

The functional connectivity between amygdala and extrastriate visual cortex activity during emotional picture processing depends on stimulus novelty

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ARTICLE INFO

Article history:

Received 24 August 2010

Accepted 26 November 2010

Available online 2 December 2010

Keywords:

Amygdala

Inferior temporal cortex

Emotional modulation

Repetition

Novelty

Significance

ABSTRACT

Enhanced perceptual processing of emotional stimuli may be accomplished via amygdala-back-projections into the inferior temporal cortex. In the current study, we investigated the influence of stimulus novelty on the covariation between these brain regions during emotional picture processing. Participants viewed repeatedly presented and novel emotional and neutral pictures during fMRI-scanning. The amygdala showed stronger activation to emotional arousing stimuli that decreased rapidly when the same pictures were presented repeatedly. Emotional modulation of the amygdala was reinstated when novel emotional and neutral pictures were presented. Inferior temporal cortex (ITC) showed increased activation during processing of emotional stimuli irrespective of picture repetition. ITC and amygdala activity were highly correlated only during processing of novel emotional pictures. Therefore, we concluded that enhanced perceptual processing of emotional stimuli is triggered by an initial significance detection and corresponding feedback information by the amygdala but is maintained by other mechanisms.

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1. Introduction

Preferential perceptual processing of emotional stimuli is an obligatory brain function that facilitates a fast motor response when necessary and, therefore, ultimately ensures survival. The emotional significance of a visual stimulus modulates its perceptual processing presumably via feedback-projections originating in the amygdala (Lang et al., 1997; Vuilleumier and Driver, 2007). This assumption is supported by neuroimaging studies showing that emotionally significant stimuli evoke enhanced activity in both the amygdala and the extrastriate visual cortex and that the activity in both regions shows a strong covariation (e.g. Morris et al., 1998; Sabatinelli et al., 2005). Furthermore, patients with amygdala lesions fail to show differential responses to emotional compared to neutral faces in their intact extrastriate visual cortex (Vuilleumier and Driver, 2007) indicating that increased activity in these visual cortical areas depends on inputs from the amygdala.

While some researchers claim that the amygdala is a core structure within the fear network – a notion primarily supported by animal experimentation (LeDoux, 1996; Rosen and Schulkin, 1998) – human neuroimaging data suggest that the amygdala is more generally involved in tagging relevant stimuli in the environment (Sabatinelli et al., 2005; Sander et al., 2003; Sergerie et al., 2008;

Whalen and Davis, 2009), rather than being specifically activated by fearful stimuli. Accordingly, not only fearful but also other unpleasant emotional stimuli (Sabatinelli et al., 2005; Stark et al., 2007) as well as pleasant stimuli (Costa et al., 2010; Hamann et al., 1999; Liberzon et al., 2003; Wendt et al., 2008) and various emotional facial expressions (Vuilleumier et al., 2001; Yang et al., 2002) reliably elicit pronounced activity in the human amygdala. Moreover, increased amygdala activation can be observed even when stimulus-significance is induced by instruction (top-down process) as investigated e.g. with a modified Go-NoGo-paradigm (Ousdal et al., 2008).

These data support the notion that the amygdala automatically tags all relevant cues in the environment to modulate the moment-to-moment vigilance level (Davis and Whalen, 2001) and, thus, facilitates efficient behavioral adjustments including enhanced perceptual processing. Hence, the concept of significance tagging as a major function of the amygdala favors a close functional relationship between the amygdala and the higher sensory processing areas in the extrastriate cortex, consisting of a dorsal pathway to the parietal and a ventral stream to the temporal lobe. The ventral pathway includes several cortical areas that respond to shapes and identities of visual objects (Desimone et al., 1984; Logothetis et al., 1995). The inferior temporal cortex (ITC) is particularly involved in the identification of complex objects (Grill-Spector, 2003) and several studies have found greater activation of these secondary visual processing areas when people view emotional compared to neutral scenes and faces (Bradley et al., 2003; Breiter et al., 1996;

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Lane et al., 1999). Supporting the assumption of a close relationship between amygdala and higher sensory processing areas, Morris et al. (1998) demonstrated that amygdala BOLD-responses during processing of emotional facial expressions predicted neural activity in the extrastriate cortex. Moreover, Sabatinelli et al. (2005) found a close relationship between activation of the amygdala and inferior temporal regions during processing of emotionally arousing scenes. Finally, Larson et al. (2009) recently reported amygdala and inferior temporal cortex coupling when using simple V-shaped stimuli to activate the perception of threat. In the same vein, a study using steady-state visual evoked potentials to explore the re-entrant connectivity of visual cortical areas (Keil et al., 2009) provided evidence for a signal flow during viewing of emotional scenes that originates from higher levels of the visual cortex and re-enters lower tiers. Underscoring the functional connectivity of these brain regions, Catani et al. (2003) reported on a major fiber bundle (the inferior longitudinal fasciculus; ILF) that arises from the lateral occipital gyrus and projects laterally to the inferior temporal cortex and medially to the amygdala.

