Research Report

Effects of spatial frequency and location of fearful faces on human amygdala activity

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ABSTRACT

Facial emotion perception plays a fundamental role in interpersonal social interactions. Images of faces contain visual information at various spatial frequencies. The amygdala has previously been reported to be preferentially responsive to low-spatial frequency (LSF) rather than to high-spatial frequency (HSF) filtered images of faces presented at the center of the visual field. Furthermore, it has been proposed that the amygdala might be especially sensitive to affective stimuli in the periphery. In the present study we investigated the impact of spatial frequency and stimulus eccentricity on face processing in the human amygdala and fusiform gyrus using functional magnetic resonance imaging (fMRI). The spatial frequencies of pictures of fearful faces were filtered to produce images that retained only LSF or HSF information. Facial images were presented either in the left or right visual field at two different eccentricities. In contrast to previous findings, we found that the amygdala responds to LSF and HSF stimuli in a similar manner regardless of the location of the affective stimuli in the visual field. Furthermore, the fusiform gyrus did not show differential responses to spatial frequency filtered images of faces. Our findings argue against the view that LSF information plays a crucial role in the processing of facial expressions in the amygdala and of a higher sensitivity to affective stimuli in the periphery.

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1. Introduction

Faces provide complex visual information at multiple spatial frequencies: Low-spatial frequency (LSF) components reveal global configurational properties sufficient to supply coarse emotional cues due to the relationship between different feature positions and shapes (e.g., eyes, mouth, and nose) (Costen et al., 1996; Schyns & Oliva, 1999; Calder et al., 2000). High-spatial frequency (HSF) components convey fine-grained features important for precise recognition of identity and for more detailed analysis of facial traits (e.g., age, expression-related wrinkles) (Liu et al., 2000; Hayes et al., 1986; Fiorentini

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et al., 1983; Norman & Ehrlich, 1987). The different spatial frequency information is dissociated by the magnocellular (M) and parvocellular (P) pathway in the visual system (Livingstone & Hubel, 1987; 1988; Bullier, 2001). M-cells have low-spatial and high-temporal resolution, large receptive fields and produce rapid, transient, but coarse visual signals. These cells have a potential advantage in the perception of suddenly appearing stimuli, stimulus location, direction of movement, and stimuli signalling potential danger. In contrast, P-cells are responsive to high-spatial and low-temporal frequency. The neurons of the P-pathway are highly sensitive to wavelength and orientation, and have small receptive fields. P-cells are crucial for sustained, analytic, and detailed processing of shape and colour. Both pathways project to distinct cortical regions, with the M-pathway projecting mostly to dorsal visual areas, including V2 and V5/MT (Shipp, 2001), and connected subcortical regions, such as the superior colliculus and pulvinar (Schiller et al., 1979; Leventhal et al., 1985; Berson, 1988; Berson and Stein, 1995), whereas the P-pathway provides input to ventral visual cortex (Merigan & Maunsell, 1993). These two pathways are not only histologically and physiologically distinct, but also possess different signal time courses in functional magnetic resonance imaging (fMRI) of human primary visual cortex (Liu et al., 2006).

These two distinct spatial frequency processing routes have been subject to a great body of research investigating the role of HSF and LSF information in the visual recognition of faces using psychophysics (Schyns & Oliva, 1999; Fiorentini et al., 1983; Blakemore & Campbell, 1969; Parker & Costen, 1999; Ojanpää & Näsänen, 2003), electroencephalographic (EEG) recording in humans (McCarthy et al., 1999; Goffaux et al., 2003b; Pourtois et al., 2005; Alorda et al., 2007; Holmes et al., 2005; Vlamings et al., 2009) and fMRI (Liu et al., 2006; Winston et al., 2003; Vuilleumier et al., 2003; Eger et al., 2004; Iidaka et al., 2004; Gauthier et al., 2005; Rotshtein et al., 2007).

