal cortex. (see Fig. 7a and Table IV).

Comparison of the negative over positive and neutral conditions

The contrast (negative related > negative unrelated) > [(neutral related > neutral unrelated) + (positive related > positive unrelated)] showed signal changes in the left posterior part of the rostral superior medial gyrus (see Fig. 7b and Table IV).

Comparison of neutral over positive and negative conditions

The interaction (neutral related > neutral unrelated) > [(positive related > positive unrelated) + (negative related > negative unrelated)] revealed no significant effects.

Influence of Emotion of the Prime

For the contrast (positive unrelated > negative unrelated)] differences were found in the left posterior part of the rostral superior medial gyrus and the right pallidum. The opposite contrast revealed differences in the left insula (see Table V).

Figure 4.

Correlates of the negative priming effects and parameter estimates. Significant activations for the comparison of negatively related and unrelated word pairs. **A:** Response enhancement (related > unrelated) was found in the left posterior part of superior medial gyrus (SmedFG). **B:** Response suppression (unrelated > related) was located in the bilateral precuneus, right hippocampus, right angular (AngG) and middle cingulate

gyri (MCC), superior frontal gyrus (SFG), and middle frontal gyrus (MFG). Plots of mean parameter estimates with 90% confidence interval showing response amplitude of all regions. Labeling of the y-axis is in arbitrary units. The coordinates are the corresponding MNI coordinates. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

DISCUSSION

The aim of the current study was to investigate the influence of emotional context on semantic processing. Behavioral data showed that only positive and neutral information lead to a priming effect under automatic processing conditions while negative information had no effect. On a neural level, we found differences between all three conditions: Emotional stimuli induced effects in left medial fronto-parietal regions in comparison to neutral stimuli. Positive affective information revealed bilateral fronto-pa-

rietal activation in comparison to negative and neutral information and the negative condition showed enhanced activation in the left superior medial gyrus in comparison to the neutral and positive condition. Overall, the current results revealed that emotional valence has a specific influence on the neural correlates of automatic semantic processing.

The behavioral data are in line with the results from Rossell and Nobre [2004]. Subjects responded faster if the stimuli were neutrally or positively related. In contrast, if there was a negative relation, there was no difference

Figure 5.

Correlates of the neutral priming effects and parameter estimates. Significant areas of activation for the comparison of neutrally related and unrelated stimuli. Response suppression was found in the left posterior cingulate (PCC), superior frontal gyrus (SFG), and the anterior part of the rostral anterior cingulate (ACC). Plots of mean parameter estimates with 90% confidence interval showing signal changes in all areas. Labeling of the y-axis is in arbitrary units. The graphs have different scaling and scaling steps. The coordinates are the corresponding MNI coordinates. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

between the related and the unrelated condition. The difference between the current study and the study of Rossell and Nobre is that they found no effect for fearful stimuli, but inhibition for sad stimuli. Anyway as the results of both studies tend towards comparable results for positive and neutral information as well as towards diverging results for negative information, the question remains if the missing priming effect of negative stimuli is a result of compensatory mechanisms or if negative information inhibits the optimization of word recognition. A possibility to answer this question on behavioral level is the comparison of both unrelated conditions. In contrast to Rossell and Nobre [2004], our unrelated stimuli started with either a positive prime (and ended with a negative target) or started with a negative prime (and ended with a positive target). The idea behind was that the prime induces a “specific” spread of activation related to the context of the prime (i.e., either positive or negative). The results showed that there was a significant difference between the positive and negative unrelated condition: Negative unrelated led to faster reaction times than positive unrelated stimuli. Hence, based on our hypotheses, compensatory mechanisms seem to be induced by negative primes rather than an inhibition of word recognition that would lead to slower reaction times for the following targets. Furthermore, these differences would also highlight a differential organization

of emotional information within the associative network [Bower, 1981]. However, another explanation might be that the way we designed our unrelated conditions, also influenced the results. That is, the unrelated positive condition (e.g., heaven – conflict) might be confounded with cognitive/emotional processes that are related to the processing of the negative target (i.e., participants might try to suppress the negative connotation while making their decision). The behavioral data showed that a negative target led to delayed performance if it was preceded by a positive prime and induce large priming effects for the positive condition. Thus, the priming effect could be related to strong semantic/emotional association between prime and target or might result from an increased processing load for negative targets preceded by positive primes. In contrast, the unrelated negative condition (e.g., grave – luck) might not be confounded since no additional costs were required for target processing. Consequently, the asymmetry between both unrelated conditions could be the cause for the differences between positive and negative priming effect.