However, these findings suggesting a close covariation of these regions are at odds with results that are obtained when the same stimuli are presented repeatedly. There is convincing evidence that the BOLD-responses in the amygdala during processing of emotional cues decrease rapidly if the stimuli are presented repeatedly (Breiter et al., 1996; Fischer et al., 2003; Wright et al., 2001). In contrast, using EEG to investigate the effects of repeated presentations of the same emotional and neutral pictures, Schupp et al. (2006) found that the emotional modulation of visual cortical areas hardly habituates. Moreover, the late positive potential (LPP), maximal in a 300–600 ms window, although decreasing in magnitude across picture repetition, is still larger for emotional compared to neutral pictures after 30 repetitions of the same stimulus (Codispoti et al., 2007). Thus, it remains unclear if enhanced perceptual processing of emotional stimuli is secondary to significance tagging in the amygdala or might also be modulated by other processes.

In the current study, we therefore investigated the course of BOLD-responses in the amygdala and the inferior temporal cortex during repeated presentations of emotionally arousing and neutral stimuli as well as during viewing of novel stimuli. If the enhanced perceptual processing of emotional stimuli is completely determined by amygdala input, the emotional modulation of the inferior temporal cortex should decrease with stimulus repetition. If, on the other hand, the enhanced perceptual processing does partially rely on other processes than amygdala input (as suggested by the EEG-evidence) we should observe a sustained emotional modulation of ITC activity. We therefore expected a close correspondence between amygdala and ITC activity only, when emotional stimuli are tagged as significant. Since amygdala shows rapid habituation due to stimulus repetition we would predict that presenting novel emotional (significant) stimuli would reinstall the initially close covariation between amygdala and inferior temporal cortex.

2. Methods

2.1. Participants

Twenty female right-handed students (mean age 24.3 (SD 2.25), range 21–29) of the University of Greifswald participated in the present study. Selection was restricted to female participants in order to reduce variability due to gender specific brain responses to emotional contents (e.g. Sabatinelli et al., 2004). Before participation, all subjects gave written informed consent to the experiment which was approved by the University of Greifswald ethics committee.

2.2. Stimulus materials and design

Overall, 20 grey-scaled emotional (ten pleasant, ten unpleasant) and ten neutral pictures were selected from the International Affective Picture System (IAPS;

Lang et al., 2008) based on their valence ratings.¹ Six pictures (two pleasant, two unpleasant, and two neutral) were presented repeatedly for 12 times each during the repetition phase of the experiment. Pictures were arranged in three blocks, such that each of the six pictures was shown four times in each of the blocks. After this repetition series, 24 novel pictures (eight from each valence category) were presented once.

Pictures were presented for 2 s and separated by a varying inter-trial-interval in which a fixation cross was shown (8–12 s).² We constructed five different presentation orders to ensure that aggregated over all participants, each picture exemplar was presented both during the repetition phase and during the novelty phase. Within each experimental phase, pictures were randomized with the constraint that there were no more than two successive presentations of the same valence category. Participants were randomly assigned to one of the five presentation orders.

2.3. Apparatus and data acquisition

MRI data were collected using a 1.5 Tesla Magnetom Symphony system (Siemens) that was additionally equipped with an 8-channel-headcoil. Field homogeneity was optimized prior to each session by using a shimming-sequence. Then a T1-weighted anatomical volume was recorded (MP-RAGE, 176 sagittal slices, TR 11 ms, TE 5.2 ms, flip angle 15°, matrix 224 × 256, voxel size 1 mm × 1 mm × 1 mm). During picture presentation, 724 volumes with 22 slices each (4 mm thick, 1 mm gap) were acquired in transversal direction parallel to the AC-PC-line using echo-planar images (EPIs; TR 2000 ms, TE 38 ms, flip angle 90°, FoV 192 mm, matrix 64 × 64, voxel size 3 mm × 3 mm × 4 mm).

