Nonlinear Relationship Between Emotional Valence and Brain Activity: Evidence of Separate Negative and Positive Valence Dimensions

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Abstract: Emotion plays a significant role in goal-directed behavior, yet its neural basis is yet poorly understood. In several psychological models the cardinal dimensions that characterize the emotion space are considered to be valence and arousal. Here 3T functional magnetic resonance imaging (fMRI) was used to reveal brain areas that show valence- and arousal-dependent blood oxygen level dependent (BOLD) signal responses. Seventeen healthy adults viewed pictures from the International Affective Picture System (IAPS) for brief 100 ms periods in a block design paradigm. In many brain regions BOLD signals correlated significantly positively with valence ratings of unpleasant pictures. Interestingly, partly in the same regions but also in several other regions BOLD signals correlated negatively with valence ratings of pleasant pictures. Therefore, there were several areas where the correlation across all pictures was of inverted U-shape. Such correlations were found bilaterally in the dorsolateral prefrontal cortex (DLPFC), dorsomedial prefrontal cortex (DMPFC) extending to anterior cingulate cortex (ACC), and insula. Self-rated arousal of those pictures which were evaluated to be unpleasant correlated with BOLD signal in the ACC, whereas for pleasant pictures arousal correlated positively with the BOLD signal strength in the right substantia innominata. We interpret our results to suggest a major division of brain mechanisms underlying affective behavior to those evaluating stimuli to be pleasant or unpleasant. This is consistent with the basic division of behavior to approach and withdrawal, where differentiation of hostile and hospitable stimuli is crucial. *Hum Brain Mapp* 31:1030–1040, 2010.

Key words: emotion; valence; fMRI; correlation

INTRODUCTION

There are two main theoretical approaches to the nature of emotions. Basic emotion theories assume that there exists a relatively small number of distinct basic emotions or emotion families that are universal for all mankind [e.g., Ekman et al., 1987]. Most proponents of such theories agree that there are at least six basic emotions: happiness, sadness, disgust, anger, fear, and surprise. Dimensional theories, on the other hand, consider that emotions are

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represented in an N-dimensional space, where the two cardinal dimensions explaining most of the emotional variation are usually named *valence* and *arousal* [Russell and Barrett, 1999]. Other dimensions include, for instance, dominance and recognition. Valence refers to pleasantness, which varies from negative (very unpleasant) values via neutral to positive (very pleasant) values. It has, however, been argued that valence is not a single dimension, but there actually are separate dimensions for negative- and positive-valence emotions [Cacioppo and Berntson, 1994; Cacioppo et al., 1997]. Arousal dimension refers to the intensity of emotions, varying from very low to very high.

These two approaches to emotions are not necessarily contradictory but rather emphasize different aspects of emotions. Names of basic emotions are linguistic categorical divisions of the emotion space, but the fine details of the emotions described by these words may vary extensively. The dimensional approach captures certain aspects of emotions in detail, since the dimensions can be characterized with high resolution. The six basic emotions can be characterized by valence and arousal in an emotional circumplex [Russell, 1980]—a framework that models categorized emotions around the two assumedly orthogonal dimensions. There exists, in other words, a nonbijective mapping between the two dimensional valence-arousal model and the six dimensional model of six basic emotions.

Functional neuroimaging provides one possibility to investigate the neural implementation of emotions. On the grounds of these techniques the medial prefrontal cortex seems to have an important general role in emotional processing, often showing activity regardless of the specific emotion [Phan et al., 2002]. Interestingly, based on brain anatomy, Nauta suggested already in 1971 [Nauta, 1971] that parts of frontal lobes form a major cortical component of limbic system participating in emotional regulation. Neural correlates of the assumed emotion dimensions have been examined by using pictures from the International Affective Picture System (IAPS) [Lang et al., 2005], as stimuli. The IAPS is an assortment of pictures, which has been collected to extensively cover the emotional valence-arousal space and consists currently of 956 pictures. The subjective ratings of the IAPS pictures by two large subject samples [Lang et al., 2005; Ribeiro et al., 2004] were in close agreement. Ratings were obtained from female and male subjects for emotional valence, arousal, and dominance. The modification of subjects' emotions during viewing of IAPS pictures is supported by results demonstrating that autonomic responses, facial muscle activity, and amplitude of the startle reflex correlate with arousal and valence dimensions [Lang et al., 1990, 1993]. As shown by Mikels et al. [2005], different IAPS pictures can be also classified to distinct emotion categories.

Obviously, IAPS provides exceptional material to study parametrically the neural correlates of emotional dimensions in the human brain. This has been done in two recent fMRI studies using an event-related paradigm. Heinzel et al. [2005] measured BOLD responses to IAPS pictures of 2-s duration and examined their correlations with valence. The authors observed a linear positive correlation between BOLD signal and valence in the orbito- and dorsomedial prefrontal cortex (OMPFC and DMPFC), medial parietal cortex, and insula. Emotional valence was associated with BOLD signal decreases, when compared with the fixation-cross baseline. For negative valences the signal decreases were larger and for positive valences smaller. Grimm et al. [2006] used in their study IAPS pictures of 4-s duration. These authors observed a positive correlation of BOLD signal with valence in the ventromedial prefrontal cortex (VMPFC) and a negative correlation in the bilateral dorsolateral prefrontal cortex (DLPFC). With arousal the correlation with BOLD signal was positive in the right ventrolateral prefrontal cortex (VLPFC) and DMPFC. The main conclusion of both Heinzel et al. [2005] and Grimm et al. [2006] was that there is a bipolar representation of valence in the brain: linear changes in valence resulted in concomitant linear changes in brain activity.

