

Amygdala activation during reading of emotional adjectives—an advantage for pleasant content

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This event-related functional magnetic resonance imaging (fMRI) study investigated brain activity elicited by emotional adjectives during silent reading without specific processing instructions. Fifteen healthy volunteers were asked to read a set of randomly presented high-arousing emotional (pleasant and unpleasant) and low-arousing neutral adjectives. Silent reading of emotional in contrast to neutral adjectives evoked enhanced activations in visual, limbic and prefrontal brain regions. In particular, reading pleasant adjectives produced a more robust activation pattern in the left amygdala and the left extrastriate visual cortex than did reading unpleasant or neutral adjectives. Moreover, extrastriate visual cortex and amygdala activity were significantly correlated during reading of pleasant adjectives. Furthermore, pleasant adjectives were better remembered than unpleasant and neutral adjectives in a surprise free recall test conducted after scanning. Thus, visual processing was biased towards pleasant words and involved the amygdala, underscoring recent theoretical views of a general role of the human amygdala in relevance detection for both pleasant and unpleasant stimuli. Results indicate preferential processing of pleasant information in healthy young adults and can be accounted for within the framework of appraisal theory.

Keywords: emotion; perception; re-entrant processing; reading; amygdala; extrastriate cortex; neuroimaging

Emotional stimuli are of particular importance for an individual and demand priority access to perception and attention (Lang *et al.*, 1997; Öhman *et al.*, 2001). Human lesion and neuroimaging studies suggest that the amygdala, a phylogenetically old brain structure located in the mediotemporal lobes, plays a key role in the facilitated processing of emotionally significant visual stimuli (e.g. Adolphs *et al.*, 1999; Vuilleumier *et al.*, 2004). Over the years many studies have shown amygdala involvement in the processing of threatening and fear-relevant stimuli, such as fearful faces or pictures of human and animal attack (see e.g. Öhman and Mineka, 2001; Adolphs, 2002; Vuilleumier, 2002). This has led to an initial conceptualization of the amygdala as a structure specialized in the detection of unpleasant and fear-relevant material, possibly even a 'fear-module' (Öhman and Mineka, 2001). But increased amygdala activation has subsequently also been found in response to happy faces (Williams *et al.*, 2005) and emotionally arousing pleasant scenes and objects (see e.g. Zald, 2003 for a review) as well as for pleasantly and unpleasantly arousing vocalizations (Fecteau *et al.*, 2007). A general role of the human amygdala beyond the processing of threat-related and fear-relevant

material, extending to the processing of arousing stimuli of both valences, has therefore been discussed in the recent literature (Davis and Whalen, 2001; Sabatinelli *et al.*, 2005; Lewis *et al.*, 2007).

In further distinction to the view of the amygdala as especially involved in fear, or the processing of emotionally arousing stimuli, enhanced amygdala activity has sometimes been found specifically to pleasurable or rewarding pleasant stimuli (O'Doherty *et al.*, 2002; see also, Burgdorf and Panksepp, 2006). It has also been found in response to biologically meaningful, but not inherently emotional stimuli such as human eye gaze (Bonda *et al.*, 1996; Baron-Cohen *et al.*, 1999; Kawashima *et al.*, 1999) and also, in response to socially and individually important stimuli (e.g. Phelps *et al.*, 2000). Moreover, individual differences in participants' motivational state and personality traits have been reported to modulate the magnitude of amygdala activation in response to emotionally pleasant and unpleasant stimuli. For instance, during viewing of pictures of food items, amygdala activation is higher when hungry than after food intake (LaBar *et al.*, 2001; Morris and Dolan, 2001; Hinton *et al.*, 2004), higher in responses to happy faces than to angry faces in highly extraverted subjects (Canli *et al.*, 2002), and higher in response to fear-relevant stimuli in highly anxious subjects than in low-anxiety subjects (Sabatinelli *et al.*, 2005). The latter findings are hard to reconcile with the aforementioned conceptualizations of the amygdala as a general 'fear module' or an 'arousal indicator'. Thus, an even

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broader conceptualization of amygdala function as a more dynamic 'evolved system for relevance detection' has been proposed (Sander *et al.*, 2003). According to this view, the human amygdala acts as a dynamic 'relevance detector'. It alerts us in principle towards both hostile and pleasurable stimuli but takes into account internal milieu states as well as current environmental and individual demands (Sander *et al.*, 2003).

The special significance of most stimuli shown to robustly elicit amygdala activation, such as emotional faces, food items or fear-relevant objects such as spiders or snakes, is at least partly innate and *phylogenetically* 'prepared' (Öhman and Mineka, 2001; Öhman, 2002). But humans as members of a social and symbolic species can also use more abstract, symbolic means to communicate emotions: written words bear no resemblance to the state or object they denote, and their emotional connotation is conveyed solely on the basis of *ontogenetically* learned associations. Thus, their significance might be analysed only after they are subjected to higher level semantic processing and *evaluation* (Vanderploeg *et al.*, 1987; Cacioppo *et al.*, 1993).

Dual process models of emotional processing in the brain suggest two distinct processing systems: an explicit processing system operating mainly on the basis of controlled emotional evaluation and an implicit processing system responding relatively automatically to emotionally significant stimuli (Cunningham *et al.*, 2003; Ochsner *et al.*, 2004; Ochsner and Gross, 2005). Current evidence indicates that the amygdala is more strongly engaged in implicit or stimulus-driven than in cognitively controlled processing of emotional stimuli (Critchley, *et al.*, 2000; Liberzon *et al.*, 2000; Cunningham *et al.*, 2003, 2004; Winston *et al.*, 2003; Lieberman *et al.*, 2007). Thus, the question arises whether the amygdala is activated during visual processing of highly symbolic emotional stimuli such as words.

Several neuroimaging studies on emotional word processing report activation in dorsolateral and medial prefrontal and middle temporal brain regions to be enhanced during processing of emotional in contrast to neutral words, but fail to find amygdala activation (Beauregard *et al.*, 1997; Crosson *et al.*, 1999, 2002; Cato *et al.*, 2004; Kuchinke *et al.*, 2005). Some lesion and intracranial recording studies, on the other hand, suggest that the amygdala may amplify perception and attention to emotionally challenging words (e.g. 'rape', 'bastard'), possibly via reciprocal feedback projections to the ventral visual processing stream (Anderson and Phelps, 2001; Naccache *et al.*, 2005). In neurologically intact subjects, however, evidence in favour of this thesis is still sparse. So far, few imaging studies demonstrate amygdala activation during visual processing of emotionally arousing words. More evidence exists for the selective processing of unpleasant words (Isenberg *et al.*, 1999; Strange *et al.*, 2000; Tabert *et al.*, 2001; Nakic *et al.*, 2006; Lewis *et al.*, 2007), although amygdala activation in response to pleasant words has also been reported (Hamann and Mao, 2002;

Canli *et al.*, 2004; Kensinger and Schacter, 2006; Lewis *et al.*, 2007). Comparing depressed patients' and normal controls' brain responses to differently valenced words in a lexical decision task, Canli *et al.* (2004) even found stronger amygdala activation in response to pleasant than to neutral words in normal controls, but not in depressed subjects.