2.4. Data processing and analysis

MRI data were preprocessed and analyzed using the statistical parametric mapping software (SPM5, Wellcome Department of Imaging Neuroscience, London, UK). Preprocessing included slice time correction, spatial realignment, co-registration, segmentation, normalization into the MNI space, and spatial smoothing (FWHM 8 mm). To correct for low-frequency components, a high-pass filter with a cut off of 128 s was applied. Statistical analyses were performed using the general linear model as implemented in SPM5. For each participant a design matrix was created using a canonical hemodynamic response function for each of the three valence categories and for each of the experimental phases (three repetition blocks, one novelty block) resulting in 12 regressors. The six movement parameters estimated during the realignment procedure were introduced as covariates into the model to control for variance caused by head displacements. The resulting beta images were then taken to the second level full factorial model.

Parameter estimates for each valence category within each experimental phase were averaged and extracted across voxels within the amygdala [6 mm sphere centered at $x = \pm 24, y = 0, z = -18$ (MNI space)] and the inferior temporal cortex [peak activation was located in the inferior temporal gyrus; 6 mm sphere centered at $x = \pm 54, y = -66, z = -6$ (MNI space)].³ To test for repetition and novelty effects, the extracted parameter estimates were entered in two different repeated measures analyses: (1) to test for repetition effects with the within-factors Repetition (block 1 vs. block 2 vs. block 3) and Valence (pleasant vs. unpleasant vs. neutral pictures) and (2) to test for novelty effects with the within-factors Novelty (repetition block 3 vs. novelty block) and Valence (pleasant vs. unpleasant vs. neutral pictures). The covariation between parameter estimates for emotional pictures extracted from amygdala and ITC clusters was tested for the four experimental phases described above using

¹ The IAPS identification numbers are as follows. Pleasant: 1440, 1460, 1710, 1722, 1750 (puppies); 4659, 4664, 4670, 4687, 4690 (erotica). Neutral: 1333, 1450, 1602, 1670, 1910 (neutral animals); 2221, 2320, 2383, 2393, 2440 (neutral humans). Unpleasant: 1050, 1120, 1300, 1525, 1930 (animal attack), 6230, 6250, 6315, 6350, 6540 (human attack). Pictures were selected to ensure a balanced proportion of human and non-human scenes as previous research revealed a processing advantage for social scenes in the amygdala (Scharpf et al., 2010).

² The current reduction of the picture presentation time from 6 to 2 s meant a divergence from the original design of Bradley et al. (1993). Therefore, we conducted a pilot study in which we applied the same paradigm and measured startle responses in two groups: one, in which pictures were presented for 6 s and one in which pictures were presented for 2 s. We replicated the findings of Bradley et al. (1993), i.e. we found a general habituation of the startle response but a preservation of the modulation as a function of the affective foreground stimulation. We found no difference in startle response habituation or modulation due to the duration of picture presentation. Thus, we chose the 2 s presentation time in order to reduce the total duration of measurements in the MRI environment.

³ We were mainly interested in the alteration of the emotional modulation of amygdala and inferior temporal cortex activity over the course of repeated picture presentation and novel presentation together with the alteration of the connectivity of the brain regions. Therefore, we chose the otherwise unfavorable approach to determine the center of the spheres by the highest activated clusters of both hemispheres during the contrast emotional vs. neutral picture contents during the first repetition block.

Table 1
Repetition block 1: brain activity elicited by emotional compared to neutral stimuli.

Region	Side	MNI-coordinates			t-Score*
		x	y	z	
Amygdala	L	-24	-3	-24	3.57
	R	24	0	-12	5.29
Inferior temporal cortex	L	-54	-60	-6	5.14
	R	51	-75	-6	4.66

* Region-of-interest-analyses, $p_{FDR} < .05$.

Pearson correlations. Unless otherwise noted, all statistical tests with extracted parameter estimates used the .05 level of significance and were accomplished with SPSS 17.0 (SPSS for Windows, SPSS Inc.). Greenhouse–Geisser adjustments of degrees of freedom were used to control for all effects involving repeated measures factors. Nominal degrees of freedom are reported along with epsilon values.