An important extension to previous studies was recently brought by Lewis et al. [2007], who studied different correlation models regarding the relationship of valence and BOLD signal. They investigated brain correlates of valence and arousal using 248 affective word stimuli, rated earlier by their valence and arousal, and fitted three different models—bipolar, independent, and U-shaped—to the data in order to explain the relation between BOLD signal strength and valence. Whereas the bipolar model, used in the previous studies, failed to explain the data, both the independent and increasing U-shaped models revealed significant correlations. This suggests that valence might have nonlinear and nonbipolar representation in the brain. The increasing U-shaped model described correlation between BOLD signal and valence in the posterior-lateral orbitofrontal cortex as well as in subgenual and anterior cingulate cortices. Complementary information was obtained from the independent model: For negative words correlation was positive in the right posterolateral and medial orbitofrontal cortices and medial subgenual cingulate, and for positive words correlation was positive in the right lateral orbitofrontal cortex and anterior insula. With negative words arousal correlated positively with BOLD signal in the midbrain, left insula, left dorsal amygdala, and putamen and with positive words correlation was positive in the ventral striatum and subgenual cingulate cortex. Importantly, both arousal and valence manifested different kind of responses to negative and positive stimuli. These results suggest that there are different valence and arousal representations in the brain for negative and positive (unpleasant and pleasant) stimuli. In such case arousal is not independent but rather correlated with valence, as earlier found by Ribeiro et al. [2004] and Grühn and Scheibe [2008].

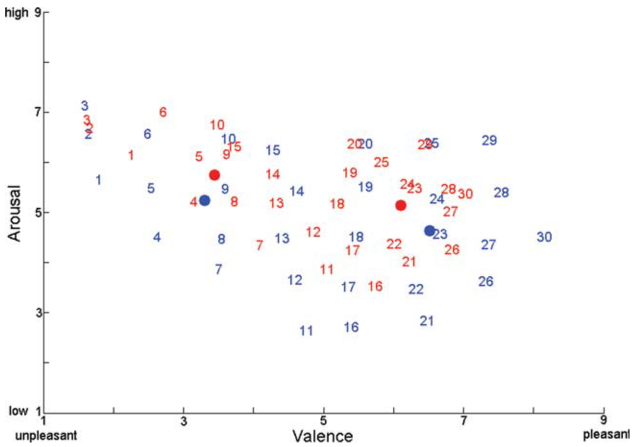

Figure 1.
Mean ($N = 9$) values of valence and arousal of the different picture sets used during fMRI-scanning, as evaluated by subjects in Lang et al. [2005] (*blue*) and our subjects (*red*). The numbers from 1 to 30 denote the different presented sets. Colored circles denote overall averages over negative and positive picture sets; Lang et al. [2005] average evaluations in *blue* and our subjects' average evaluations in *red*. Our subjects evaluated the stimuli on average as slightly more arousing and showed less variance between picture sets along the valence and arousal dimensions.

The aim of the present study was to find further evidence for the hypothesis that emotions are represented in brain by valence and arousal dimensions and to extend earlier results by generating a more detailed and elaborate pattern especially of the valence- but also of the arousal-dependencies. We used pictures, selected from IAPS, which extensively covered the emotional valence-arousal space. Short 100 ms stimulus presentation times were used to emphasize processing of intuitive emotional in contrast to consciously processed aspects of the pictures [Carlsson et al., 2004; Williams et al., 2004]. However, 100 ms is still enough for a clear conscious recognition of the stimuli [Seamon et al., 1984; Williams et al., 2004]. We studied the correlation of the two emotional dimensions to the BOLD signal changes, across all pictures, but also separately for pictures evaluated to be unpleasant and pleasant. Valence-dependent modulations were expected in the prefrontal cortical regions, amygdala, and insula. Our specific hypothesis was that, in at least some of emotion-related brain areas, correlation of brain activity is different for stimuli evaluated as negative versus positive. Such finding would support the major positive-negative division of brain mechanisms underlying affective processing. This would be in accordance with basic division of behavior to approach and withdrawal, which requires evaluating the environmental objects to good and bad [see e.g. Alexandrov and Sams, 2005].

METHODS

The study was approved by the ethical committee of Helsinki and Uusimaa district for healthy subjects and basic healthcare and it was carried out in accordance with the Helsinki declaration.

Subjects

We studied 17 healthy adults (9 women, 8 men; mean age 23, range from 21 years to 26 years), all of which gave their written informed consent after thorough explanation of the study design. Fifteen of the subjects were right- and two were left-handed. All subjects had normal or corrected-to-normal visual acuity. All subjects were naive to the experiment and they were recruited amongst the students of Helsinki University of Technology and the personnel of Laboratory of Computational Engineering.

Stimuli

The stimuli were 270 pictures from IAPS, presented in fMRI for 100 ms with 2 s interstimulus interval. Short presentation time was used to force the subjects to evaluate and process the pictures on the basis of first impression, based more on intuition than on conscious evaluation. The stimuli were presented in sets of nine pictures using a block design. We selected pictures to cover the valence-arousal space, from highly unpleasant to highly pleasant (valence) and from soporific to highly arousing (arousal).