Behavioral studies found a differential sensitivity to HSF and LSF contents of emotional expression. According to the aforementioned differences between spatial frequency ranges, it seems plausible that a precise judgment of expression should require precise HSF cues, whereas the cruder expressive versus non-expressive judgment would not need such precision. However, the opposite has been shown (Schyns & Oliva, 1999): An expressive versus non-expressive task was biased to HSF, whereas a categorization of the expression itself such as happiness and anger was biased to LSF. Furthermore, LSF contents provide rapid attentional responses to fearful stimuli (Holmes et al., 2005). In contrast, a recent psychophysical study reported that at low-spatial frequencies emotion discrimination is impaired thereby indicating that in order to interpret another person's facial expression (specifically happiness, sadness and fear) HSF information must be present (Goren & Wilson, 2006). It has to be pointed out that different stimuli have been used in these behavioral studies. In the study of Schyns and Oliva (1999) hybrid stimuli, which simultaneously present two faces, each associated with a different spatial scale, have been used, while Goren and Wilson (2006) created synthetic faces of different spatial frequencies. Therefore, it has to be taken into account that using these specific stimuli might limit the reported biases in emotion categorization towards certain

frequency domains as they might not all apply to the normal perception of faces. Additionally, it has been demonstrated that faces containing predominantly LSF compared to HSF information are detected faster (Winston et al., 2003; Vlamings et al., 2009; Coin et al., 1992). However, the studies done to discover which SFs are necessary for face recognition have not produced conclusive results (Ruiz-Soler & Beltran, 2006), since an extensive range of SFs seems to play a role in recognition. It has been proposed that a flexible spatial frequency integration mechanism might account for the various results, which depends on the interaction between the demands of the task and the information in the image (Sergent 1986, 1994; Costen et al., 1996; McSorley & Findlay, 1999).

EEG studies investigating the effect of SF of negative expressions on the amplitude and latency of various early event-related potential (ERP) components related to face processing like P1 (Gomez Gonzales et al., 1994; Heinze et al., 1994; Rossion et al., 1999) and N170 (Jacques & Rossion, 2004, 2006; Henson et al., 2003) showed an increased P1 at occipitotemporal electrodes for LSF fearful relative to neutral facial expressions (Pourtois et al., 2005) and pictures (Alorda et al., 2007). It has further been demonstrated that an early modulation of P1 and N170 by facial expression is primarily driven by LSF (Vlamings et al., 2009).

Recent fMRI studies focused on the processing of different emotional expressions at low and high SF ranges in the amygdala (Vuilleumier et al., 2003), which is well known to be implicated in the processing of emotional stimuli (Sergerie et al., 2008; Zald, 2003; Phan et al., 2002), and fusiform gyrus (Winston et al., 2003; Rotshtein et al., 2007). The amygdala has been proposed to receive inputs from ventral visual cortical pathways (in its lateral nucleus) on the one hand (LeDoux, 1996; Vuilleumier, 2005), but also subcortical inputs from the thalamus via a retinal–collicular–pulvinar pathway (Morris et al., 1999; de Gelder et al., 1999) providing fast signals about threat-related stimuli prior to complete processing in cortex. The superior colliculus and pulvinar receive LSF inputs from magnocellular visual pathways showing increased activity in response to LSF fearful expressions (Vuilleumier et al., 2003). While LSF information is preferentially carried to the amygdala by the magnocellular visual pathway, the HSF information in faces travels via parvocellular inputs into the ventral cortical pathway resulting in a higher sensitivity to LSF stimuli in the amygdala and to HSF stimuli in the fusiform cortex (Vuilleumier et al., 2003). These distinct response properties delineate segregated anatomical routes for facial and emotional processing.

Another fMRI study (Rotshtein et al., 2007) revealed dissociable processing in occipitotemporal cortex, with distinct regions specialized in processing LSF and HSF components from faces. Specifically, HSF faces evoked increased activation in the right inferior occipital gyrus and left inferior temporal gyrus, whereas bilateral middle occipital gyrus responded stronger to LSF information. A common effect of HSF and LSF was observed in the right fusiform gyrus. A connectivity analysis suggested a direct influence of the middle occipital, inferior temporal and inferior occipital gyrus on the fusiform gyrus responses. These findings show that different regions within occipitotemporal cortex extract distinct visual features at different spatial frequencies in faces

and that this information is passed on to the right fusiform gyrus, where these different visual cues may converge.