3. Results

As expected, the emotional pictures elicited significantly stronger activations than neutral pictures bilaterally in the amygdala and in the inferior temporal cortex (ITC) during the first repetition block (see Table 1 and Fig. 1A). The peak activation of the ITC was located within the inferior temporal gyrus. The respective coordinates were used for region-of-interest-analyses as described in the method section. Amygdala and ITC BOLD-responses to repeatedly presented and novel emotional and neutral stimuli are displayed in Fig. 1B and C.

3.1. Amygdala and ITC responses to repeatedly presented and novel emotional stimuli

Activity in the amygdala and the inferior temporal cortex rapidly declined across the repetition phase for all picture foregrounds (amygdala: $F(2,38) = 6.47, p < .01$, partial $\eta^2 = .25$; ITC: $F(2,38) = 5.16, p < .05$, partial $\eta^2 = .21$). Increased amygdala activity to emotional relative to neutral materials persisted as a trend during repetition block two ($F(2,38) = 2.60, p = .09$, partial $\eta^2 = .12$), but was no longer maintained during block 3 ($F(2,38) = 1.37$, n.s.). In contrast, increased activation of the ITC to emotional pictures relative to neutral contents was maintained throughout the entire phase of repetition (Valence: $F_s(2,38) = 9.93, p < .01$, partial $\eta^2 = .34$, 12.03, $p < .001$, partial $\eta^2 = .39$, 4.44, $p < .05$, partial $\eta^2 = .19$ for blocks 1, 2, and 3, respectively).

Viewing of novel pictures elicited significantly stronger activation of the amygdala compared to repeatedly seen old pictures ($F(1,19) = 4.55, p < .05$, partial $\eta^2 = .19$). The novelty effect was pronounced for unpleasant stimuli ($F(1,19) = 6.31, p < .05$, partial $\eta^2 = .25$) and marginal significant for pleasant stimuli ($F(1,19) = 3.21, p = .09$, partial $\eta^2 = .15$). No significant increase was found for neutral novel stimuli ($F < 1$). This effect was substantiated by a significant Novelty \times Valence interaction, $F(1,19) = 6.05, p < .05$, partial $\eta^2 = .24$ (quadratic trend). Furthermore, viewing of novel emotional pictures elicited significantly stronger amygdala activity than viewing novel neutral pictures ($F(2,38) = 5.32, p < .05$, partial $\eta^2 = .22$); see Fig. 1B.