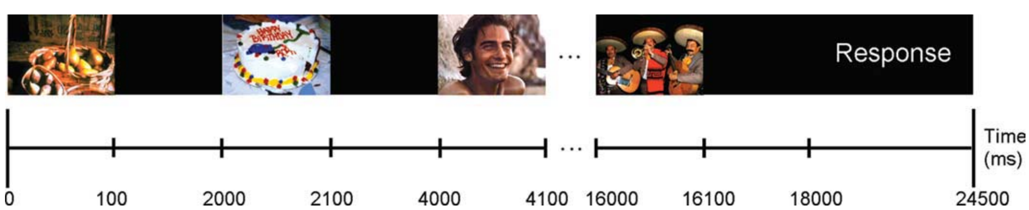

Figure 2.
Schematic presentation of a single stimulus block during scanning. Nine 100 ms IAPS pictures alternate with black screen followed by a 6.5-s evaluation period. In each block instruction to give the response was given in the subjects' mother tongue (Finnish).

The valence-arousal space was covered as thoroughly as possible on the basis of ratings published in Lang et al. [2005]. Nine different IAPS pictures with similar valence and arousal values were put in the same block. The difference between blocks was at least close to one unit in either emotion dimension on the used 1–9 scale, as judged by the subjects of Lang et al. [2005]. The means of valence and arousal evaluations for the 30 nine-picture blocks are shown in Figure 1, as evaluated in Lang et al. [2005] with 6 s stimulus presentation time and as evaluated by our subjects in a separate behavioral session with 2 s stimulus presentation time. The Pearson correlation between the block means of the present subjects and those of Lang et al. [2005] was 0.984 for valence and 0.975 for arousal ($P < 0.01$ for both).

Experimental Paradigm

During scanning, the IAPS pictures were presented in sets of nine pictures. Every set was balanced so that the valence and arousal values of the pictures within the set were approximately equal; the values of valence and arousal within each set were within a range of one unit (on 1–9 scale) according to Lang et al. [2005]. After each picture set the subjects saw a forced-choice evaluation screen, and they had to indicate by button press whether the preceding picture set was pleasant or unpleasant. Because of the block design, no stimulus-wise judgment was included. We also wanted to avoid movement-related activity in our BOLD signals. There were altogether 30 picture sets, each having a specific average level of valence and arousal (see Fig. 1).

Each picture was presented for 100 ms and followed by 1900 ms black screen. The duration of one block, including the valence evaluation, was 24.5 s. The time line of one block is presented in Figure 2. The blocks as well as the pictures within each block were presented in a random order. Before the experiment, the subjects were familiarized with the stimuli with a few random blocks, which were also used in the experiment.

Scanning Procedure and Image Analyses

During scanning subjects viewed the stimuli through a mirror positioned on the head coil. Visual angle was 13.2–22.7 degrees horizontally and 14.0–16.4 degrees vertically. The subjects were asked not to move with the exception of button presses when evaluating the valence of the stimuli. The subjects had a single response pad in either of their hands and they were asked to press the right button for pleasant judgment and the left button for unpleasant judgment. Head movement was minimized by padding and restraint.

The scanning was performed with a 3.0-T GE Signa scanner with Excite upgrade using an eight-channel head coil. A gradient-echo T2*-weighted echo-planar imaging sequence was used for fMRI with the following parameters: TR = 1,750 ms, TE = 32 ms, matrix = 64 × 64, NEX = 1, FOV = 20 cm, flip angle = 70 degrees, slice thickness = 3.0 mm. We acquired 29 contiguous axial slices covering the entire brain apart from the cerebellum and the extreme superior part of the cerebrum. The first four acquisitions were discarded due to T1-saturation effects. After the functional MR sequence, an anatomical data set was acquired using a T1-weighted gradient echo pulse sequence with the following parameters: FOV = 26 cm, matrix 256 × 256, voxel size = 1 mm^3.

Image processing and statistical analyses were performed with BrainVoyager software [Goebel, 1997]. On subject level, all volumes were realigned to the first volume, motion corrected and smoothed temporally and spatially. For temporal filtering a linear trend removal was made and a three-cycles-in-time-course high-pass filter was used for smoothing. For spatial smoothing we used a 6-mm full-width-at-half-maximum Gaussian kernel. After these preprocessing steps the volumes were coregistered with the subject's corresponding anatomical image and transformed into Talairach space. The adjusted measures were subjected to the statistical analyses. We used regular general linear model (GLM) with subjective and postscan given valence and arousal values (see Behavioral measures), that were averaged within blocks, as study predictors and random effects (RFX) group analysis. Reaction times from the behavioral valence and arousal evaluations were used as nuisance covariates in the GLM for valence and arousal, respectively. For the RFX analysis a %-transform was made for the time-courses and separate predictors were used for each subject. The predictors were derived from the individual postscan valence and arousal evaluations of the subjects. They included linear modulation of valence and arousal, second-order nonlinear modulation of valence and, as a separate model, linear modulations of negative valence and positive valence. Every stimulus block was convolved with a canonical hemodynamic response function (HRF). Voxel-wise t-scores for the group analysis (with 16 degrees of freedom) were calculated and thresholded using $P < 0.001$ (uncorrected), followed by 135 voxel cluster size thresholding (resampled 1 × 1 × 1 mm voxels; corresponding to five original 3 × 3 × 3 mm voxels). The threshold of contiguous voxels was set to tackle the problem of multiple comparisons and to avoid false positives [Forman et al., 1995].