On a neural level, the neutral condition induced response suppression in mainly left-lateralized fronto-parietal regions including the anterior part of the rostral anterior cingulate cortex [rACC; Amodio and Frith, 2006]. These signal changes are in line with earlier studies. For example, Matsumoto et al. [2005] found RS in the ACC assuming that it reflects a response competition that is higher for unprimed words [see also Wible et al., 2006], i.e., less routine to process those stimuli [Mummery et al., 1999]. Other studies [e.g., Copland et al., 2007; Phelps et al., 1997; Tivarus et al., 2006; Warburton et al., 1996] suggested that activation of the left ACC reflects the attentional focus and the involvement of attentional demands. Our study showed that the integration of emotional and neutral stimuli in one session might enhance the task demands leading to enhanced involvement of attentional processes. In addition, this suggestion is supported by Rossell et al. [2001] who found that the more caudal regions of the ACC ($z = 31$ and 37 mm) are related to controlled priming while the more rostral regions ($z = 9$ and 15 mm) are related to automatic priming. This is in line with our results ($z = 12$ mm) and the results of Mummery et al. [1999]. Hence, the anterior part of the rostral ACC seems to support an automatic attentional system [Rossell et al., 2001]. In addition, the left fronto-parietal signal changes reflect the retrieval from semantic memory and the involvement of episodic memory contents during semantic processing as several earlier studies have shown [Binder et al., 2009; Cabeza and Nyberg, 2000; Cavanna and Trimble, 2006; Muller et al., 2003; Sass et al., 2009a; Shallice, 1988]. Nevertheless, according to earlier studies on semantic priming, we expected activation in classical “semantic” areas, e.g. middle temporal gyrus, inferior frontal gyrus or parietal regions [see Binder et al., 2009]. A possible explanation could be that participants were biased towards emotional aspects of word meaning because the majority of our stimuli had either a positive or negative

TABLE II. Brain regions showing semantic priming effects

Anatomical Region	BA	Coordinates			z-value	No. voxels
		x	y	z		
Positive priming effect: unrelated > related (excl. masked nonword)						
Right fusiform gyrus	20	42	−34	−16	3.78	9
Positive priming effect: related > unrelated (excl. masked nonword)						
Left superior medial gyrus ^a	10	−4	60	12	4.32	568
Left posterior cingulate gyrus	23	−2	−54	24	4.03	150
Left middle frontal gyrus	8	−30	24	46	4.09	108
Right angular gyrus	39	52	−70	38	3.75	26
Right cerebellum		42	−66	−50	4.13	25
Right inferior temporal gyrus	20	64	−8	−28	4.17	22
Right parahippocampal gyrus	36	22	−38	−12	3.70	13
Right middle occipital gyrus	19	44	−80	34	3.41	9
Left precuneus						
Negative priming effect: unrelated > related (excl. masked nonword)						
Right precuneus	7	14	−54	46	4.36	257
Left precuneus	7	−8	−62	54	4.05	164
Right angular gyrus	19	42	−74	36	4.76	241
Right middle cingulate gyrus	31	14	−34	42	4.42	195
Right superior frontal gyrus	6	24	6	66	3.82	48
Right middle frontal gyrus	8	28	18	48	3.80	22
Right hippocampus		36	−10	−18	3.77	8
Negative priming effect: related > unrelated (excl. masked nonword)						
Left superior medial gyrus ^b	8	−8	42	42	3.96	101
Neutral priming effect: unrelated > related (excl. masked nonword)						
Left anterior cingulate gyrus ^a	32	−2	46	12	4.14	56
Left posterior cingulate gyrus	29	−2	−46	8	3.67	22
Right fusiform gyrus	37	36	−52	−10	4.33	22
Left superior frontal gyrus	6	−22	0	52	3.71	11
Right cuneus	18	10	−88	20	3.48	11