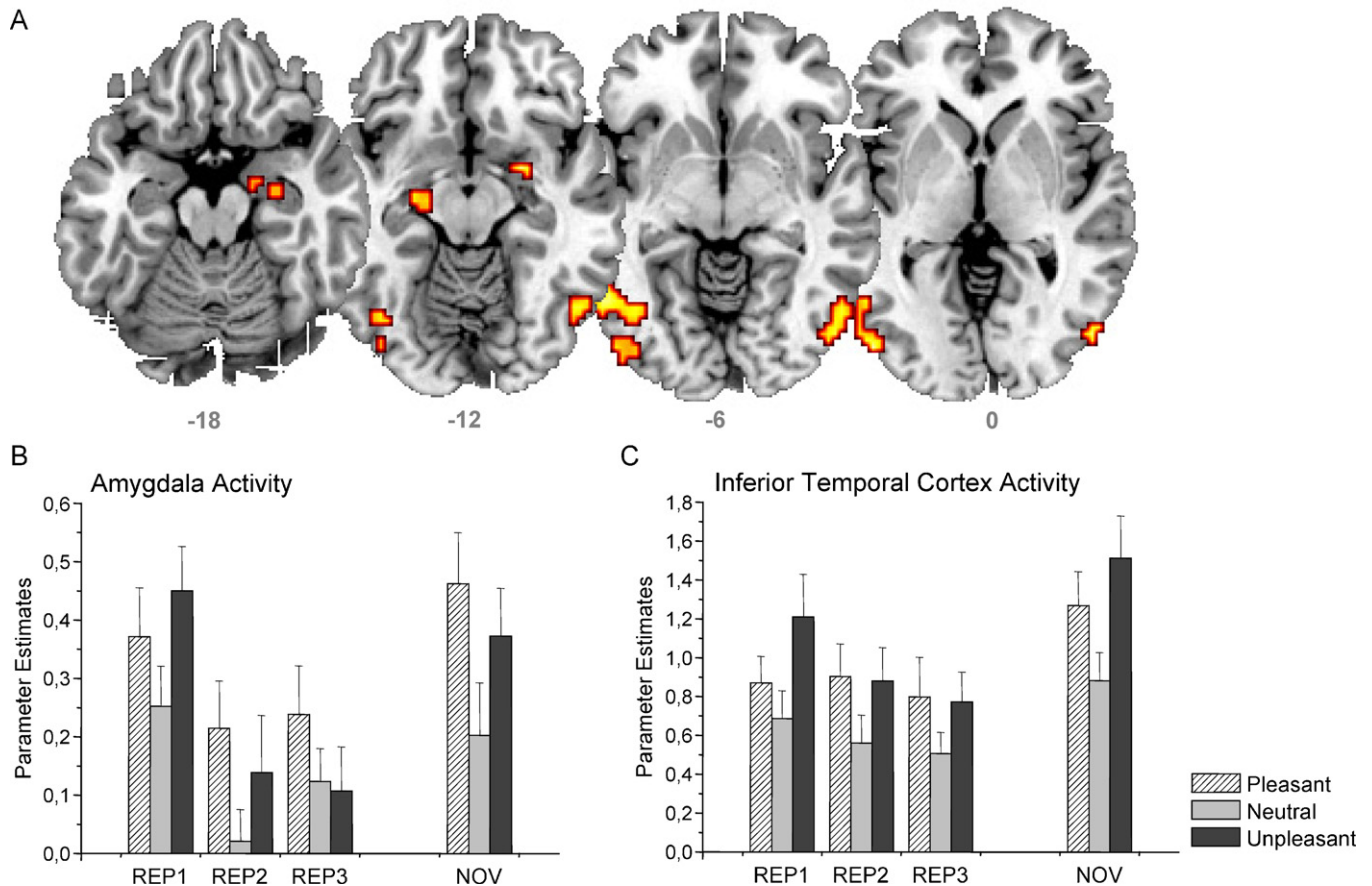


Fig. 1. (A) Whole-brain activity during processing of emotional compared to neutral visual stimuli during the first repetition block. The activation map was thresholded at $p_{uncorr.} < .001$ (for visualization purposes only) and $k = 5$ and projected on Collins’s reference brain as provided by MRIcro. The numbers under each slice indicate axial location (MNI-space). (B) Amygdala activity (parameter estimates extracted at $\pm 24 0 -18$ with a 6 mm sphere) and (C) inferior temporal cortex activity (parameter estimates extracted at $\pm 54 -66 -6$ with a 6 mm sphere) during viewing of repeatedly presented and novel emotional and neutral pictures; REP = repetition phase, NOV = novelty phase.