To sum up, behavioral studies investigating the dependence of recognition and categorization of facial expression on spatial frequency provided diverse results; while the temporal ordering of spatial scale processing in vision is quite clear (lowest spatial frequencies in an image are processed relatively quickly while progressively finer spatial information is processed more slowly). EEG studies found evidence for an early modulation of ERP components related to face processing in favor of LSF information. On a neuronal level, neuroimaging studies demonstrated differential responses in the amygdala according to various spatial frequencies with higher sensitivity to LSF, while the results on the influence of spatial frequency on face selective regions is inconsistent.

Based on the aforementioned fMRI studies and the fact that M-cells are sensitive to peripheral stimuli due to their large receptive fields, it has been proposed that the amygdala might be especially sensitive to affective stimuli in the periphery in order to direct attention to emotionally relevant stimuli, outside the current focus of attention (Palermo & Rhodes, 2007). Indeed, a recent magnetoencephalographic study (Bayle et al., 2009) investigating the spatio-temporal dynamics of the neural processing of danger related stimuli as a function of the stimuli position in the visual field, revealed fast responses (as early as 80ms of latency) to fearful stimuli occurring in the peripheral visual field in the frontal lobes and the right internal temporal lobe, including the amygdala. However, no fMRI study to date, investigated the effects of spatial frequency and stimulus eccentricity on amygdala activity. Therefore, the aim of the present study was to further explore the contribution of LSF and HSF to emotional processing of faces in respect to stimulus eccentricity in the amygdala and the fusiform gyrus using fMRI.

Greyscale faces with fearful expressions were bandpass filtered resulting in two categories of stimuli: LSF and HSF filtered faces (Fig. 1A). As control stimuli non-filtered (broad-band, BSF) faces and images of faces with unchanged
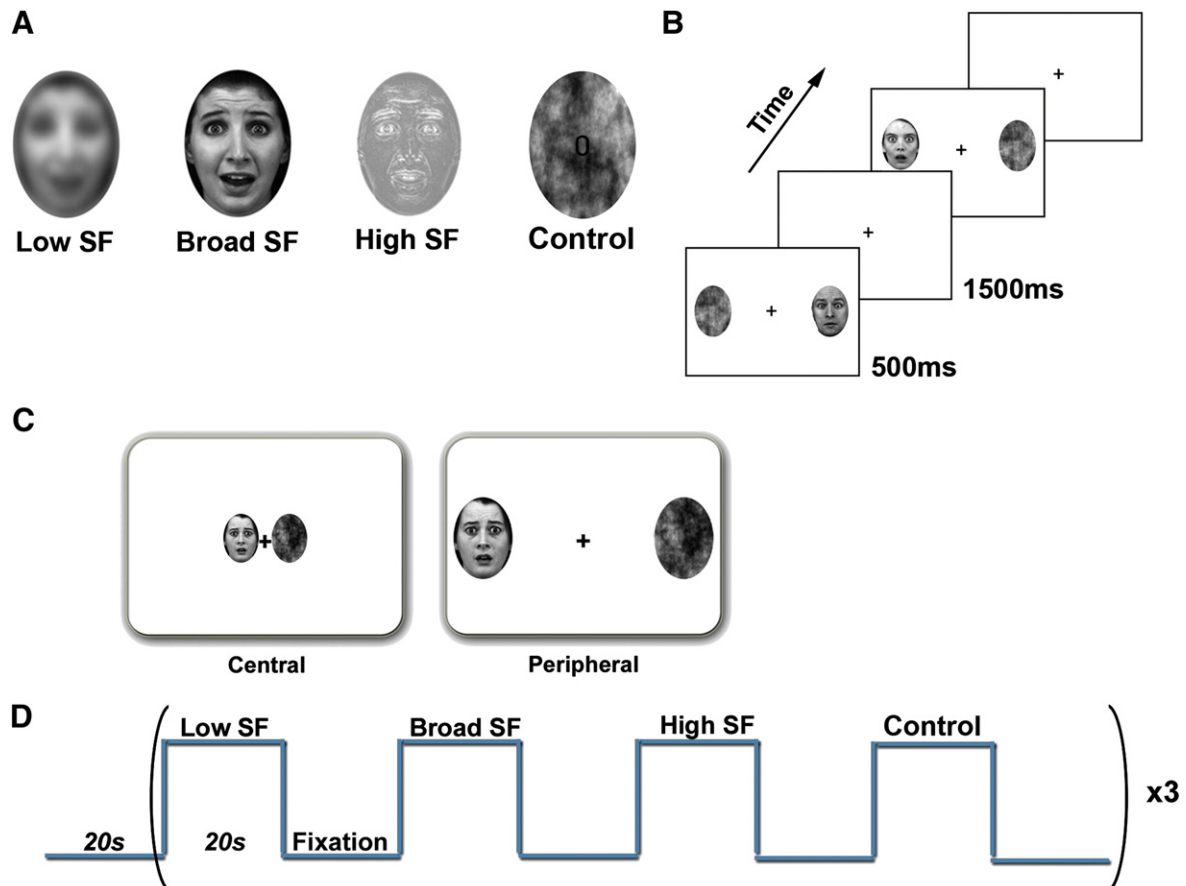
Fig. 1 – (A) Stimuli. Stimuli consisted of bandpass filtered fearful faces. Spatial frequency (SF) content of the original stimuli (broad-band, BSF) was either high-pass (HSF) or low-pass (LSF) filtered. A face stimulus with unchanged amplitude spectra but scrambled face spectra (phase-scrambled image) was used during the control condition. (B) Tasks. A pair of images, one face (LSF, HSF or BSF) and one phase-scrambled image, was presented for 500 ms with an interstimulus interval of 1500 ms. Subjects had to indicate on which side of the screen the face appeared. As control condition two phase-scrambled images were displayed, one containing a black oval-shaped circle as target. (C) Spatial location of the stimuli. In the central location images were located 1.7° and in the peripheral location 9.5° from central fixation. (D) The stimulation paradigm employed for functional imaging. One block consisted of four different tasks, each lasting 20 s, separated by a Fixation condition and repeated three times.