Two of the studies reporting amygdala activation during emotional word processing suggested a modulatory role of the amygdala on other brain regions sub-serving word perception. Comparing highly aversive (threat) words to neutral words, Isenberg *et al.* (1999) using Positron Emission Tomography (PET) and Tabert *et al.* (2001) using functional magnetic resonance imaging (fMRI) found enhanced processing of unpleasant words in the visual cortex to be paralleled by enhanced amygdala activation for unpleasant in comparison to neutral words. Both authors therefore assume that the amygdala amplifies perceptual processing of threat words via direct feedback connections to the visual cortex. Tabert and colleagues (2001) provide tentative support for this suggestion by showing in nine female subjects that amygdala and occipital activity was significantly correlated during processing of unpleasant words.

The assumption that the amygdala amplifies perceptual processing of at least threat words is consistent with findings of bidirectional modulatory connections between the amygdala and extrastriate cortex, so-called 're-entrant processing' loops, in non-human primates (Amaral and Price, 1984), and is supported by human lesion data on the processing of emotional faces and words (Anderson and Phelps, 2001; Vuilleumier *et al.*, 2004).

'Re-entrant processing' has been favoured by many authors as a model to explain facilitated sensory processing of faces and pictures in the visual cortex (Lane *et al.*, 1997, 1999; Morris *et al.*, 1998; Bradley *et al.*, 2003; Winston *et al.*, 2003; Sabatinelli *et al.*, 2005) and some imaging studies provide empirical support for this model by showing that activity in amygdala and extrastriate cortex is correlated or at least that the two brain structures show parallel response patterns, particularly during processing of emotional faces (e.g. Morris *et al.*, 1998, 1999; Pessoa *et al.*, 2002).

Extrastriate cortex regions located in the ventral and lateral parts of the inferior temporal and occipital lobes respond to word stimuli (Petersen *et al.*, 1990; Nobre *et al.*, 1994; Cohen *et al.*, 2002; Jobard *et al.*, 2006; Vigneau *et al.*, 2005; Gaillard *et al.*, 2006) and are sensitive to a word's lexical and semantic aspects. Therefore, as previously suggested (Tabert *et al.*, 2001; Isenberg *et al.*, 1999), these brain areas might represent sites of amygdala-driven re-entrant processing during word processing, affording a mechanism by which facilitated visual processing could occur for content with evolutionarily prepared as well as learned emotional significance.

But, as mentioned above, amygdala activation in response to emotional words is in itself not uncontroversial. Differences in task demands may account for some of the

conflicting findings: previous hemodynamic imaging studies on emotional word processing have all used 'active tasks' in which subjects were explicitly asked to categorize the words according to emotional, lexical or semantic aspects. Although, attention often facilitates emotional perception (Isenberg *et al.*, 1999; Lane *et al.*, 1999; Vuilleumier *et al.*, 2001; Pessoa *et al.*, 2002; Bradley and Lang, 2007), cognitively demanding experimental tasks can mitigate stimulus-driven perceptual processing due to higher order controlled processing (Hariri *et al.*, 2000; Ochsner *et al.*, 2002; Phan *et al.*, 2002 for an overview). Recent evidence even suggests that linguistic processing is especially suited to down-regulate stimulus-driven affective responses (Lieberman *et al.*, 2007; Tabibnia *et al.*, 2008). In particular, attaching word labels to emotional stimuli reduces amygdala activation and instead increases prefrontal, particularly right ventrolateral prefrontal cortex activation (Lieberman *et al.*, 2007).

Surprisingly, to date no fMRI study has investigated emotional word processing during conditions of natural reading, that is, without any instructions other than to read the words silently. Word reading is a highly over-learned automated skill. We perceive the meaning of written words without being told to attend to their content, and we cannot help but process their meaning (LaBerge and Samuels, 1974; Logan, 1988). Silent word reading is probably the most natural task to study brain activation patterns underlying enhanced stimulus-driven processing of emotional words, as it occurs spontaneously and implicitly as soon as a word is perceived. Silent word reading has recently successfully been used in investigations of category-specific divisions of the semantic system (Hauk *et al.*, 2006, 2008). In emotion research, 'passive' picture viewing has been used repeatedly to measure spontaneous and naturalistic responses to emotional stimuli (e.g. Bradley *et al.*, 2003; Sabatinelli *et al.*, 2005; Junghofer *et al.*, 2006), because such uninstructed processing may model processing in everyday life more closely than experimentally imposed, often highly artificial, cognitive tasks. A possible drawback of this approach is reduced control over or assessment of subjects' cognitive activity, which may introduce more variability and 'noise' (i.e. activity of no interest) in the data. On the other hand, if relevant activity (e.g. amygdala) can still be identified under such conditions of implicit emotional processing, this should increase confidence in such activation occurring naturally outside the laboratory.

Finding amygdala activation during spontaneous processing of unpleasant and particularly also pleasant words would help to establish several facts about its functional role: first, amygdala activation during reading would underscore that the amygdala spontaneously responds to a broad class of emotionally relevant stimuli even when their particular relevance is conveyed by abstract symbolic stimuli.

Second, the overall activation pattern in the amygdala may inform general theories of affective processing: if activation

were restricted to unpleasant stimuli, results would be in line with the view that the amygdala is specialized for detecting unpleasant stimuli. Enhanced activation during the processing of both pleasantly and unpleasantly arousing words would indicate that, at least during reading, amygdala activity is driven by the arousal value of the stimuli. Stronger amygdala activation during reading of pleasant than of neutral and unpleasant words might be more in line with the view that the amygdala acts as a 'dynamic relevance detector', neither specifically responding to negative valence nor exclusively driven by arousal. Instead, its response patterns might be determined by situation-specific and individual factors, as suggested by considerations from appraisal theory (Sander *et al.*, 2005).

Third, examining the functional relationship between the amygdalae and extrastriate visual areas would provide further empirical data on the validity of the concept of re-entrant processing during emotional perception. Although, this concept is often theoretically called upon, supportive experimental data are scarce.

Extending previous findings from experimentally instructed tasks to more natural processing conditions and from negatively to positively valenced symbolic stimuli, the present study first delineates the overall pattern of cerebral activation during reading of words varying in emotional content. Then, it clarifies whether silent reading of emotionally arousing pleasant and unpleasant words induces enhanced activation in the amygdala and the ventral visual system, relative to neutral words. Primary regions of interest (ROIs) of this second, more focused analysis, therefore, comprise the left and right amygdala and the extended bilateral extrastriate cortex. Additionally, the functional relationship between these ROIs is examined by correlation analysis to examine evidence for re-entrant processes. Finally, as in previous silent reading studies (Kissler *et al.*, 2007; Herbert *et al.*, 2008), a surprise free recall test assesses incidental recall of the presented words to verify adequate task involvement and investigate whether reading emotional *vs* neutral words has a measurable and lasting differential impact on memory. Research suggests that increased amygdala activation during stimulus perception is related to superior subsequent recall (Cahill *et al.*, 1994; Canli *et al.*, 2000).