Notes: Significance level and the size of the respective activation cluster (number of voxels) at $P < 0.05$, Monte Carlo corrected. Coordinates are listed in MNI space. BA is the Brodmann area nearest to the coordinate and should be considered approximate.

^aThe coordinates of the anterior cingulate gyrus refer to the anterior rostral part [Amodio and Frith, 2006].

^bThe coordinates of the anterior cingulate gyrus refer to the posterior rostral part [Amodio and Frith, 2006].

emotional connotation. Additionally, the neural correlates are also dominated by activation in medial fronto-parietal regions—similar to the network that engages in emotion (i.e., positive) priming. These results would underline the findings of earlier studies on the emotion-induced recognition bias [Kuchinke et al., 2006; Windmann and Kutas, 2001], i.e., participants have an automatic recognition bias towards emotional information based on implicit emotional evaluation.

The positive emotional information induced enhanced activation in a large network including frontal, temporal, parietal and occipital regions. The largest cluster was localized in the left superior medial gyrus extending through the anterior part of the rACC. This region was found in several studies before and is thought to reflect semantic and emotional processing. For example, Cabeza and Nyberg [2000] found activation of the superior medial frontal gyrus (incl. ACC) during retrieval from semantic memory and hypothesized that it reflects the matching of congruent stimuli [Assaf et al., 2006]. During emotional processing, the superior medial frontal gyrus reflects the

processing of emotional connotated words and the evaluation of emotional significance of behavior [Cato et al., 2004]. This suggestion is supported by activation of the anterior part of the rACC that reflects the mediation of affective responses and of different emotional processes including the assignment of emotional valence to positive stimuli [Ashby et al., 1999; Barch et al., 1997; Devinsky et al., 1995; Kuchinke et al., 2005], the regulation of affective functions and assessment for emotional salience [Bush et al., 2000; Critchley, 2003]. Additionally, its activation is strongly related to attention [Copland et al., 2007; Kondo et al., 2004; Luks et al., 2002; Phelps et al., 1997; Rossell et al., 2001; Tivarus et al., 2006; Warburton et al., 1996], i.e., activation reflects attentional demands of the task. Overall, this medial frontal cluster for positively related word pairs might reflect the processing of emotional associations that recruit additional attention related processes.

The processing of positive emotional associations is also mirrored by the signal changes in the left posterior cingulate (PCC). During semantic priming, the left PCC is thought to reflect the automatic spread of activation

Figure 6.

Neural correlates of the comparison between the emotional and neutral condition. Significant activations for emotional > neutral were found in the left anterior cingulate gyrus (ACC), the posterior cingulate (PCC), and the superior frontal gyrus (SFG). Parameter estimates (90% confidence interval) showing signal changes for all conditions. Labeling of the y-axis is in arbitrary units. The coordinates are the corresponding MNI coordinates. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

between associations in semantic memory as well as episodic memory functions [Binder et al., 2009; Rossell et al., 2001]. For emotional stimuli, activation of PCC has been found when subjects make valence judgments on emotional stimuli or evaluate external stimuli with emotional salience [Cato et al., 2004; Maddock et al., 2003a], i.e., reflects the interaction between emotion and episodic memory [Dolcos et al., 2004a; Kuchinke et al., 2005; Maddock et al., 2003a; Smith and Wheeldon, 2004]. The episodic component is supported by activation of the precuneus as several studies assumed that activation reflects the involvement of episodic memory contents and retrieval from episodic memory during semantic processing [Cavanna and Trimble, 2006; Sass et al., 2009a; Shallice et al., 1994]. The right-hemispheric signal changes in temporo-parietal regions might be related to the strong semantic

associations that are correlated with greater activation as well as response to emotionally significant stimuli [Blair et al., 1999; Chou et al., 2006; Tovee, 1994]. To sum up, the signal changes for positive stimuli indicate an interaction between emotional processing and semantic as well as episodic memory reflected through widespread bilateral activation clusters.