amplitude spectra but scrambled phase spectra (phase-scrambled image) were used (Fig. 1A). Pairs of images, one face (LSF, HSF or BSF) and one phase-scrambled image, were presented either 1.7° (central location) or 9.5° (peripheral location) from central fixation for 500 ms, with an interstimulus interval of 1500 ms (Fig. 1B and C). A face was presented either in the left or right visual field at the two different locations and subjects had to simply report on which side the face stimulus appeared. As control condition (Control) two phase-scrambled images were displayed, one containing a black oval-shaped circle as target. As performance declines towards the visual field periphery in most tasks when a constant stimulus size is used (Weymouth, 1958), we scaled the photographs by the human cortical magnification factor to activate an approximately equivalent portion of early visual cortex at the two eccentricities (Van Essen et al., 1984; Tolhurst & Ling, 1988; Rovamo & Virsu, 1979). The four task conditions (LSF, BSF, HSF and Control) were implemented in a blocked design and separated from each other by a fixation condition (fixation cross in the middle of a white screen) (Fig. 1D).

On a behavioral level, we hypothesized that (1) subjects would respond faster to LSF compared to HSF faces as LSF information has been found to be processed faster (Vlamings et al., 2009; Alorda et al., 2007; Winston et al., 2003; Kveraga et al., 2007) and (2) there should be no effect of stimulus location on accuracy as we increased stimulus size according to the human cortical magnification factor. Furthermore, we hypothesized that (3) LSF in contrast to HSF faces would be associated with a stronger signal increase in the amygdala when presented foveally (Winston et al., 2003; Vuilleumier et al., 2003), (4) within the LSF domain peripherally rather than foveally presented faces would be associated with a stronger response in the amygdala (Palermo & Rhodes, 2007), (5) the LSF and HSF filtered images would result in no differential signal change in the fusiform gyrus (Rotshtein et al., 2007), and (6) the foveally compared to peripherally presented faces would be associated with a higher signal change in the fusiform gyrus in LSF and HSF ranges (Levy et al., 2001; Liu et al., 2006).

2. Results

2.1. Behavioral data during scanning

To assess behavioral performance, mean reaction times (RTs) and response accuracy for each experimental condition and each subject were computed. RT results were computed only on accurate responses. The behavioral data were analyzed using 2×4 repeated measures ANOVA with location (central, peripheral) of the emotional stimuli and task (LSF, BSF, HSF and Control) as within-subject factors. Differences were tested using paired t-tests.