Behavioral Measures

Three to 10 days after the scanning the subjects evaluated each of the 270 IAPS pictures by its valence and arousal (ranging from 1 to 9) in a separate behavioral session. Each picture was presented for 2 s. The presentation time was longer than in the scanner, because we wanted to make the behavioral session better comparable to the procedure in Lang et al. [2005] who used 6 s presentation

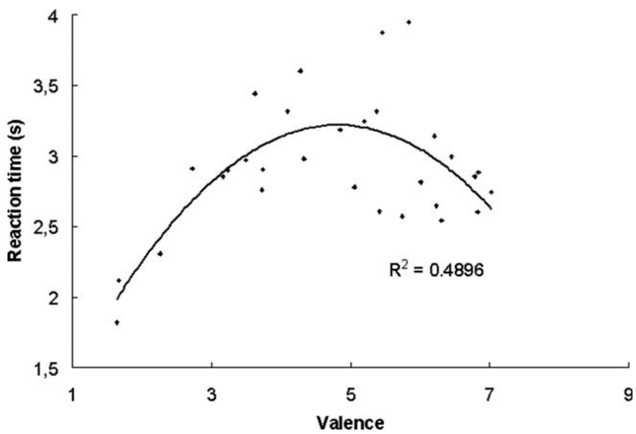

Figure 3.
Mean (N = 9) reaction times of the subjects for valence evaluations in the different picture sets as function of valence and a second-order polynomial fit.

times and to the experiments by Heinzel et al. [2005] (2 s presentation) and Grimm et al. [2006] (4 s presentation). The Pearson correlation between the postscan behavioral valence ratings and the positivity versus negativity judgments in the scanner was 0.912, indicating that the postscan ratings did not substantially change due to differences in presentation times. Because evaluation of mean valence and arousal of a block of different stimuli would have been difficult to the subjects, they rated each picture separately in the behavioral session.

The subjects were told to make all their evaluations based on the first impression, but evaluation time was not limited. Reaction times (RTs) to the evaluations were measured. Valence rating was always done first and arousal rating thereafter. The valence scale ranged from 1 (very unpleasant) to 9 (very pleasant), 5 indicating neutral valence. For arousal the scale ranged from 1 (soporific) to 9 (highly arousing). To familiarize the subjects with the used scale, they were shown before the session facial expressions of a female that represented different values of valence and arousal. Before the actual behavioral session the subjects also practiced with a few stimuli from the IAPS.

RESULTS

We calculated the means of the RTs to the stimuli presented in the same block in the fMRI measurement. RTs measured during valence evaluations in the behavioral session are shown in Figure 3. As the figure shows, RTs showed an inverted U-shaped type ($R^2 = 0.49$; $P = 0.0003 < 0.01$) dependency on valence: the most negative pictures were the fastest to evaluate, then the most positive pictures, and evaluating the neutral pictures took longest. This is probably because the pictures at the middle of the valence scale are most ambiguous [see Schimmack, 2001] in their emotional content. Since this could manifest in the BOLD signals as a task difficulty effect, RTs were taken as a covariate in the valence correlation analyses. The task during fMRI scanning was to judge whether preceding block of stimuli had been negative or positive, being most difficult for the neutral stimuli. RTs for arousal evaluations showed a small but significant ($P = 0.017 < 0.05$) positive linear correlation with arousal and were also taken into account in the fMRI-analysis. For both valence and arousal evaluations, RTs over 15 s were considered as outliers.

Strengths of the BOLD signals were correlated with the valence and arousal evaluations of individual subjects. First, we examined the correlation between the stimulus valence and the linear change of the BOLD signal, separately for unpleasant and pleasant blocks (as judged during scanning). Activity in several brain regions showed positive linear correlation to valence with unpleasant pictures and negative linear correlation to valence with pleasant pictures. In other words, for both negative and positive stimuli BOLD signal levels increased when the pictures became subjectively more neutral. Therefore, we performed also a second-order curve fit to describe the nonlinear dependency between the BOLD signal and valence. Results are summarized in Table I, which shows regions with significant ($P < 0.001$, uncorrected, cluster size = 135 with $1 \times 1 \times 1$ mm voxels) correlations.

Linear correlation of the strength of the BOLD signal and viewing pictures with negative valence was consistently positive, with the only exception in the left postcentral gyrus, and was the most significant in the right lateral sulcus, bilateral insula, right dorsolateral prefrontal cortex (DLPFC), and right amygdala. On the other hand, linear correlation of the strength of the BOLD signal and viewing pictures with positive valence was consistently negative, again with the exception of the left postcentral gyrus, and was the strongest in the dorsomedial prefrontal cortex/anterior cingulate cortex (DMPFC/ACC; bilaterally), bilateral insula, and midbrain tegmentum. Also bilateral DLPFC showed negative correlation. Many regions showed an inverted U-shaped relation between the BOLD signal and valence across all pictures (t values of the nonlinear correlation were negative). The most significant inverted U-shaped activations appeared in the left DLPFC, left insula, and bilateral DMPFC/ACC other areas including the right DLPFC, bilateral occipitotemporal gyrus, and right parahippocampal gyrus. Bilateral inverted U-shaped activations were found particularly in DMPFC, DLPFC, and insula, as depicted in Figure 4. The region of postcentral gyrus showed bilaterally significant upright U-shaped relation between BOLD signal and valence (i.e. in this area BOLD signal diminished when the stimuli changed toward more neutral). There were no significant linear correlations across all valences (from most negative to most positive).