The negative condition induced response suppression in mainly right-hemispheric fronto-parietal regions. The parietal activation comprises the precuneus and the angular gyrus that indicate an interaction of episodic memory and processing of emotional negative stimuli. Thereby, the precuneus might act as “mediator” between episodic memory [Platel et al., 2003] and emotional processing as well as attentive processing of emotional stimuli, respectively [Habel et al., 2005; Leichnetz, 2001; Paradiso et al., 1999; Schmahmann and Pandya, 1990; Yeterian and Pandya, 1985, 1988, 1993]. Moreover, the angular gyrus is involved in semantic processing and therefore reflects the semantic component of processing [Binder et al., 2009]. The middle cingulate and frontal clusters are suggested to reflect the detection of emotional stimuli [Buchanan et al., 2000], emotional regulation and suppression [Beauregard et al., 2001; Levesque et al., 2003; Ochsner et al., 2004; Ohira et al., 2006], i.e., it is assumed that subjects “build up” a distance from the stimulus and inhibit the emotional reaction to the stimulus [Blair et al., 2007]. The assumption would be in accordance to the behavioral results as subjects showed no priming effect on negative stimuli. Furthermore, RE was found in the left superior medial gyrus. In contrast to the positive condition, the activation was located in the posterior part of the rostral medial frontal cortex. The posterior region is associated with cognitive tasks recruiting attention and action monitoring [Amodio and Frith, 2006]. Interestingly, enhanced activation was found during response inhibition and conflict monitoring leading to the conclusion that the related condition of the negative information induced an inhibition of emotional reaction as already suggested. Overall, the negatively valenced word pairs led to signal changes in regions responsible for emotion and semantic processing as well as

TABLE III. Comparison of emotional and neutral priming effects

Anatomical Region	BA	Coordinates			z-value	No. voxels
		x	y	z		
Enhanced emotional > suppressed neutral (excl. masked nonword)						
Left anterior cingulate gyrus ^a	32	−4	46	12	4.20	168
Left posterior cingulate gyrus	29	−2	−48	8	4.10	45
Left superior frontal gyrus	9	−14	40	42	3.82	82
Enhanced neutral > suppressed emotion						
No further differences						

Notes: Significance level and the size of the respective activation cluster (number of voxels) at $P < 0.05$, Monte Carlo corrected. Coordinates are listed in MNI space. BA is the Brodmann area nearest to the coordinate and should be considered approximate.

^aRostral anterior cingulate cortex [Amodio and Frith, 2006].

Figure 7.

Neural correlates of the comparison between all conditions. **A:** Significant activations for positive over neutral and negative were found in the left cingulate gyrus (anterior [ACC], middle [MCC], posterior [PCC]), superior medial gyrus and right hippocampus. Parameter estimates (90% confidence interval) showing signal changes for all conditions. **B:** Significant signal changes for nega-

tive over positive over neutral were found in the left posterior rostral medial frontal gyrus. Parameter estimates (90% confidence interval) showing signal changes for all conditions. Labeling of the y-axis is in arbitrary units. The coordinates are the corresponding MNI coordinates. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

episodic memory. In contrast to the positive condition, these effects are mainly localized in the right hemisphere.