First, we examined task effects on RTs considering the spatial location of the stimuli. Repeated measures ANOVA (two-sided) revealed a significant main effect of stimulus ($F(3,60)=26.75$, $p<0.001$) and a significant interaction between stimulus and location ($F(3,60)=12.51$, $p<0.001$). Testing hypothesis 1, the comparison of filtered faces revealed significant faster RTs for the LSF faces ($F(1,20)=5.09$, $p=0.035$) (Fig. 2A). Subjects' RTs were also significantly faster in
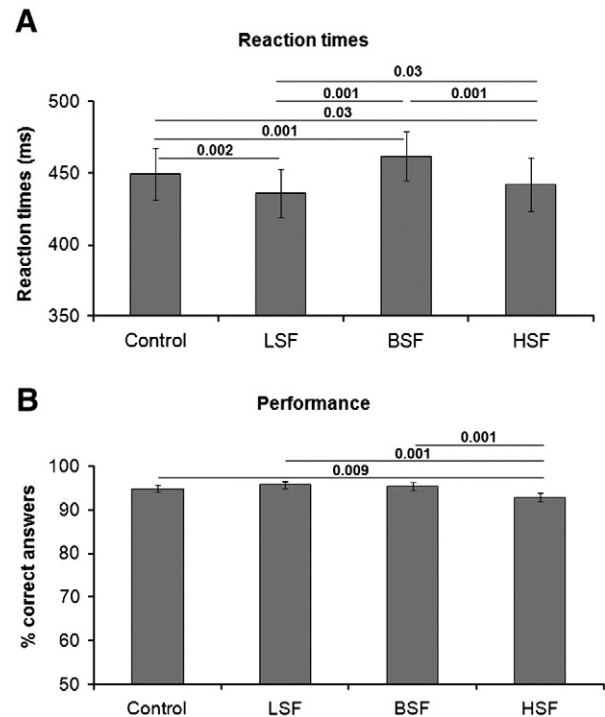
Fig. 2 – Behavioral results for each task condition. (A) Reaction times (mean ± S.E.) (B) Percent correct answers (mean ± S.E). LSF: low-spatial frequency; BSF: broad spatial frequency; HSF: high-spatial frequency.

response to the filtered compared to the intact faces at both frequencies ranges (LSF: $F(1,20)=113.03$, $p<0.001$; HSF: $F(1,20)=59.79$, $p<0.001$). The recognition of filtered face stimuli resulted in shorter RTs compared to the control images (LSF: $F(1,20)=13.25$, $p=0.002$; HSF: $F(1,20)=4.90$, $p=0.039$).

Second, we assessed the accuracy of the different tasks considering the spatial location of the stimuli. The accuracy results were analyzed separately for each location because we wanted to show that performance did not decline with eccentricity. Testing hypothesis 2, repeated measures ANOVA (two-sided) revealed no effect of stimulus location, but only a significant main effect of stimulus ($F(3,60)=7.72$, $p=0.002$). As expected, mean task performance for all conditions was very high (mean performance=95% correct answers) and was not affected by the location of the stimuli. Therefore, data from the two locations were pooled (Fig. 2B). Subjects were less accurate during the HSF task compared to all other conditions (LSF: ($F(1,20)=24.01$, $p<0.001$); BSF: ($F(1,20)=14.54$, $p=0.001$); control: ($F(1,20)=8.40$, $p=0.009$)).

2.2. Imaging data

fMRI data were analyzed within the framework of a random effects general linear model. Two regions of interest (ROIs), the amygdala and fusiform gyrus, were identified. The ROIs of the amygdala were determined anatomically on a single subject level. The fusiform gyrus ROIs were defined individually on the basis of a functional localizer experiment contrasting face and house stimuli (for a detailed description see methods and materials). Data extracted from the ROIs in these areas were analyzed with a two factors repeated measures ANOVA with

location of the emotional stimuli (central, peripheral) and stimulus (LSF, BSF, HSF and Control) as within-subject factors. Finally, we computed the mean percent signal change averaged across participants for each experimental condition with respect to the spatial locations of the emotional stimuli. Differences were tested using paired *t*-tests.

2.3. Amygdala region of interest analysis

The ROIs of the left and right amygdala were analyzed separately. To investigate habituation effects in the amygdala, we split the experimental blocks within one run into early and late blocks allowing us to probe how the neuronal response in these regions is influenced by presentation time. As one run consisted of 12 blocks (each task was repeated three times in one run, Fig. 1D), the first block of each task condition within one run was assigned early, whereas the last block of each task condition within one run was labeled late (blocks between early and late were grouped as intermediate).