MATERIALS AND METHODS

Participants

Fifteen healthy right-handed native speakers of German (eight males, seven females; mean age 26 years) without history of drug abuse, chronic bodily or neurological and psychiatric diseases, or medication for any of these participated in the fMRI experiment. Handedness was determined with the Edinburgh Handedness Inventory (Oldfield, 1971), and all subjects had normal or corrected to normal vision. All participants gave written informed consent prior to participation, and the study was approved by University of

Tübingen Institutional Review Board. Subjects were paid 15 euros for participation.

Stimulus material

The stimulus set consisted of 102 adjectives taken from a larger corpus of words, previously collected by this research group.¹ This corpus provides arousal, valence and concreteness ratings from 45 adult native speakers of German for a set of about 800 German words. Valence and arousal ratings were obtained on the Self-Assessment Manikin scale (SAM, Bradley and Lang, 1994) in analogy to the Affective Norms for English Words (ANEW), a standardized list of affective norms for English words (ANEW, Bradley and Lang, 1999) and the international affective picture system (IAPS) (Lang *et al.*, 2005). Subsets of these words have been used in previous studies of emotional word processing (Ethofer *et al.*, 2006; Herbert *et al.*, 2006, 2008; Kissler *et al.*, 2007, 2008).

Thirty-four pleasant, 34 unpleasant and 34 neutral adjectives were selected. Pleasant and unpleasant adjectives were matched in emotional arousal, and both were more arousing than neutral adjectives. Mean valence differed appropriately (pleasant > neutral > unpleasant). Pleasant and unpleasant adjectives described a broad range of affective traits and states (e.g. successful, happy, in love, chilling, brutal, tortured, anxious, nervous, sick, etc.). Neutral adjectives described less arousing and salient traits and states (e.g. neutral, normal, civilian, formal, etc.). Additionally, word categories were comparable on non-emotional attributes such as concreteness, word frequency, word length, orthographic neighbourhood density and bigram frequency. Word frequency was assessed using frequency counts for written language from the CELEX database (Baayen *et al.*, 1995). Neighbourhood density and bigram frequency were analysed with WordGen software (Duyck *et al.*, 2004). Word categories did not differ significantly in concreteness, word length, orthographic neighbourhood density or bigram frequency. Pleasant and unpleasant adjectives had somewhat lower word frequency counts than neutral adjectives, although pleasant and unpleasant adjectives did not differ significantly in word frequency. Descriptive statistics of the word stimuli are summarized in Table 1.

Experimental design

The 102 adjectives were randomly assigned to one of two sets of 51 experimental stimuli presented in two separate imaging runs of silent word reading. Each run contained 17 highly arousing pleasant, 17 highly arousing unpleasant and 17 low arousing neutral adjectives. No word occurred twice. Adjectives were presented for 1000 ms. Each was followed by a baseline consisting of an array of eight unpronounceable letter strings (xxxxx). Intertrial intervals (word offset to word onset) ranged from 7.5 s to 12.75 s in order to facilitate an event-related fMRI analysis. Stimulus

Table 1 shows mean valence, arousal and concreteness values, as well as mean word length, word frequency, orthographic neighbourhood size and bigram frequency counts for pleasant, neutral and unpleasant adjectives

	Adjectives		
	Pleasant	Neutral	Unpleasant
Valence	6.6 (0.14) ^a	5.2 (0.09) ^b	2.5 (0.06) ^c
Arousal	6.0 (0.11) ^a	3.0 (0.06) ^b	6.1 (0.10) ^a
Concreteness	4.7 (0.16) ^a	4.6 (0.29) ^a	4.0 (0.20) ^a
Word length	8.5 (0.42) ^a	7.4 (0.36) ^a	8.4 (0.34) ^a
Word frequency	24.0 (6.2) ^a	95.9 (25.6) ^b	16.0 (4.2) ^a
Orthographic neighbourhood size	0.61 (0.20) ^a	0.79 (0.25) ^a	0.47 (0.16) ^a
Bigram frequency	27 651.3 (2853.0) ^a	245 61.0 (2539.7) ^a	31 374.5 (3004.6) ^a

The range and direction of the valence, emotional arousal and concreteness values are as follows: valence = 9 (extremely pleasant) to 1 (extremely unpleasant), emotional arousal = 9 (extremely arousing) to 1 (not at all arousing), concreteness = 1 (extremely concrete) to 9 extremely abstract. Same superscript alphabets (a) on numbers within each row indicate that the means are not significantly different ($P > 0.05$) from each other using planned comparison tests. Standard errors are in parentheses.

presentation order was randomized within runs, and run order was counterbalanced across subjects. Each run began with a baseline trial of random letter strings presented for 5 s. Experimental runs were controlled using 'Presentation' software (Neurobehavioral Systems Inc. <http://www.neurobs.com>).

Participants were instructed to read each word silently. No reference to emotional content was made. Fifty minutes after scanning, participants were given a surprise memory test. They were asked to recall as many of the presented adjectives as they could. Valence labels ('pleasant', 'unpleasant' and 'neutral') were given as category cues, and subjects were asked to write down as many of the previously presented words as they could remember. Across subjects, the order of emotional category cues given at recall test was randomized.

Physiological data collection and reduction

Image acquisition. Functional and anatomical images were recorded on a 1.5 T-whole body scanner (Siemens Vision, Erlangen, Germany). T1-weighted, high-resolution ($1 \times 1 \times 1.5 \text{ mm}^3$ voxel size) structural brain images were obtained for each subject using a magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence (192 slices, no gap, TR = 9.7 s, TE = 4 ms, $\alpha = 8^\circ$, FOV = $256 \times 256 \text{ mm}^2$). Functional images were acquired by using a T2-weighted multislice echo-planar imaging (EPI) sequence (28 axial slices acquired in descending direction, 4 mm thickness, 1 mm gap, TR = 3 s, TE = 39 ms, $\alpha = 90^\circ$, FOV = $192 \times 192 \text{ mm}^2$, 64×64 matrix, $3 \times 3 \times 5 \text{ mm}^3$ voxel size).

Image analysis. Imaging data were analysed with Statistical Parametric Mapping software (SPM99, Wellcome Department of Imaging Neuroscience, London, UK). The first five EPI images of each run were

¹ The complete list of the words used in this study (original and translation) together with valence and arousal ratings is available from the authors upon request.

discarded from further analysis to exclude images preceding T1 saturation. Pre-processing of functional images included slice time correction, 3D motion correction and normalization to MNI space (Montreal Neurological Institute, Collins *et al.*, 1994; resampled voxel size $3 \times 3 \times 3 \text{ mm}^3$). Data were smoothed spatially with an isotropic Gaussian Filter of 12 mm full width at half maximum (FWHM) to remove high-frequency artefacts and smoothed temporally (4 s FWHM) to permit application of random field theory for statistical inference (Worsley *et al.*, 1996).