The neural correlates of the different priming effects revealed partially overlapping but also different areas. To directly compare the differences, we contrasted both emotional over the neutral condition and found enhanced activation of left fronto-parietal regions. The activation of the anterior part of the rACC and the signal changes of the PCC for emotional over neutral relationships were mainly based on the difference between positive and neutral information (see parameter estimates in Fig. 6). Hence, the suppression for neutral and enhancement for positive information in the anterior rACC could be explained by the involvement of different processes. During semantic priming, RS is thought

to reflect the consequence of priming, i.e., less effort in processing primed targets or faster processing of primed stimuli [Henson, 2003]. In contrast, RE reflects the cognitive processes that index the spread of activation between related concepts [Henson, 2003; Marinkovic et al., 2003]. According to the current results, we would suggest that the RS for neutral word pairs is related to the automatic attentional system, i.e., more effort is needed to process unrelated neutral items while RE for positively related items is related to the enhanced spread of activation for emotional associations and the additional involvement of attention processes during the processing of related associations. Furthermore, the signal changes in PCC (RE for positive and RS for neutral) reflects the enhanced involvement of episodic memory

TABLE IV. Comparison of all conditions with each other

Anatomical Region	BA	Coordinates			z-value	No. voxels
		x	y	z		
Enhanced positive > suppressed neutral + negative (excl. masked nonword)						
Right superior parietal lobule		22	-40	40	4.41	30
Right hippocampus		20	-38	-12	3.97	34
Left calcarine gyrus		-6	-48	6	3.97	33
Left posterior cingulate gyrus		-6	-48	20	3.92	75
Left superior medial gyrus		-2	62	12	3.91	35
Left anterior cingulate gyrus ^a		0	46	6	3.61	98
Right inferior parietal cortex		42	-78	34	3.59	32
Left middle cingulate gyrus		-6	-36	38	3.48	9
Enhanced negative > suppressed neutral + positive (excl. masked nonword)						
Left superior medial gyrus ^b		-8	40	44	3.71	62

Notes: Significance level and the size of the respective activation cluster (number of voxels) at $P < 0.05$, Monte Carlo corrected. Coordinates are listed in MNI space. BA is the Brodmann area nearest to the coordinate and should be considered approximate.

^aAnterior part of rostral anterior cingulate cortex [Amodio and Frith, 2006].

^bPosterior part of rostral anterior cingulate cortex [Amodio and Frith, 2006].

retrieval that is more prominent for positive words. A possible explanation is that positive words are better elaborated and interconnected than negative words in the cognitive emotional system [Ashby et al., 1999; Isen, 1985; Kuchinke et al., 2005] and therefore, they rather recruit episodic memory contents. The only cluster that showed enhanced activation for both positive and negative over neutral stimuli was located in the left superior frontal gyrus (SFG). This frontal region is related to semantic processing [Demonet et al., 1992; Petersson et al., 2003] and processing of emotional valence during explicit semantic memory tasks [Cato et al., 2004; Crosson et al., 1999] as well as during judgements of emotional responses [Stowe et al., 2004]. According to this study, we suggest that the left SFG supports higher-level semantic processes as well as processing of emotional information. Because parameter estimates revealed enhancement for both emotional conditions and suppression for neutral relations, this region might be related to some interaction processes of semantics and emotion. To conclude, the results revealed that emotional connotated words (especially positive) recruit mainly left-hemispheric regions that reflect the

processing of emotion and show enhanced attention related processes that are necessary to process those relations in comparison to neutral stimuli. According to our first research question our results therefore show that brain regions partially overlap but seem to function differently (e.g., ACC is engaged in RS in neutral trials but RE in positive trials).

The second main question referred to the same or different neural networks involved in processing of positive and negative emotions. First, we directly compared positive over neutral and negative information. Beside the above mentioned effects in the anterior rACC and PCC, activation was found in the right hippocampus, i.e., while positive emotions induced enhanced activation, negative and neutral information lead to suppressed activation. The hippocampus is related to enhanced encoding of emotional stimuli through the interaction between amygdala and hippocampus [Dolcos et al., 2004b; McGaugh, 2000; Pare, 2003]. Thereby, the hippocampus is primarily related to negative emotion [Maratos et al., 2001; Phillips et al., 1998] and to episodic memory [Fernandez et al., 1998]. Hence, the access to

TABLE V. Comparison of positive and negative unrelated word-pairs

Anatomical Region	BA	Coordinates			z-value	No. voxels
		x	y	z		
Positive > negative						
Left superior medial gyrus ^a	8	−10	32	44	4.10	56
Right pallidum		18	−2	−2	3.77	9
Negative > positive						
Left insula	13	−26	28	8	3.65	10

Notes: Significance level and the size of the respective activation cluster (number of voxels) at $P < 0.05$, Monte Carlo corrected. Coordinates are listed in MNI space. BA is the Brodmann area nearest to the coordinate and should be considered approximate.