We applied a three-factors repeated measures 3 (time) by 3 (stimulus) by 2 (location) ANOVA analysis (two-sided) to test for habituation effects in both ROIs. The results of the ANOVA showed no main effect of time and no interaction effects between time and the other two factors. Therefore, all blocks were grouped together regardless of the time of their presentation within a run and used for further analysis. Furthermore, we tested for laterality effects by adding the additional factor "side" of the ROI (left, right) to the ANOVA. As no significant difference in signal change was observed between the left and right amygdala, both ROIs were combined for further analysis.

Next we examined the main and interaction effects between stimulus and location. This revealed a significant main effect of stimulus ($F(3,60) = 8.29$, $p < 0.001$), but no significant main effect of location and no significant interaction effect between stimulus and location.

According to the hypotheses, we tested the effects of spatial frequency of the emotional stimuli on amygdala activity (hypothesis 3). As the ANOVA revealed no effect of location we refrained from further statistical testing regarding this factor (hypothesis 4). In order to determine activity directly related to any face-specific information within the different spatial frequency ranges, the phase-scrambled images of the control condition served as baseline.

2.3.1. Effect of spatial frequency
Fig. 3A reveals signal increases in the amygdala during the LSF, BSF and HSF task (Table 1 lists all statistically significant comparisons). Testing hypothesis 3 stating that the spatial frequency of filtered faces presented foveally differentially influences amygdala responses, we observed no differential signal change in response to LSF compared to HSF faces in the central location. Enhanced amygdala responses were found during the presentation of intact compared to LSF faces in the peripheral location and to HSF faces at both stimulus locations.

2.3.2. Effect of stimulus eccentricity
According to hypothesis 4, stimulus location should affect the signal change in the amygdala within the LSF domain. However, the response in the amygdala was not influenced by the location of the face stimuli (Fig. 3A).
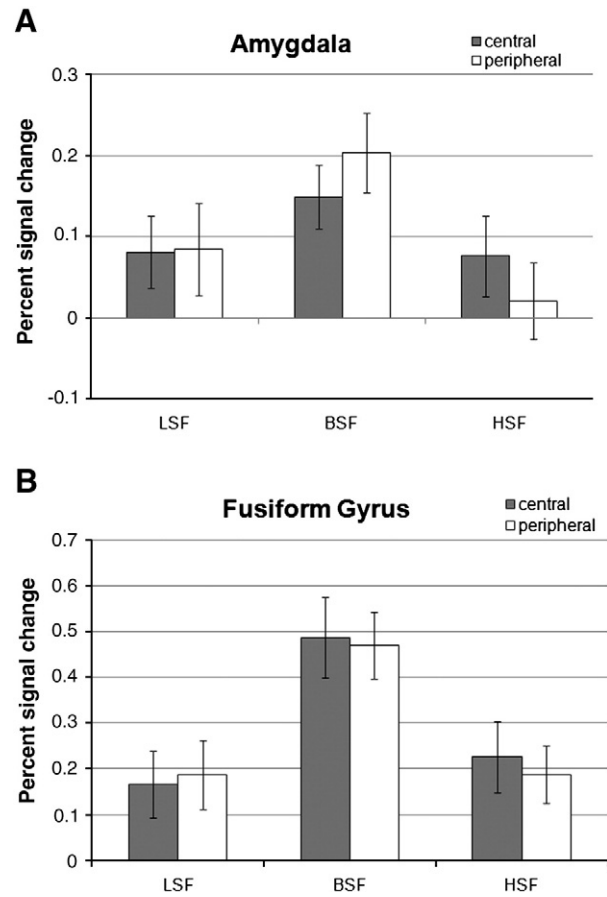
Fig. 3 – Mean percent signal changes (±S.E.) relative to the control condition in the amygdala (A) and the fusiform gyrus (B) during the different task conditions (LSF, BSF, HSF) as a function of the spatial location of the face stimuli. See text and Tables 1 and 2 for between-task comparisons.
LSF: low-spatial frequency; BSF: broad spatial frequency; HSF: high-spatial frequency.