Statistical analysis was based on the general linear model (Friston *et al.*, 1995). Hemodynamic responses during adjective presentation were modelled using a stick function (time-locked to stimulus onset) convolved with the canonical hemodynamic response function of the SPM99 software package. Stick functions were time-locked to the onset of the stimuli, and separate regressors were used to model each condition (pleasant, unpleasant and neutral adjectives). To account for signal changes due to head movements during scanning, six regressors representing estimated head movements were added as covariates of no interest into the statistical model (Friston *et al.*, 1996).

Group data were analysed with random-effect analyses (Holmes and Friston, 1998). For each contrast of interest (see below), individual contrast images were averaged across the two runs and entered into a second-level one-sample *t*-test, each analysing activity associated with reading of pleasant, unpleasant or neutral adjectives in the entire brain. Activation is reported for clusters reaching a spatial threshold of at least 20 contiguous voxels each at a significance threshold of $P < 0.005$ (uncorrected). These criteria correspond to what has been used in similar previous functional imaging studies on the processing of emotional words (e.g. Hamann and Mao, 2002; Cato *et al.*, 2004).

Four different contrasts were calculated: (i) emotional *vs* neutral, (ii) unpleasant *vs* neutral, (iii) pleasant *vs* neutral and (iv) pleasant *vs* unpleasant adjectives.

ROI analysis and correlation analysis

A second, more focused analysis specifically examined the effects of emotional content on activity in visual areas and the amygdala and their functional relationship: ROIs for this analysis comprised the left and right amygdala and the bilateral extrastriate cortex, where a large extrastriate ROI included the infero-temporal gyrus (BA20), the fusiform gyrus (BA37) and the extrastriate occipital cortex (BA18 and BA 19). This ROI was chosen to be relatively large, in view of the variability concerning the localization of word-specific visual activity reported in the fMRI literature (for review, see Jobard *et al.*, 2006). Note that larger ROIs also lead to more conservative assessment when the small volume correction (SVC) procedure is applied. Anatomical masks for volume extraction were generated on the basis of a priori anatomical criteria as defined in the automatic anatomical labelling atlas integrated in SPM99 (Tzourio-Mazoyer

et al., 2002). Activity within these regions was statistically evaluated using the SVC procedure (Worsley *et al.*, 1996).

The functional relationship between amygdala and visual activation during reading of emotional adjectives was tested by entering mean signal change in the voxels of peak activity in these regions into correlation analysis (Pearson's *r*). Mean signal change was calculated on the basis of beta values of the voxels in the amygdalae and extrastriate visual cortices that across regressors and participants showed maximal activation. In order to obtain a reasonably representative and stable estimate, activity was extracted from spheres of 6 mm around the peak voxels. As a consistency check, the analysis was repeated entering only the peak activity voxels from the amygdala and extrastriate cortex.

Memory performance

Free recall memory performance for correctly remembered pleasant, unpleasant and neutral adjectives was statistically tested with a one-way repeated-measures analysis of variance.

RESULTS

Imaging data

Emotional > neutral adjectives. Reading emotional compared to reading neutral adjectives significantly increased activity in the left middle and inferior occipital (BA 18, BA 19) cortex, the left amygdala and adjacent left parahippocampal regions. Additional clusters of activation were found in prefrontal (supplementary motor cortex) and parietal cortex (precuneus), bilaterally, as well as the cerebellum (Table 2).

Neutral > emotional adjectives. There was also a small and regionally distinct activity enhancement during reading of neutral *vs* emotional adjectives in the superior and middle temporal gyri, parts of the parietal lobe and the inferior frontal gyrus. These activities are summarized in Table 2.

Pleasant > neutral. Visual and limbic activation of the left hemisphere, encompassing the inferior and middle occipital gyrus, the inferior temporal and fusiform gyrus, and amygdala and anterior parahippocampal gyrus, were most pronounced for the contrast comparing pleasant against neutral adjectives (Table 3 and Figure 1A). Processing of pleasant compared to neutral adjectives also accounted for signal increase in bilateral inferior parietal cortex (BA 40) including the left middle cingulate (BA 23, BA 31) cortex, as well as frontal lobe and cerebellar activation.

Unpleasant > neutral. For the contrast comparing unpleasant against neutral adjectives, no clearly significant supra-threshold voxels were found within the amygdalae, although activation of the left amygdala was detectable at a very lenient significance threshold of $P = 0.05$ uncorrected (see also Figure 1A). There was significantly enhanced activity in the left visual brain, the right supplementary motor area (SMA) and the left cerebellum during reading of

Table 2 Comparisons of overall brain activity obtained during silent reading of emotional (pleasant and unpleasant) versus neutral adjectives. The upper part of this table indicates which brain regions exhibited a significant increase in activity during reading of emotional compared to neutral adjectives. The lower part displays the reverse contrast (neutral > emotional)

Hemisphere	Brain Region	Brodman area (BA)	T-value	Coordinates <i>x, y, z</i> MNI	Cluster
Emotional adjectives > neutral adjectives					
<i>Temporo-occipital lobe extrastriate cortex</i>					
Left	Inferior/middle occipital gyrus <i>Limbic system</i>	BA 18/19	6.31	−14, −100, −4	295
Left	Amygdala/anterior parahippocampus <i>Parietal lobe</i>		4.60	−16, −4, −24	72
Left and Right	Superior parietal, precuneus	BA 5/7	3.46	−8, −44, 74	21
			4.00	8, −50, 72	22
<i>Frontal lobe</i>					
Left	Superior frontal gyrus, medial	BA 9	3.63	−10, 54, 36	23
Left and Right	SMA	BA 6/8	3.47	−16, 10, 58	24
			4.20	12, −6, 56	66
<i>Cerebellum</i>					
Left and Right			3.92	14, −56, −18	142
			3.54	−14, −76, −20	55
Neutral adjectives > emotional adjectives					
<i>Temporal lobe</i>					
Left and Right	Superior/middle temporal gyrus	BA 21/22	4.85	−60, −22, −6	128
			4.90	−42, −30, 4	44
				50, −26, 8	185
<i>Parietal lobe</i>					
Left and Right	Supramarginal/angular gyrus	BA 22	4.00	−32, −64, 36	20
			3.58	44, −50, 32	32
<i>Frontal lobe</i>					
Left and Right	Inferior frontal gyrus	BA 45/47	3.13	−58, 24, 10	20
			3.65	58, 28, 18	44

unpleasant *vs* neutral adjectives (Table 3), but the extent of the activation was considerably smaller than for the pleasant *vs* neutral comparison.

