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

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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.

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, Welcome 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

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[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.