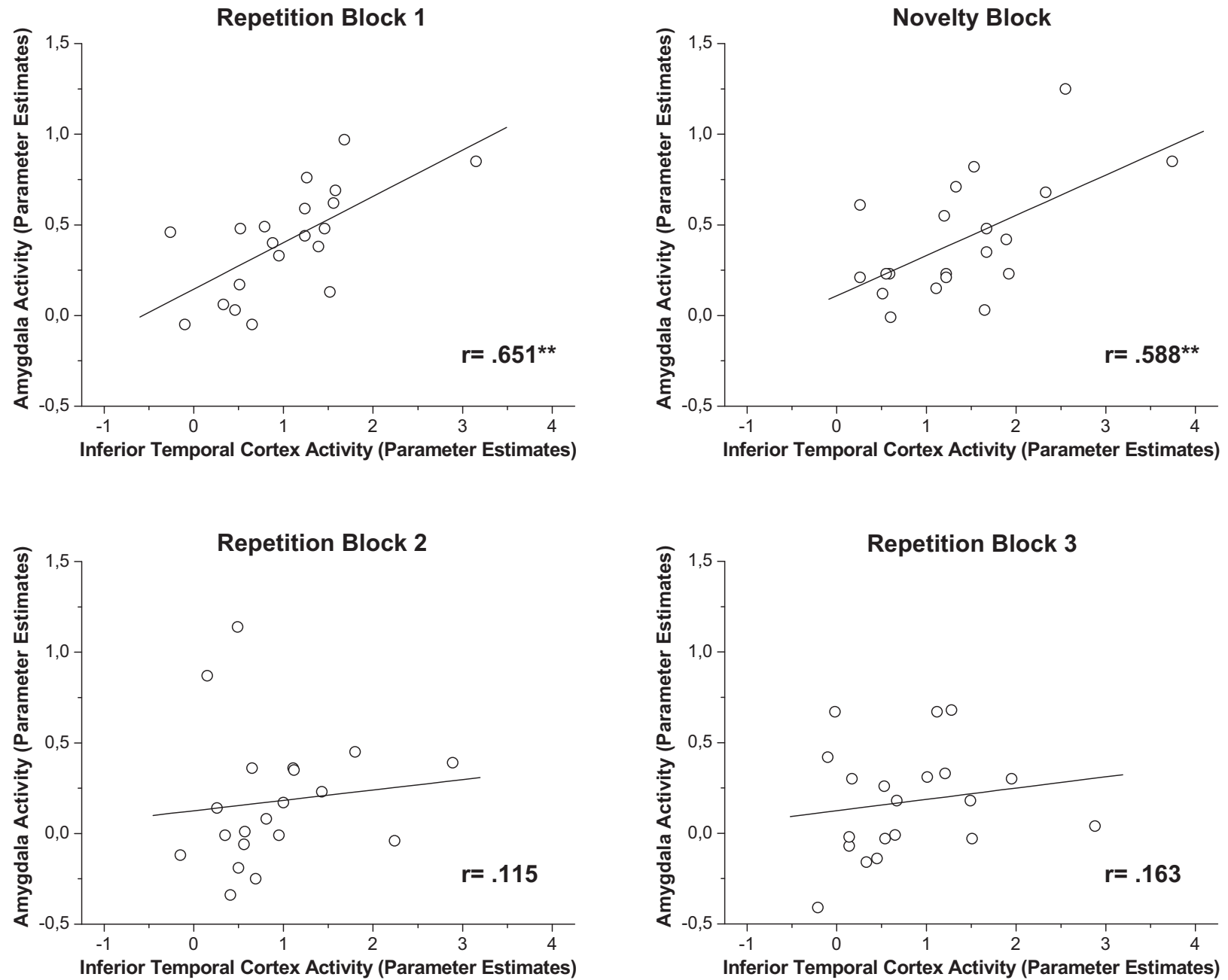


Fig. 2. Correlations between the extracted parameter estimates from the amygdala and the inferior temporal cortex during viewing of emotional pictures during repetition block 1 and during the presentation of novel emotional pictures (upper panel) as well as during repetition blocks 2 and 3 (lower panel); $**p < .001$.

Novel pictures also elicited significantly stronger inferior temporal cortex activity than repeatedly seen pictures during the third (last) repetition block ($F(1,19)=44.57, p<.001, \text{partial } \eta^2=.70$). Again this novelty effect was stronger for emotional compared to neutral pictures supported by a significant Novelty \times Valence interaction ($F(1,19)=4.83, p<.05, \text{partial } \eta^2=.20$). ITC activity increased significantly during viewing of both novel unpleasant ($F(1,19)=28.98, p<.001, \text{partial } \eta^2=.60$) and pleasant stimuli ($F(1,19)=29.03, p<.001, \text{partial } \eta^2=.60$). In contrast to the amygdala, there was also a significant increase in ITC activity for neutral stimuli ($F(1,19)=19.78, p<.001, \text{partial } \eta^2=.51$) suggesting that the novelty effect in the ITC was stronger than in the amygdala. Paralleling the amygdala findings viewing of novel emotional pictures evoked far more pronounced ITC activity than processing of novel neutral stimuli ($F(2,38)=17.56, p<.001, \text{partial } \eta^2=.48$); see Fig. 1C.

Post-hoc *t*-tests revealed that amygdala activity elicited by pleasant and unpleasant stimuli differed in none of the experimental phases. In contrast, viewing unpleasant stimuli elicited significantly more ITC activity than viewing pleasant pictures during repetition block 1 ($t(19)=2.35, p<.05$) as well as during the novelty block ($t(19)=2.47, p<.05$).

3.2. Correlation analyses

During processing of emotional pictures, amygdala and ITC activity correlated significantly during the first repetition block ($r_{\text{Pearson}}=.651, p<.01$) and during presentation of novel emotional pictures ($r_{\text{Pearson}}=.588, p<.01$). In contrast, no significant correlations between amygdala and ITC activity were observed for the emotional pictures presented during the second and the third block of the repetition phase (see Fig. 2).