Figure 5 depicts the major brain regions that correlated with stimulus valence. Ventral parts of the prefrontal frontal cortex (VMPFC and VLPFC) were more strongly related to

TABLE I. Brain regions, corresponding Talairach coordinates (peak activity) and peak t-values in valence correlation analyses, where reaction time was used as a nuisance covariate

		Negative valence				Positive valence				U-shaped valence			
Brain region	L/R	*x*	*y*	*z*	*t*-Value	*x*	*y*	*z*	*t*-Value	*x*	*y*	*z*	*t*-Value
Postcentral gyrus	L	−63	−40	34	−4.775878	−57	−43	46	4.763835	−57	−40	43	6.678865
DLPFC	R	42	20	25	5.433650	42	17	25	−5.119899	45	23	28	−5.509978
Insula	L	−30	23	−2	6.018400	−33	20	−2	−6.992431	−42	14	7	−8.757505
Insula	R	30	23	1	6.078242	42	26	4	−5.575615	30	20	1	−5.160250
VLPFC	L	−45	47	−2	4.936033								
VLPFC/VMPFC	R	21	50	1	4.880065								
VMPFC	L	−15	53	−2	4.757486								
Lateral sulcus	R	33	17	−17	6.753970								
Amygdala	R	18	−1	−17	5.298195								
DMPFC/ACC	L					−6	11	55	−5.829142	−3	14	46	−6.833297
DMPFC/ACC	R					12	23	46	−7.788039	9	20	43	−7.690048
ACC	R					12	17	31	−6.916986				
DLPFC	L					−33	8	37	−5.742520				
DLPFC	L					−45	17	22	−4.795809	−57	23	16	−9.194703
Caudate nucleus	L					−9	8	10	−5.097876	−12	14	13	−5.378715
Caudate nucleus	L					−15	−7	22	−4.624615				
Caudate nucleus	R					12	5	19	−5.226375				
Occipital gyrus	L					−33	−79	10	−4.961071	−33	−82	10	−5.970357
Occipital gyrus	R					36	−73	10	−4.673096	33	−76	10	−6.404235
Middle temporal gyrus	L					−60	−37	1	−5.078028				
Thalamus	R					3	−16	4	−5.300222				
Midbrain tegmentum	–					0	−22	−8	−6.007562				
Occipito-temporal gyrus	R					36	−46	−11	−5.784977	30	−43	−14	−7.349181
Lingual gyrus	L					−27	−46	−14	−5.289441	−21	−58	−2	−5.094453
Postcentral gyrus	R									60	−28	49	6.260209
Precentral gyrus	R									39	−1	34	−4.687090
Circular sulcus	R									48	−7	16	4.889324
Parahippocampal gyrus	R									12	−46	1	−7.210532
Occipito-temporal gyrus	L									−27	−43	−14	−6.523684

Negative valence indicates linear correlation with unpleasant pictures, positive valence with pleasant pictures, and U-shaped valence shows the second-order correlation across all pictures. Threshold $P < 0.001$, uncorrected, cluster size = 135. Positive t values denote positive correlation and negative t values negative.

negative valences. Dorsal parts of the prefrontal cortex, DMPFC and DLPFC, correlated with positive valences and exhibited an inverted U-shaped relation across all valences. Activity in the right amygdala correlated with negative valences, whereas activity in the bilateral insula correlated with both positive and negative valences. Activity in ventromedial part of the right lateral sulcus correlated strongly with negative valences (see also Table I).

We also examined the correlation between the arousal and the linear change of the BOLD signal, again separately for unpleasant and pleasant blocks. BOLD signal covaried significantly with arousal in the ACC (3, 26, 13; peak t value −5.44) for pictures with negative valence and in the right substantia innominata (30, 17, −11; peak t value 4.79) for pictures with positive valence. In the ACC increase in arousal elicited diminished BOLD signal, whereas in the substantia innominata there was an opposite effect. However, across all pictures there were no significant arousal correlations. These results suggest that brain mechanisms of valence and arousal are not independent. The RFX analysis did not reveal any gender-related differences in response to valence or arousal.

DISCUSSION

The purpose of this study was to investigate how viewing and evaluating pictures of different valence and arousal, and possibly corresponding feelings, activate the brain. Previous studies using pictures, smells, and emotional concepts as stimuli, have revealed several regions showing linear correlation between BOLD signal and valence or arousal [Anderson et al., 2003; Cunningham et al., 2004; Grimm et al., 2006; Heinzel et al., 2005]. We aimed to confirm and refine these results by examining BOLD signal changes separately for IAPS pictures evaluated to be pleasant and unpleasant, using a block instead of event-related design to enhance signal-to-noise ratio. To emphasize emotional in contrast to more cognitive evaluation of the stimuli, IAPS pictures were shown only for 100 ms. Interestingly, several brain areas showed an inverted U-shaped relationship