2.4. Fusiform gyrus region of interest analysis

In addition to the amygdala we investigated the signal changes in the fusiform gyrus to ascertain the reliability of the stimulus manipulation. The fusiform gyrus was also

Table 1 – Region-of-interest analysis of the amygdala.			
Effect of spatial frequency in the amygdala			
Contrast			
	Position [a]	F(1, 20)	P-value
BSF > HSF	Central	5.5	0.029
	Peripheral	18.3	0.001
BSF > LSF	Peripheral	6.4	0.02

Only statistically significant comparisons are listed in the table (paired *t*-test).
[a] Position of the face stimuli in the visual field.

tested for habituation and laterality effects like the amygdala (for details of the analysis see amygdala region of interest analysis). The results of the ANOVA clearly demonstrated a habituation effect in the fusiform gyrus (for detailed results see supplementary data). Therefore, only the early blocks of each task condition were included for further analysis and as no significant difference in signal change was observed between the left and right fusiform gyrus, both ROIs were combined.

First, we applied a two factors repeated measures 4 (stimulus) by 2 (location) ANOVA analysis. This revealed a significant main effect of stimulus ($F(3,60)=26.47$, $p<0.001$) and a significant main effect of location in the fusiform gyrus ($F(1,20)=23.08$, $p<0.001$).

According to the hypotheses, we tested the effects of spatial frequency (hypothesis 5) and stimulus eccentricity (hypothesis 6) of the emotional stimuli on fusiform gyrus activity. Overall, an increase in response was found during all task conditions in the fusiform gyrus compared to the control condition.

2.4.1. Effect of spatial frequency

According to hypothesis 5, the fusiform gyrus is not preferentially tuned to LSF or HSF filtered faces illustrated by Fig. 3B (Table 2 lists all statistically significant comparisons). In line with this hypothesis, the comparison between the LSF and HSF task revealed no significant difference. Intact faces were associated with significantly higher signal changes compared to filtered faces in both frequency domains in the central and peripheral location.

2.4.2. Effect of stimulus eccentricity

Hypothesis 6 is based on the assumption that centrally presented stimuli compared to peripherally ones are associated with an increase in fusiform gyrus activity during the LSF and HSF tasks. However, within the LSF and HSF domain no significant differences between the two stimulus locations were observed (Fig. 3B).

2.5. Behavioral ratings of facial expression

To assess whether fearful filtered faces were perceived as negative, we asked a separate group of healthy participants to rate the images on a scale from 1 (very negative) to 9 (very positive) for each of the intact, HSF and LSF faces also including neutral faces. The ratings showed a main effect of expression (mean, 3.5 for fearful and 4.7 for neutral; $F(1,19)=244.72$, $p<0.001$) without a main effect of spatial frequency content, but with a significant interaction of these two factors ($F(2,38)=70.54$, $p<0.001$). Intact fearful faces were rated significantly more negative than the filtered images (LSF: $F(1,20)=15.84$, $p<0.001$; HSF: $F(1,20)=54.17$, $p<0.001$).

2.6. Behavioral data on emotion recognition

In order to test if expression perception is affected by spatial frequency and stimulus location, we performed an additional behavioral experiment in the same group of participants which rated the images. A similar task design as in the fMRI experiment was used: fearful, happy and neutral faces of BSF, LSF and HSF were either presented at the central or peripheral location. A three-alternative forced choice paradigm was used in which the target face was presented, followed by a choice screen. Subjects were instructed to identify the expression of the face (possible expressions were happy, neutral and fearful). The results revealed a main effect of frequency domain ($F(2,38)=82.53$, $p<0.001$), facial expression ($F(2,38)=78.84$, $p<0.001$) and stimulus location ($F(1,19)=5.11$, $p=0.036$). Furthermore, a significant interaction effect was observed between spatial frequency and facial expression ($F(4,133)=25.16$, $p<0.001$) and between all three factors ($F(4,133)=7.22$, $p<0.001$). The results showed that subjects had difficulties in discriminating filtered fearful from neutral faces and that happy and neutral faces were easier to identify (mean, 67% correct for fearful; 91% correct for neutral; 92% correct for happy faces). However, the mean task performance was very high (mean=83% correct answers). Regarding the stimulus location, performance was higher for fearful LSF and intact faces when the faces were presented in the peripheral rather than the central position. The same effect was found for HSF neutral and happy faces.