4. Discussion

The current study investigated the influence of stimulus repetition and novelty on the association between amygdala and inferior temporal cortex activity during emotional picture processing. As expected, both the amygdala and the ITC initially showed increased responses to emotional compared to neutral picture contents. Replicating previous findings, the emotional modulation of amygdala activity faded with stimulus repetition (e.g. Breiter et al., 1996; Phan et al., 2003), whereas the emotional modulation of the ITC activity remained unchanged. Amygdala and ITC activity elicited by emotional stimuli closely covaried during the first trials of stimulus repetition as well as during the presentation of novel pictures but not during later trials of stimulus repetition.

4.1. Amygdala and significance detection

In line with previous findings (e.g. Sabatinelli et al., 2005; Wendt et al., 2008), emotional pictures elicited significantly stronger activation in the amygdala than neutral pictures during the first trials of stimulus repetition. When, however, the same pictures were presented repeatedly, we found a fast habituation of the emotional modulation of amygdala activity. These findings seem to be at odds with the finding of continuous potentiation of the startle reflex to unpleasant pictures throughout a habituation series (Bradley et al., 1993; replicated in our pilot study), since animal data consistently show that the potentiation of the startle reflex during processing of fear cues is mediated by the central nucleus of the amygdala (see Davis, 2000). On the other hand, one has to keep in mind that the spatial resolution of the current neuroimaging data does not allow to differentiate between the different subnuclei of the amygdala. Thus, the habituation of the emotional modulation of

the amygdala activation might be a result of decreasing activity in the larger basolateral nucleus which is the input region of the amygdaloid complex. Supporting this assumption, the presumed location of the basolateral nucleus corresponds with the sphere chosen for the current analyses (cf. Whalen et al., 2001). Therefore, the lack of emotional modulation of amygdala activity after stimulus repetition could be interpreted as a decrease in significance detection (which decreases with the diminishing novelty of the cue) rather than as a decrease in response mobilization which would be reflected by activity of the central nucleus of the amygdala and – subsequently – in the startle response. Whereas significance detection is a brain function that comes in need as soon as a situation changes but not when the situation remains the same, response mobilization once initiated may be maintained as long as the relevant stimulus is around. Correspondingly, certain well known stimuli have to trigger a fast response if the environment changes; say if, for example, the glass of the terrarium suddenly vanishes and sets free the poisonous snake.

In accordance with the assumption that BOLD-activity of the amygdala mainly reflects significance detection, the presentation of emotional novel stimuli resulted in significantly stronger activations in the amygdala than repeatedly shown stimuli. While neutral novel pictures also evoked increased activation in the inferior temporal cortex (albeit less pronounced than emotionally significant stimuli), amygdala activation only significantly increased during processing of novel emotional stimuli. Thus, in contrast to previous reports (Dubois et al., 1999; Schwartz et al., 2003; Wright et al., 2003), we did not find an increase of amygdala activity during viewing of neutral pictures. In contrast to these studies, we, however, did not use neutral faces as visual stimuli but rather neutral animals and pictures from people at work. Such stimuli might be less significant than faces directing their gaze towards the observer, even if the facial expression is neutral. Assuming that emotional relevance and novelty both contribute to the significance of a stimulus, the amygdala responses during processing of repeatedly presented and novel emotional stimuli strengthen the notion of amygdala BOLD-responses as reflecting the process of significance detection.

4.2. Amygdala – extrastriate visual cortex coupling during significant picture processing

The observed covariation between amygdala and ITC activity during processing of emotional stimuli corresponds with previous functional neuroimaging findings (Morris et al., 1998; Sabatinelli et al., 2005; Larson et al., 2009). Moreover, these data are consistent with reports of a direct anatomical path between the amygdala and the inferior temporal cortex as found in non-human primates (Amaral et al., 1992) as well as in diffusion tensor imaging data in humans: Catani et al. (2003) reported on a major fiber bundle (the inferior longitudinal fasciculus; ILF) that arises in extrastriate visual association areas and projects to lateral and medial anterior temporal regions. While stating that the function of this pathway is still unclear, the authors suggested that it plays a role not only in the fast transfer of visual information to the anterior temporal regions but also in modulatory back-projections from the amygdala to visual cortex areas. Consistent with this hypothesis, it was reported that damage to the ILF impairs the recognition of emotional facial expressions (Philippi et al., 2009) a function to which encoding in the amygdala appears to be critical (Adolphs and Spezio, 2006). In the context of these findings, the observed close covariation between amygdala and extrastriate visual cortex areas during processing of novel emotional stimuli suggests a functional connectivity of these brain areas that may be mediated by re-entrant processing from the amygdala into inferior temporal cortical areas.