Pleasant > unpleasant. Contrasting pleasant against unpleasant adjectives corroborated significantly enhanced responses for pleasant adjectives in the left amygdala and the left extrastriate cortex (Table 4). In addition, an increase of activation for pleasant adjectives occurred in anterior parahippocampal gyrus regions adjacent to the left amygdala and in inferior parietal and parietal somatosensory cortex regions as well as in right-hemisphere temporal brain regions including areas in the superior (BA 21) and middle (BA 37) temporal gyrus and the anterior temporal pole (BA 38).

Unpleasant > pleasant. There was increased activation in the cerebellum, but no other brain region showed larger activation for unpleasant adjectives than for pleasant adjectives.

Effects of emotional content on word processing are summarized in Figure 1A.

ROI analysis and correlation analysis

Although, hypotheses had covered bilateral amygdalae and extrastriate regions, results are reported only for the left

hemisphere, as no corresponding right-hemisphere above-threshold activation was found for right extrastriate regions and the right amygdala, respectively (see above and Tables 2 and 3). ROI analysis and correlation analysis of the left amygdala and left extrastriate cortex showed significant effects for pleasant adjectives. Activation peaks were located in the left amygdala (peak at MNI: −20, 2, −18) and in the inferior occipito-temporal gyrus (peak at MNI: −48, −76, −2) of the left extrastriate cortex, respectively. The magnitude of activations in the left limbic and extra-striate ROIs is detailed in Table 5 (emotional > neutral; pleasant > neutral and pleasant > unpleasant). After small volume correction, no significantly activated voxels within the ROIs were found for the unpleasant > neutral and unpleasant > pleasant contrasts.

Correlation analysis was restricted to the left amygdala and left extrastriate cortex since no corresponding right-hemispheric main effects were found. Left amygdala activation was significantly correlated with perceptual processing in the left extrastriate cortex for pleasant adjectives (Pearson's $r=0.65$; $P<0.01$). There were no significant correlations between left amygdala and left extrastriate cortex

Table 3 Comparisons of overall brain activity obtained during silent reading of pleasant, unpleasant and neutral adjectives. Upper part: Regions showing enhanced brain activity during reading of pleasant versus neutral words. Lower part: Regions showing enhanced brain activity during reading of unpleasant versus neutral words

Hemisphere	Brain Region	Brodman area (BA)	T-value	Coordinates <i>x, y, z</i> MNI	Cluster
Pleasant adjectives > neutral adjectives					
	<i>Temporo-occipital lobe extrastriate cortex</i>				
Left	Inferior/middle occipital gyrus	BA 18/19	6.47	-14, -100, -6	405
Left	Inferior temporal gyrus, fusiform gyrus	BA 19/37 BA 20	4.14 3.77	-42, -68, -16 -36, -8, -26	69 43
	<i>Limbic system</i>				
Left	Amygdala/anterior parahippocampus		5.52	-14, 0, -24	105
	<i>Parietal lobe</i>				
Left	Middle cingulate	BA 23/31	3.90	-6, -24, 44	98
Left and Right	Inferior parietal gyrus	BA 40	3.57 3.83	-40, -38, 44 24, -46, 46	53 64
	<i>Frontal lobe</i>				
Left	Superior/middle frontal gyrus	BA 8/9	4.23	-18, 12, 60	111
	<i>SMA</i>				
	<i>Cerebellum</i>				
Left and Right			4.39 4.08	-26, -54, -26 12, -74, -36	184 240
Unpleasant adjectives > neutral adjectives					
	<i>Occipital lobe extrastriate cortex</i>				
Left	Middle occipital gyrus	BA 18	3.50	-20, -96, -4	40
	<i>Frontal lobe</i>				
Right	SMA	BA 6	3.68	14, -6, 56	43
	<i>cerebellum</i>				
Left			4.20	22, -84, -34	90

activity for unpleasant (Pearson's $r = 0.31$, $P > 0.2$) or neutral adjectives (Pearson's $r = 0.33$, $P > 0.2$). An additional analysis, correlating for each subject only the peak voxels in the left amygdala and the left extrastriate cortex, yielded very similar results (pleasant: $r = 0.58$, $P < 0.03$; unpleasant: $r = 0.23$, $P > 0.2$; neutral: $r = 0.10$, $P > 0.2$). Results from the ROI analysis and correlation analysis are presented in Figure 1B.

Memory performance

Incidental memory performance differed depending on the emotional content of the previously read words [$F(2,28) = 13.7$, $P < 0.01$]. *Post hoc* tests revealed that pleasant adjectives were better remembered than unpleasant and neutral adjectives ['Valence': pleasant > neutral: $F(1,14) = 23.6$, $P < 0.001$; pleasant > unpleasant: $F(1,14) = 12.9$, $P < 0.005$; Figure 2].

DISCUSSION

The present fMRI study delineated brain structures active during silent reading of arousing pleasant and unpleasant in contrast to neutral adjectives. Beyond identifying the general brain structures more active during reading of emotional

adjectives than during neutral ones, the present study was particularly interested in three questions: first, does amygdala activation occur during spontaneous processing of highly symbolic emotional stimuli such as words? Second, if so, is it restricted to one emotional valence, or does it occur in response to arousing verbal stimuli regardless of their valence? Third, can we find evidence for a functional relationship between activity in the amygdala and extrastriate visual areas? The behavioural consequences of selective processing of emotional and neutral words during reading were assessed in a free recall test after scanning.

Overall, modulation of brain activity by the words' emotional content was identified in the visual cortex and comprised extrastriate cortex regions in the left middle and inferior occipital and temporal gyrus including the left posterior fusiform gyrus. These regions form part of the ventral visual processing stream responsible for the recognition of objects (Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994), letters and words (Petersen *et al.*, 1990; Posner and Abdullaev, 1999; Cohen *et al.*, 2002; Gaillard *et al.*, 2006).

Moreover, an enhancement of limbic-system activity, specifically in the left amygdala and left peri-amygdaloid regions, was observed during reading of emotional,