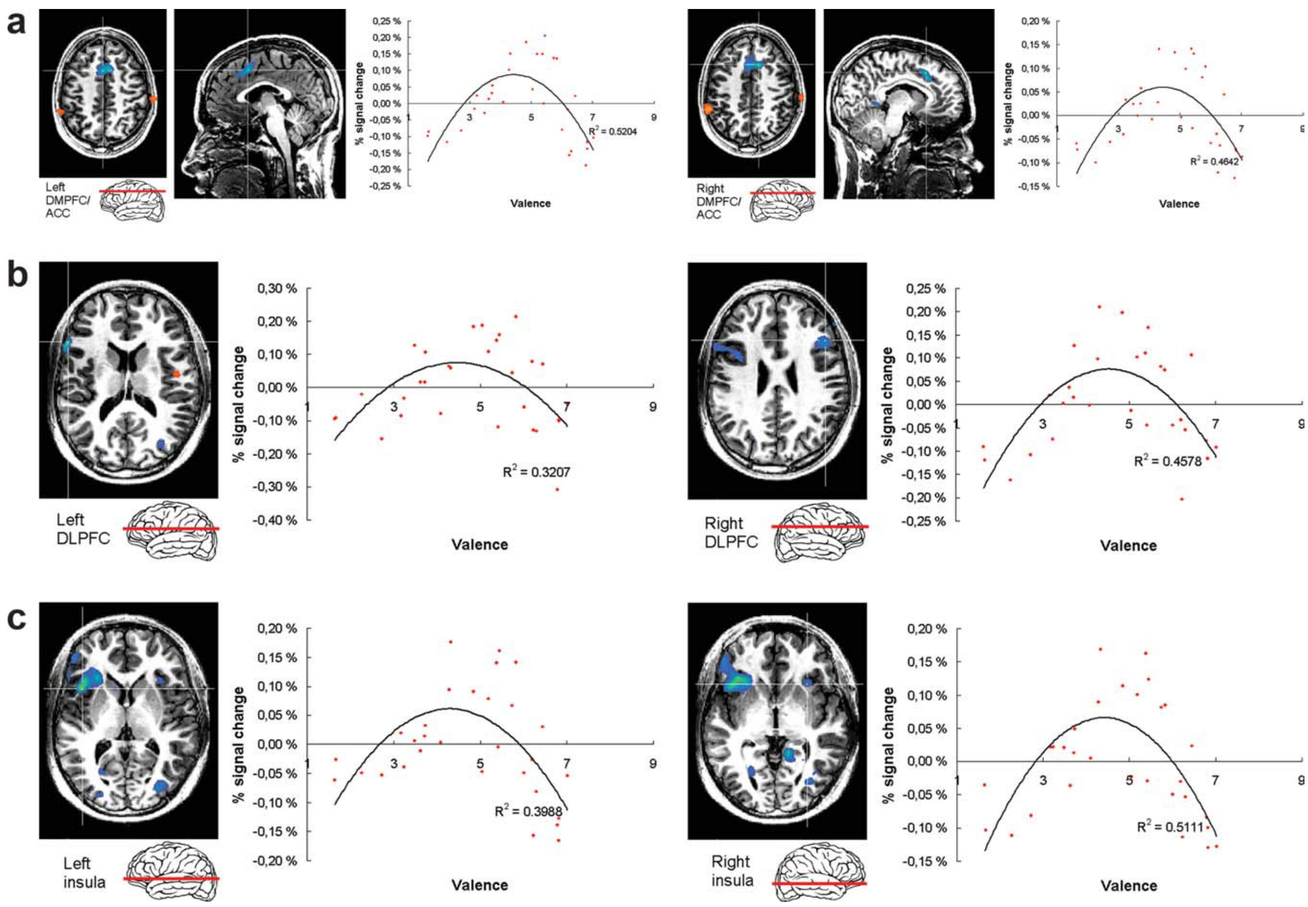

Figure 4.

Statistical maps from the correlation analysis which takes into account both linear and second-order fit. Correlation between BOLD signal and valence was of inverted U-shape in bilateral DMPFC (**a**), bilateral DLPFC (**b**), and bilateral insula (**c**). Blue colors denote negative correlation and orange colors denote positive correlation. Brain images have been presented in neurological orientation and thresholded with $P < 0.001$, uncorrected. R^2 values in the diagrams show the multiple correlation squared, depicting the level which variations in the percent BOLD signal change can be explained by the variations in valence. DMPFC = dorsomedial prefrontal cortex, ACC = anterior cingulate cortex, DLPFC = dorsolateral prefrontal cortex.

between the BOLD signal and stimulus valence: signals were strongest for neutral stimuli and progressively weaker for both negative- and positive-valence stimuli. In addition, in other areas BOLD signal strength correlated with only positive or negative valences.

Correlations With Valence

In previous studies, correlations of IAPS picture valence and BOLD signals were calculated over the whole negative-to-positive valence scale. Heinzel et al. [2005] observed a linear positive correlation between BOLD signal and valence in the OMPFC, DMPFC, and medial parietal cortex, and, as we did for unpleasant pictures, in the insula. We found negative linear dependence of valence and BOLD signal for pleasant pictures, as well as inverted U-shaped dependence across all pictures, in the DMPFC. Nonlinear valence dependence could be a reason why valence related activity in the DMPFC was not seen by Grimm et al. [2006]. Northoff et al. [2004] and Gusnard et al. [2001] have found DMPFC activations during emotional judgment. Our results suggest that mere perception and crude block-wise evaluation of emotional figures is sufficient to activate this area.

The bilateral DLPFC was activated in our study by perception and block-wise evaluation of emotional figures, whereas earlier studies have reported DLPFC activation during emotional judgment [Hariri et al., 2000; Nakamura et al., 1999]. Grimm et al. [2006] found a negative correlation between valence and BOLD signal in the bilateral DLPFC during picture judgment. They examined valence also separately for negative and positive pictures, finding a negative correlation in the left DLPFC for positive-valence pictures, but only during picture judgment. In

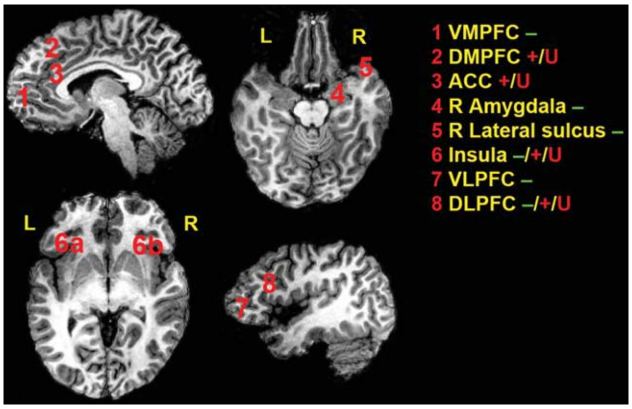

Figure 5.