^aPosterior part of rostral anterior cingulate cortex [Amodio and Frith, 2006].

negative emotions might be easier if there is a relation between them inducing RS. In contrast, the spread of activation between positively related items and the particular involvement of episodic memory contents during the processing of positive information induced RE. To conclude, the comparison between the conditions revealed activation differences between positive over negative and neutral information leading to the suggestion of differently organized contents within the associative network.

Second, the comparison of negative over positive and neutral word pairs revealed activation in the posterior part of the rostral medial frontal cortex—a region that we earlier related to inhibition of emotional reaction. Hence, the division of more anterior activation for positive and more posterior activation for negative within the rostral medial frontal cortex point to a more effortful and attention-related processing of negative emotions. Additionally, also the priming effects for positive and negative information showed that positive vs. negative emotions evoke different neural response: while positive emotions primarily lead to RE, negative stimuli relate to RS in a completely different network (see Figs. 4 and 5). These activations might allow for interferences on the cognitive processes that underlie positive vs. negative priming (e.g., spreading activation, strategic processing).

The comparison of both unrelated conditions revealed activation of the left posterior part of the rostral superior medial gyrus for positive over negative and left insula for negative over positive. On the one hand, the insula is commonly associated with processing of disgust [e.g., Calder et al., 2000; Phillips et al., 1997], fear [Critchley, 2003; Phelps et al., 2001] and viewing of emotional pictures [Kuniecki et al., 2003], among other processes. Therefore, according to our data we would suggest that negative primes induce activation of the insula because this region is connected to processing of negative emotion in demanding cognitive tasks [Phan et al., 2003]. On the other hand, the posterior part of left superior medial gyrus might reflect the enhanced cognitive efforts that are necessary to process an emotional incongruent condition if this condition starts with a positive prime. This interpretation would be in line with the behavioral results as (a) stronger activation was observed for the cognitively/emotionally more demanding unrelated positive condition in parts of the left medial superior frontal gyrus and (b) the slowest reaction times for unrelated positive stimuli presumably caused by the higher processing load.

Finally, according to our hypothesis we did not find activation of the amygdala. Hence, the current study supports the assumption that there is a distinction between an arousal dependent amygdala-hippocampal and valence-dependent prefrontal-hippocampal network [Kensinger and Corkin, 2004; Kuchinke et al., 2005]. As the current study involved decision influenced by valence rather than arousal, as well as a focus on non-emotional decision (i.e., lexical decision) no amygdala activation was suggested.

CONCLUSION

This study revealed an influence of emotional context on semantic priming. The results highlighted a distributed brain network—primarily involving attentional, mnemonic and emotional processing areas in medial frontal-parietal cortices—which were sensitive to the processing of additional emotional information during semantic priming. Some of the components in this network were specifically linked to the type of affective manipulation, i.e., positive vs. negative. Hence, according to Bower [1981] there might be an associative network with different organization of emotional material, i.e., positive relations might be better elaborated and interconnected than negative ones [Isen, 1985, 1987]. A direct comparison showed that emotional context compared to neutral words revealed partially overlapping (e.g., ACC, PCC) but also different areas. However, those areas that are shared seem to function differently according to the direction of signal changes (RE vs. RS in the rACC). A second major finding was that positive and negative emotions evoke different neural responses in the rostral ACC: positively valenced recruit more anterior parts and negatively valenced stimuli recruit more posterior parts—a result that underlines the involvement of cognitive demands during automatic processing of negative information. Thus, negative emotions seem to induce compensatory mechanisms and inhibition of emotional reaction to the stimulus under automatic processing conditions.

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