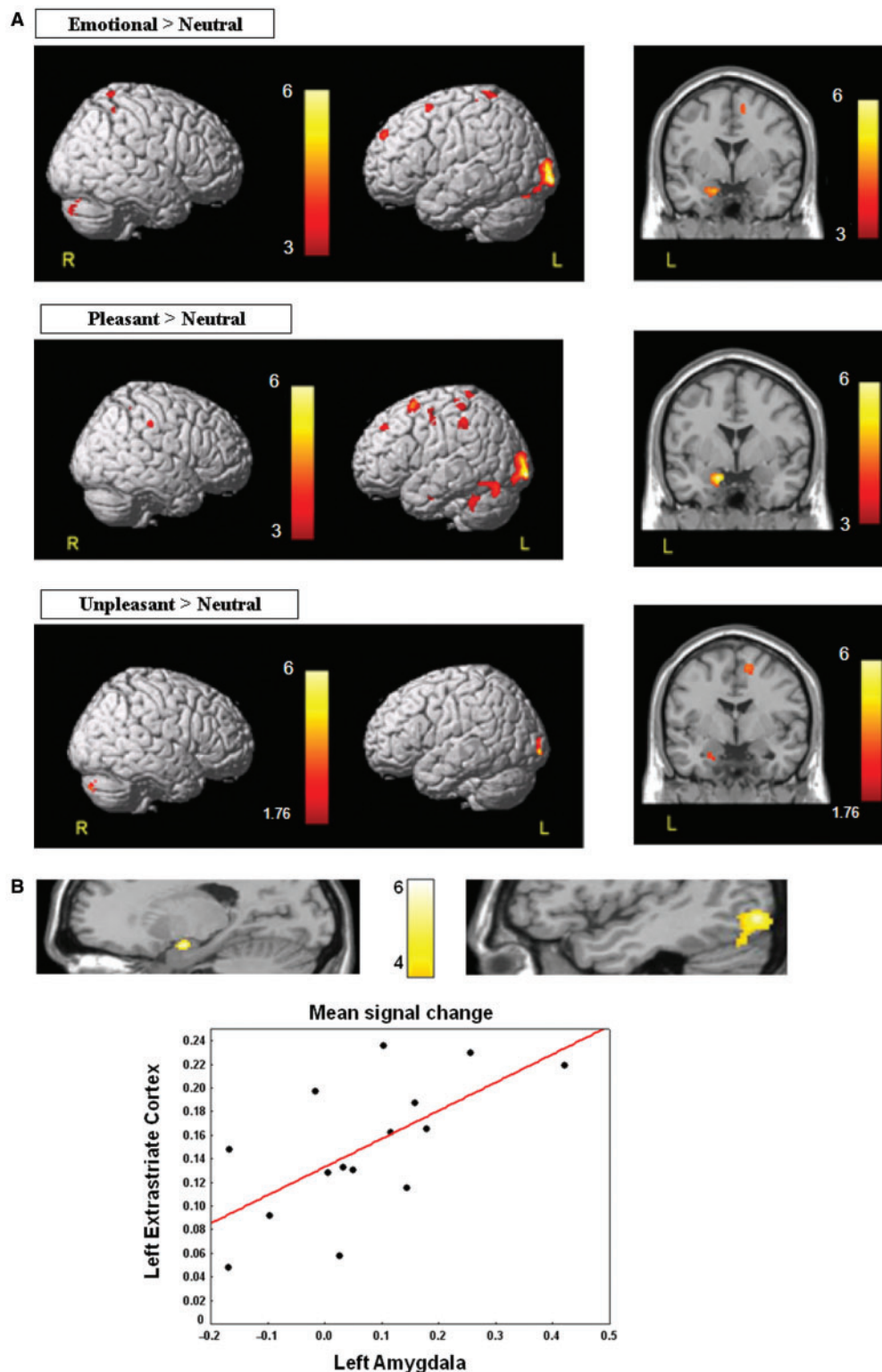


Fig. 1 (A) Shows brain activity elicited by emotional as compared to neutral adjectives during silent reading. Right panels provide an overview on cortical activation and left panels on amygdala activation for contrasts between neutral adjectives and emotional, pleasant or unpleasant adjectives, respectively. For visualization, functional brain activation maps are superimposed on a rendered brain incorporated in the SPM99 software package and on T1-weighted images from MRIcro software (<http://www.sph.sc.edu/comd/rorden/micro.html>). Effects are displayed at a threshold of $P < 0.005$ uncorrected, (T -score > 3) with a spatial extend threshold of 20 contiguous voxels. For contrasts comparing unpleasant against neutral adjectives, activation is displayed at a more lenient threshold of $P = 0.05$ uncorrected (T -score > 1.76) to illustrate the general pattern. (B) Amygdala and extrastriate activity obtained from a ROI analysis of the left amygdala and the left extrastriate cortex. Significant correlation ($r = 0.66$; $P < 0.001$) between peak signal change in the left amygdala and the left extrastriate cortex (peak at $-48 -76 -2$) elicited by pleasant adjectives relative to baseline conditions.

Table 4 Comparisons of overall brain activity obtained during silent reading of pleasant, unpleasant and neutral adjectives. This table displays the brain structures that were more active during reading of pleasant compared to unpleasant adjectives

Hemisphere	Brain region	Brodman area (BA)	T-value	Coordinates <i>x, y, z</i> MNI	Cluster
Pleasant adjectives > unpleasant adjectives					
<i>Temporo-occipital lobe extrastriate cortex</i>					
Left	Inferior occipital gyrus	BA 19	4.37	−46, −74, −6	73
Right	Middle temporal gyrus	BA 37	3.67	54, −60, 16	50
	Superior temporal gyrus anterior temporal pole	BA 21/28/38	5.21	64, −2, −10	32
			3.54	26, 12, −24	42
<i>Limbic system</i>					
Left	Amygdala/anterior parahippocampus		3.77	−16, 2, −24	38
<i>Parietal lobe</i>					
Left and right	Superior parietal gyrus, postcentral, supramarginal	BA 4/40	3.90	−38, −10, 36	69
			4.10	−54, −10, 48	137
			4.71	50, −26, 40	135
Left	Inferior parietal gyrus, precuneus	BA 5	3.82	−10, −52, 60	59

Tables 5 T-values, MNI coordinates and corresponding Brodman areas (BA) of highest activated voxels within two pre-defined brain ROIs, the extended extra-striate cortex and amygdala, respectively. Upper panel: ROI sub-regions showing stronger activation during reading of emotional (pleasant and unpleasant) versus neutral adjectives. Middle panel: ROI sub-regions showing stronger activation during reading of pleasant versus neutral adjectives. Bottom panel: ROI sub-regions showing stronger activation during reading of pleasant versus unpleasant adjectives.

Hemisphere	Brain regions of interest	Brodman area (BA)	T-value	Coordinates <i>x, y, z</i> MNI	Cluster
Emotional adjectives > neutral adjectives					
Extra-striate ROI					
Left	Occipital lobe				
	Extra-striate cortex	BA 18/19	6.15	−18 −98 −2	198**
	Inferior temporal lobe				
Left	Inferior temporal gyrus	BA 20	3.20	−38 −10 −28	3
	Fusiform gyrus	BA 20	3.13	−38 −12 −26	8
	Amygdalar ROI				
Left	Amygdala		4.14	−20 −2 −24	25**
Pleasant adjectives > neutral adjectives					
Extra-striate ROI					
Occipital lobe					
Left	Extra-striate cortex	BA18/19	5.25	−20 −98 −4	311**
	Inferior temporal lobe				
Left	Inferior temporal gyrus	BA 20	4.19	−36 −8 −26	18
	Fusiform gyrus	BA 19	3.77	−42 −68 −16	43*
	Amygdalar ROI				
Left	Amygdala		4.77	−20 −2 −24	20**
Pleasant adjectives > unpleasant adjectives					
Extra-striate ROI					
Occipital lobe					
Left	Extra-striate cortex	BA 19	4.37	−46 −74 −6	73**
	Amygdalar ROI				
Left	Amygdala		3.25	−18 2 −22	6*

^aROI-effects characterized by a significant increase (after small volume correction ~ SVC) during reading emotional adjectives compared to reading neutral adjectives.