Approximate locations of the most interesting brain regions that correlated significantly with stimulus valences are depicted. The green minus-signs denote positive correlation with negative valence; the red plus-signs denote negative correlation with positive valence; the red U-signs denote negative second-order correlation with the whole valence scale. VMPFC = ventromedial prefrontal cortex, DMPFC = dorsomedial prefrontal cortex, ACC = anterior cingulate cortex, amygdala, lateral sulcus, insula, VLPFC = ventrolateral prefrontal cortex, DLPFC = dorsolateral prefrontal cortex.

contrast, during picture viewing they observed opposite, positive correlation in this area. Our results revealed a multitude of brain areas correlating negatively to valence with positive pictures (see Table I). These regions included the bilateral DLPFC, which also showed an inverted U-shaped dependence on valence across all pictures. For negative pictures, instead of the negative correlation in the right DLPFC/VLPFC (during picture judgment) found by Grimm et al. [2006], we found positive correlation in the right DLPFC.

Grimm et al. [2006] observed a positive linear correlation of BOLD signal with valence in the VMPFC. We found also positive correlation in the bilateral VMPFC, but only for negative pictures. This is contrary to an earlier parametric study with positron-emission tomography (PET) by Zald et al. [2002], who discovered that high levels of negative affect tend to cause high level of activation in the VMPFC. Also in the bilateral VLPFC we observed significant positive correlation with valence for negative pictures. Grimm et al. [2006] found positive correlation with arousal for this area, albeit only in the right hemisphere. Northoff et al. [2004] found this region to be related to emotional-cognitive interaction. The present results additionally suggest that the bilateral VLPFC is involved in perception of negative valences.

As did Grimm et al. [2006], we found a positive linear correlation for negative-valence stimuli in the right amygdala. Anderson et al. [2003] found amygdala activations as a function of emotional intensity, not valence, of odors. Therefore, both valence and arousal appear to be factors in amygdala activation. Actually, Winston et al. [2005] suggested that amygdala has an integrated representation of valence and arousal, where the combination of these two forms the actual emotion dimension. Another well-known emotion processing region, bilateral insula, showed in our study an inverted U-shaped dependence across the whole valence scale (and significant positive correlation for negative pictures and negative correlation for positive pictures). While this region is involved in seeing and feeling disgust [Jabbi et al., 2008; Wicker et al., 2003], also others have found evidence of its more general role in valence processing [Cunningham et al., 2004; Heinzel et al., 2005; Small et al., 2003].

Morgane et al. [2005] demonstrated existence of projections from amygdala to VMPFC and from ACC to DMPFC, and also suggested that the prefrontal cortex in general can be divided into interconnected dorsal and ventral divisions, which might underlie the activities found in the present study (see Table I). Our results indicate that negative valences are dominantly processed in the ventral and positive valences in the dorsal parts of the prefrontal cortex. However, the dorsal prefrontal cortex also exhibits U-shaped activations across all valences.

Positive and Negative Valence Dimensions

Our results showed two general trends. First, negative-valence pictures had a positive correlation with BOLD signal (Table I). BOLD signal strength increased from negative towards neutral pictures in multiple regions and for these pictures diminished from low to high levels of emotional arousal in the ACC. Second, positive-valence pictures had a negative correlation with the BOLD signal (Table I). BOLD signal strength decreased from neutral toward positive pictures and for these pictures increased from low to high levels of emotional arousal in the substantia innominata. In many regions BOLD signal appeared to show a non-monotonic inverted U-shaped relation with valence; not only did we find positive correlations with unpleasant pictures and negative correlations with pleasant pictures but also negative second-order correlations across all pictures.

Cacioppo et al. [1997] suggested that the valence dimension is not bipolar but actually consists of two separately varying and functionally distinguishable dimensions. For example, in racial judgments some people rate low or high on both pro-African-American and anti-African-American scales, meaning that positive and negative sentiments about the African-American people can vary independently [Hass et al., 1991]. Goldstein and Strube [1994] found that students exhibit uncoupled positive and negative affective reactions with regard to their academic success. Larsen et al. [2001] showed several occasions where approximately half of the participants felt simultaneously both happy and sad. Gardner [1996] showed that positive and negative evaluative processes underlying various attitudes are stochastically independent. Supporting evidence for separate positive and negative emotion mechanisms comes from animal experiments: Miller showed already in 1959 [1959] that rats can exhibit simultaneously approach and withdrawal behavior with respect to an ambiguous goal containing both rewarding and punishing elements.

Our results suggest anatomical difference in mechanisms for processing pleasant and unpleasant pictorial stimuli. In the regions with (inverted) U-shaped valence dependency, the present fMRI data do not allow concluding whether the same or different neural populations are involved in the processing of pleasantness and unpleasantness. However, our data revealed several areas that did not show the U-shaped dependency but showed correlation only for either negative- or positive-valence pictures. This tendency was particularly prominent in the right lateral sulcus and right amygdala for the negative pictures (positive correlation) and the midbrain tegmentum for the positive pictures (negative correlation). Further, representation of arousal appeared to be dichotomically valence dependent, agreeing with Ribeiro et al. [2004] and Grühn and Scheibe [2008]. Hence, our results show evidence of at least partially separate brain mechanisms for evaluating visual objects as positive or negative.