4.3. Sustained emotional modulation of inferior temporal cortex activity

Different from the amygdala, the inferior temporal cortex hardly showed habituation of modulation by emotional and neutral pictures.⁴ Thus, even without activating input from the amygdala (that is after the emotional modulation of the amygdala habituated), the inferior temporal cortex still showed increased activity in response to emotional compared to neutral pictures. These results correspond with findings from Codispoti and coworkers demonstrating that the LPP hardly shows habituation effects when pictures are presented repeatedly (Codispoti et al., 2006, 2007). According to Codispoti et al. (2007) such sustained emotional modulation of the LPP seems to reflect resource allocation due to the different motivational relevance of affective and neutral stimuli. Interestingly, the amplitude of the late posterior potential (LPP) during viewing emotionally arousing pictures was found to be significantly correlated with visual cortical BOLD activity in the ITC (Sabatinelli et al., 2007), supporting the view that allocation of attentional resources is at least in part independent of back-projections from the amygdala.

Possible explanations for the amygdala independent emotional modulation of ITC activation might be that (1) emotional and neutral stimuli contain different feature compositions (e.g. complexity) of the stimulus categories, (2) modulating input from brain regions other than the amygdala, or (3) that amygdala input is only necessary initially to trigger differential processing in the ITC.

- (1) The inferior temporal cortex (ITC) encompasses the neural representation of both complex object components and semantic categories (Tanaka, 1996). Thus, one could speculate that emotional natural scenes may, on average, encompass more complex physical and/or semantic properties than neutral scenes. There is a recent discussion in the literature that the increased early negativity evoked by emotional pictures over the occipital cortex, a component labeled as 'early posterior negativity' is more sensitive to feature composition (i.e. the complexity) of the stimulus material than to differences in valence (Bradley et al., 2007). That is, heightened stimulus complexity itself may also contribute to the enhanced ITC activity observed in the current experiment. As a caveat, post-hoc complexity ratings of the stimulus material used in the present study do not indicate a higher complexity of the emotional pictures.
- (2) Alternatively, the differential ITC processing could be triggered by other brain regions that encode stimulus significance and generate a map that topographically represents stimulus salience. As reviewed by Itti and Koch (2001), there is evidence for such a saliency map in different brain regions, for example in the pulvinar, the superior colliculus, the frontal eye fields or the posterior parietal cortex. Post-hoc analyses of these brain regions, however, did not reveal any emotional modulation of the brain activity in these areas.
- (3) Finally, it is possible that enhanced perceptual processing actually depends on an initial significance labeling provided by the amygdala. If, however, the same stimulus features are presented again, neurons within the ITC that are primed with a certain feature representation by previous experiences might

ensure a prolonged enhanced perceptual processing that would no longer depend on amygdala input. Therefore, future research should address the question if an initial detection of significance as provided by the amygdala is crucial for enhanced perceptual processing of such significant stimuli in the extrastriate visual cortex (as would be suggested by the lesion studies on emotional facial expression conducted by Vuilleumier and Driver, 2007) which is then maintained even when the initial activation of the amygdala is already turned off.

5. Conclusions

Taken together, the present data provide further evidence that the amygdala and the inferior temporal cortex are functionally connected during processing of emotional stimuli. The decrease of amygdala discrimination between emotional (pleasant and unpleasant) and neutral stimuli with repetition supports the assumption that the amygdala serves as a first-stage significance detector that enhances cortical processing of significant stimuli. Once, stimulus significance is detected and further processing initiated, amygdala responses towards that same stimulus decline whereas the cortical discrimination between significant and insignificant stimuli is preserved. Thus, inferior temporal cortex discrimination between emotional and neutral stimuli does not rely on sustained amygdala input. Therefore, the emotional modulation of the ITC seems to be initiated by significance detection and corresponding back-projections by the amygdala but is maintained by other mechanisms.

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⁴ Contrasting emotional vs. neutral pictures during the first repetition block revealed ITC activity that peaked within the inferior temporal gyrus. The emotion-related activity we found is less widespread and located more lateral and posterior than those reported in previous papers (Bradley et al., 2003; Sabatinelli et al., 2005). The more focal activity found in our study might be due to the comparably small number of stimuli included in this contrast.

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