^bComparison of reading pleasant with reading neutral adjectives. ^cComparison of reading pleasant with reading unpleasant adjectives. Asterixes (** and *) indicate that effects are significant at cluster level corresponding to ** $P < 0.005$ and * $P < 0.05$ corrected for multiple comparison within small volumes (SVC) in each of the two ROIs. Because the extra-striate ROI comprised several different anatomical structures, the locations of clusters of significant activity within this ROI are further detailed in the tables. SVC was applied across all voxels of the ROIs, separately for the amygdala and the extra-striate ROI. ROI analysis did not reveal any supra-threshold activity for the contrasts unpleasant > neutral, unpleasant > pleasant, neutral > pleasant or neutral > unpleasant.

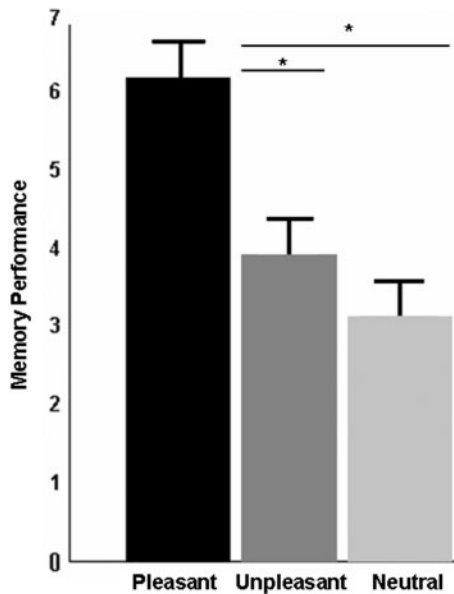


Fig. 2 Memory advantage for pleasant adjectives during the surprise free recall test. Bars (\pm s.e.) represent numbers of correctly remembered pleasant, unpleasant and neutral adjectives. Significant differences are marked with asterisks.

particularly pleasant, adjectives. Peak activation in the peri-amygdaloid cortex could be assigned to the anterior parahippocampal gyrus (anterior PHG), a region which has recently been related to enhanced memory encoding of emotional salient visual stimuli (Dolcos *et al.*, 2004). It is generally agreed that amygdala activation boosts memory encoding for emotionally arousing stimuli by adrenergic activation of the parahippocampus and hippocampus (McGaugh, 2004; for reviews see Hamann, 2001 or LaBar, 2007). Therefore, enhanced amygdala activity during stimulus perception should result in better subsequent recall. More efficient memory encoding of pleasant adjectives is supported by present behavioural data: pleasant adjectives were spontaneously better remembered than unpleasant and neutral adjectives. In the literature, the pattern of memory modulation by emotion varies: studies report superior recall of unpleasant (Ochsner, 2000) or emotionally arousing pleasant and unpleasant stimuli (e.g. Bradley *et al.*, 1992; Hamann *et al.*, 1999; Dolcos *et al.*, 2005). Gruhn *et al.* (2005) report different recall patterns for pleasant and unpleasant emotional words, depending on whether unpleasant and pleasant stimuli are presented together in the same list or in separate lists at study. Yet other studies report better recall for pleasant than unpleasant or neutral material (Kissler and Hauswald, 2008; Koenig and Mecklinger, 2008), especially in designs that, like in the present study, use incidental encoding conditions (Kiefer *et al.*, 2007; Herbert *et al.*, 2008). This thesis is corroborated by a series of studies specifically addressing the role of depth of processing at encoding for recall of emotional words (Ferré, 2003). Ferré's studies suggest that, at least in memory for single words, incidental encoding conditions drive a memory

advantage for pleasant items (see Ferré, 2003 for a review). As discussed in more detail below, spontaneous processing of emotional words in a silent reading task, especially when it entails amygdala activation, is likely to contribute to differential subsequent memory for pleasant, unpleasant and neutral stimuli.

Silent reading of emotional adjectives also increased activity in a number of other brain regions such as the bilateral parietal cortex, premotor and SMAs as well as in right anterior, superior (BA 38/28) and middle temporal (BA 21) brain regions. Frontal activation might signal action preparation in response to behaviourally challenging words. This has been reported both with regard to action words (Grafton *et al.*, 1997; Hauk *et al.*, 2004) and words with emotional connotation (Isenberg *et al.*, 1999). According to prior studies of emotional processing, bilateral parietal and right temporal lobe activity may reflect a more detailed attentive and integrative conceptual processing of emotional visual stimuli (e.g. Lane *et al.*, 1997, 1999; Canli *et al.*, 2004). Again, particularly the parietal and temporal lobe structures were more strongly activated during reading of pleasant adjectives compared to neutral or unpleasant adjectives. However, in the absence of a clear a priori prediction, activation of these brain regions should be interpreted with caution.

In the visual cortex and the amygdala, which were the focus of the present study, the BOLD signal was increased during reading of adjectives with emotional, particularly pleasant content. These findings demonstrate, apparently for the first time, enhanced activation of the human amygdala during reading of emotional, particularly pleasant, words. Both visual cortex and amygdala activity were predominantly left-lateralized. This is in agreement with a stronger contribution of the language-dominant left hemisphere (Crosson *et al.*, 1999, 2002) and the left amygdala in emotional word processing (Markowitsch, 1998; Phelps *et al.*, 2001) and in line with neuroanatomical findings on ipsilateral connections between the amygdalae and visual cortex (Amaral *et al.*, 2003).

Indeed, we also found evidence for a functional interplay between the left amygdala and left extrastriate regions during reading of pleasant adjectives. 'Re-entrant processing', according to which the amygdala amplifies perception by means of reciprocal feedback connections to the visual cortex has been suggested as a plausible explanation for findings of such bidirectional relationships between amygdala and extrastriate cortex activation during processing of emotional pictures (Bradley *et al.*, 2003; Sabatinelli *et al.*, 2005), fearful faces (Morris, *et al.*, 1998, 1999; Pessoa *et al.*, 2002) and unpleasant words (Tabert *et al.*, 2001). The present correlation between amygdala and extrastriate activity is well in line with this thesis. These results extend findings of a functional relationship between the magnitude of amygdala and extrastriate cortex activation in the processing of emotionally salient unpleasant words (Tabert *et al.*, 2001) to the processing of pleasant words.

Taken together, present findings indicate that, during silent reading of adjectives varying in emotional content, pleasant words in particular take advantage of a primarily left amygdala-mediated enhanced perceptual processing. They may additionally draw on right temporal lobe structures and recruit bilateral parietal attention networks. Behaviourally, pleasant words enjoy a memory advantage when recalled after scanning.