We suggest that the (inverted) U-shaped dependency of valence and BOLD signal is also a manifestation of segregated positive- and negative-valence processing dimensions. For example, DMPFC/ACC, bilateral DLPFC, and bilateral insula (see Fig. 4) encode both positivity and negativity of pictorial stimuli, possibly by different neuronal subpopulations. The two sides of emotional valence are represented differently, yielding a non-linear dependency across the whole scale. Heinzel et al. [2005] suggest that U-shaped valence dependency could merely reflect distinction between emotional and non-emotional processing. Our data do not allow ruling out this possibility, but the neutral stimuli in our experiment caused the highest activation and the most emotional stimuli caused the least activation, and not vice versa.

Inverted U-shaped dependency could also reflect the amount of ambiguity (and thus emotional ambivalence) in the stimuli. Ito et al. [1998] had their subjects evaluate 472 IAPS pictures in several respects, including positivity and negativity. If ambivalence is defined as the minimum of these two properties [see Schimmack, 2001], the stimuli show a negative second-order correlation of 0.544 between valence and ambivalence. In other words, there is a relatively strong inverted U-shape dependency between the valence and ambivalence in IAPS stimuli, something that could manifest itself in the BOLD signal. It is possible that increased ambivalence results in increased difficulty in evaluating stimulus valence. However, we did take into account the variations in reaction time in our analysis, which should cancel effects of ambiguity-related task-difficulty in our study.

Our study is neither the first to find a U-shaped relationship of valence and brain activity nor the first to suggest a separation of pleasant and unpleasant dimensions. Lewis et al. [2007] found that independent and U-shaped models explained relationship between BOLD signal and valence for word stimuli. We argue that the independent model of Lewis et al. [2007] with an independent way of activation for positive and negative valences is in fact a model of two valence dimensions and that their U-shaped model may also reflect variations along the unpleasant and pleasant dimensions. Even though Lewis et al. [2007] did not find the same areas as in the present study and even though the U-shaped dependency was increasing, not inverted, the results support the notion that there exists nonlinear relationship between emotional valence and brain activity. Thus, valence can be divided into negative and positive dimensions. Further, arousal associated with unpleasantness seems to be different from arousal associated with pleasantness.

Laterality of Valence Processing

It has been suggested that the left hemisphere predominates in processing positive, and the right hemisphere in processing negative emotions [e.g. Best et al., 1994; Davidson, 1992]. However, on the basis of their meta-analysis of fMRI and PET studies, Wager et al. [2003] concluded that the lateralization hypothesis does not hold for the whole brain. We failed to see any general lateralization patterns of valence-related activity. Our results are more consistent with the idea that there are specific brain structures processing predominantly negative or positive valences bilaterally. However, Best et al. [1994] have suggested that hemispheric differences can be found only for experience and expression of emotions, not for recognition of different emotions. The meta-analysis of Wager et al. [2003] suggested that males have more lateralized activations to emotions than females, especially in the frontal cortical and limbic areas. However, our study did not reveal any gender-related effects with respect to valence or arousal.

Methodological Remarks

Our task in the scanner was chosen to be convenient for the subjects. The fact that they merely judged whether the preceding block had been negative or positive in valence most likely had some effect on the emotional processing (i.e. experiencing and evaluating the stimuli). Our task could have led to more focused attention on the valence dimension, which, for one, can influence emotional processing. Feldman [1995] found that valence focus emphasizes the negative correlation between the ratings of "Negative Affect" and "Positive Affect," whereas increase in arousal focus has the opposite effect. Thus, by having the subjects judge the valence of the stimuli, we probably made the differences in experiencing negative and positive valences more enhanced. However, the affective focus does not seem to have statistically significant effects on the BOLD signal, as evidenced by Narumoto et al. [2001]. It is, hence, unlikely that more attention on valence due to task would have influenced our subjects' BOLD signals either.

The IAPS pictures, used in the present study, have been selected to be emotionally evocative [Lang et al., 2005], and viewing these pictures very likely also induces emotional feelings in the subjects. Our subjects were asked to evaluate crudely the valence (positive or negative) during the scanning. Therefore, we cannot argue that the BOLD correlations with valence and arousal reflect purely the brain mechanisms underlying emotional feelings. The activation patterns we found probably reflect brain mechanisms underlying feelings, recognition of the emotional flavor of the visual scenes, and their cognitive evaluation. It is likely that the complexity of similar tasks is also reflected in the differences in the results obtained in different experiments. The differences in results can also emanate from different presentation times of stimuli, different stimulus modalities and differences between the event-related and block design paradigms.

CONCLUSIONS

Our study is in line with the idea that there are two core emotional mechanisms in the brain: one processing emotionally negative stimuli and the other processing emotionally positive stimuli, supporting the theory proposed by Cacioppo et al. [1997] and Cacioppo and Berntson [1994]. This kind of behavior was seen across a multitude of brain regions, likely coupled to a network processing emotional information. We found several valence-responsive brain regions, but only a few regions which were arousal responsive. Our results add evidence to the idea that there are at least partly separate neural mechanisms for emotional valence and arousal, yet valence-dependency of arousal was also observed.

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