Studies have shown that both task demands and emotional arousal critically determine the amount of processing of emotional stimuli in the visual cortex (Lane *et al.*, 1999; Bradley *et al.*, 2003) and the degree to which the amygdala responds to pleasant and/or unpleasant stimuli (Phan *et al.*, 2002, 2003, 2004; Sabatinelli *et al.*, 2005). Differences in emotional arousal between pleasant and unpleasant stimuli, but also the task at hand, can affect neural responses to pleasant and unpleasant stimuli (Zald, 2003; Kuchinke *et al.*, 2005).

In the present study, pleasant and unpleasant adjectives were matched for emotional arousal, they did not differ with respect to many linguistic visual properties, and interference from cognitive processes imposed by additional attention or categorization tasks can be excluded during silent reading. The difference in word frequency between arousing and neutral words is not likely to have accounted for the present results: if indeed less frequent words had led to larger brain activations, this should have been particularly true for unpleasant words, which had somewhat lower frequency counts than pleasant words, i.e. more brain activity would have been expected during processing of unpleasant words. But this is not observed. Moreover, activity evoked by pleasant and unpleasant words should not have differed and neither superior recall for pleasant words nor a specific correlation between amygdala and extrastriate activity is a likely consequence of differences in word frequency. Neutral words had somewhat higher and unpleasant words somewhat lower frequency counts than pleasant words. Also, a recent study explicitly addressing the effects of word emotionality and word frequency in a lexical decision task (Nakic *et al.*, 2006) found no interaction between the main effects of word frequency and emotion.

These findings argue against both the view that the amygdala selectively responds to unpleasant material (e.g. Öhman and Mineka, 2001) and the view that stimulus arousal will determine the magnitude of the amygdala response (Davis and Whalen, 2001; Sabatinelli *et al.*, 2005; Lewis *et al.*, 2007). To what may this processing advantage for pleasant adjectives be attributable? Visibility and attention can bias amygdala responses to either pleasant or unpleasant stimuli: Williams and colleagues (2005) report larger amygdala responses to happy faces when faces were fully attended, whereas responses to fearful faces were enhanced when subjects' attention was diverted away from the faces to competing stimuli. In the present, study there was no competition for spatial attention between stimuli, which may have biased neural responses in favour of pleasant contents. Also, an

exposure time of 1 s per stimulus does not impose severe temporal processing constraints under which processing may be biased towards unpleasant material.

Canli *et al.* (2002) found amygdala responses to happy faces to increase with higher extraversion scores, suggesting that personality factors may play a role in modulating the relative magnitude of amygdala activation to aversive or pleasant stimuli. Although, we did not measure extraversion scores, in healthy people stronger cerebral responses to pleasant relative to unpleasant and neutral stimuli may arise from a general mood-congruent processing bias. Mood-congruent processing biases can account for differential responsiveness to pleasant and unpleasant stimuli and affect perception, attention, memory and overt behaviour (Deldin *et al.*, 2001; Ferré, 2003; Fredrickson and Branigan, 2005, for review; Kuchinke *et al.*, 2005; Kiefer *et al.*, 2007). While increased amygdala activation in response to pleasant stimuli may be larger when positive mood is induced experimentally (Schneider *et al.*, 1997) or in more extraverted subjects (Canli *et al.*, 2002), similar mood-congruent 'preferences' for pleasant material may operate in the absence of any experimenter-induced task, mildly positive mood being the modal experience in healthy people (Diener and Diener, 1996).

Healthy people tend to view positive information as more self-relevant and self-descriptive than negative information (Deldin *et al.*, 2001; Tagami, 2002; Lewis *et al.*, 2007). This may implicitly bias visual processing towards pleasant adjectives, as these words describe positive emotional states or traits that may match more closely participants' ongoing mood, expectations and intentions than adjectives describing negative traits or states. To follow up on this possibility we obtained independent ratings from 22 student subjects (11 males, 11 females) with similar biographic background and age as the participants in the present fMRI study. Subjects rated on 9-point scales, analogous to the SAM, the degree to which the words used in the present study were descriptive of personality traits or states in general and to what extent subjects thought the meaning of these words was relevant for themselves: pleasant and unpleasant adjectives were both rated as more descriptive of personal traits and states than neutral adjectives were. But only the pleasant adjectives were judged as more self-relevant than the unpleasant adjectives [pleasant–unpleasant, $F(1,98) = 73.29$, $P < 0.001$] or the neutral adjectives [pleasant–neutral, $F(1,98) = 14.1$, $P < 0.001$].

Recent results also indicate that normal subjects hold overly optimistic views about themselves and their future, the amygdala being involved in mediating this illusory optimism bias (Sharot *et al.*, 2007). Such mood-dependent or self-concept congruent processing biases in favour of pleasant stimuli may explain why in the present study pleasant adjectives elicited more activity in the amygdala and the visual system than unpleasant or neutral adjectives. In support of the reality of the phenomenon, EEG studies investigating silent reading of and incidental recall for emotional

adjectives have found a pattern similar to that of the present fMRI study (Herbert *et al.*, 2006, 2008; Kissler *et al.*, 2008). In these studies, a larger set of adjectives was used, and they were conducted with different subjects and in a different laboratory. Still, similar to the present study, higher incidental recall for pleasant adjectives as well as a larger late positive event-related potential in response to pleasant adjectives were observed. The late positive potential in the ERP and BOLD responses in the fMRI have recently been found to be correlated in a study investigating fMRI and electrophysiological correlates of affective picture processing in the same group of subjects (Sabatinelli *et al.*, 2007).

Among current emotion theories, appraisal theories (e.g. Scherer, 2001; Sander *et al.*, 2005) can account for such dynamic regulation of central nervous responses to emotional stimuli by postulating that emotional processing depends on a cascade of stimulus-evaluation checks: situational and individual relevance checks are proposed to determine whether stimuli will elicit emotional responses and what kind of response will result. This approach is well able to account for the empirical variability in responses to emotional stimuli which is becoming increasingly evident in the literature. In line with this view, the present results suggest that cerebral responses to pleasant adjectives during reading are enhanced because these stimuli were viewed as more self-relevant than either the unpleasant or the neutral adjectives.

Altogether, the present results indicate a modulatory role of the human amygdala in processing of symbolic emotional concepts during silent reading. This demonstrates that the role of the amygdala goes well beyond that of boosting visual processing for highly aversive unpleasant words (Isenberg *et al.*, 1999; Anderson and Phelps, 2001; Tabert *et al.*, 2001). The fact that pleasant adjectives provoke larger neural responses in the amygdala relative to unpleasant and neutral words is in line with recent theoretical views of the human amygdala as a structure for relevance detection (Sander *et al.*, 2003). According to this view, the human amygdala alerts the organism towards a much broader class of stimuli than suggested by traditional models, including a wide range of symbolic, ontogenetically acquired representations of emotional significance. Moreover, the direction of the response may be biased by current needs, personal goals and individual preferences that converge with participants' ongoing mood, expectations and intentions.

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