3. Discussion

In this study, fearful faces were presented at different eccentricities and were filtered to exaggerate selectively low- or high-spatial frequencies in order to test the hypothesis that the amygdala is tuned to low-spatial frequency stimuli presented in the periphery, whereas the fusiform gyrus responds to high- as well as low-spatial frequency ranges.

On a behavioral level, a LSF advantage for processing faces is reflected in shorter RTs and higher accuracy during the fMRI experiment in line with our hypotheses that LSF information is processed faster (Bar, 2003; Goffaux et al., 2003a; Schyns & Oliva, 1994) (hypothesis 1). Accordingly, previous fMRI and EEG studies using filtered faces (Winston et al., 2003; Vlamings et al., 2009), objects (Kveraga et al., 2007) and pictures (Alorda et al., 2007) reported slower reaction times for HSF than LSF information. Furthermore, stimulus location did not affect behavioral performance during the fMRI experiment in line with hypothesis 2, which could be lead back to the performed image size-adjustment.

Table 2 – Region-of-interest analysis of the fusiform gyri.			
Effect of spatial frequency in the fusiform gyri			
	Contrast		
	Position [a]	$F(1, 20)$	P-value
BSF>LSF	Central	17.4	0.001
	Peripheral	12.1	0.002
BSF>HSF	Central	13.5	0.001
	Peripheral	12.8	0.002

Only statistically significant comparisons are listed in the table (paired t-test).
[a] Position of the face stimuli in the visual field.

Taken together, the behavioral results ascribe a special role of the LSF range in face processing for rapid and successful extraction of facial expression information in demonstrating shorter RTs on the one side and higher performance during LSF compared to HSF fearful faces on the other side during the fMRI experiment.

However, the differential processing of distinct spatial frequency features in faces found on a behavioral level is not reflected in the imaging data. According to hypothesis 3, we expected that the amygdala primarily responds to LSF compared to HSF faces presented in the center of the visual field (Vuilleumier et al., 2003). In contrast to this assumption no dissociable processing of LSF and HSF faces in the central location was found in the amygdala. We further hypothesized that within the LSF range, responses in the amygdala would increase with increasing eccentricity (Palermo & Rhodes, 2007). However, in contrast to hypothesis 4 no differential amygdala response was observed contrasting the two spatial locations within the LSF domain. According to the literature, the fusiform gyrus preferably responds to stimuli of both frequency ranges (Rotshtein et al., 2007). Consistent with hypothesis 5, the results showed that the fusiform gyrus responded to both types of spatial frequency information in faces, but is not affected by the stimulus location, which is in contrast to hypothesis 6.

3.1. Amygdala

Contrary to Vuilleumier et al. (2003), the absent effects of spatial frequency modulation of amygdala response do not support the hypothesis of preferential activation of this emotion-sensitive area due to LSF stimuli: LSF and HSF resulted in similar signal changes in the amygdala when the stimuli were presented in the central location. Furthermore, no differential response between LSF and BSF was observed in the amygdala when the stimuli were presented centrally in agreement with Vuilleumier et al. (2003). We further extend previous findings in demonstrating that amygdala activity in response to LSF and HSF filtered faces is not associated with the location of the affective stimuli. In other words, neither centrally nor peripherally presented LSF and HSF faces differentially modulate amygdala responses. Therefore, our findings do not provide evidence for the idea that the amygdala is especially sensitive to affective LSF stimuli in the periphery, but rather suppose that it is implicated in the processing of emotional information located within the current spotlight of attention in general. During the experiment subjects were explicitly asked to direct their attention either to the central or the peripheral stimulus position, thereby favoring and enhancing the processing of the relevant stimuli at both locations. Thus, the idea that the amygdala may direct attention to the periphery could not exactly be addressed with this task design as no unattended location was employed as reference. However, the finding of amygdala activation being independent of stimulus location further highlights the important role of magnocellular and parvocellular information in the activation of amygdala-related circuits.

One main difference between our study and the study of Vuilleumier et al. (2003) is that we did not include neutral faces as control stimuli. Previous results showed that amygdala response was only modulated by fearful facial expressions (Vuilleumier et al., 2003). Given these findings, we declined to use neutral faces as a control as we expected effects of spatial frequency only in the fear context. Though, the use of fearful faces only strongly limits the interpretation of the observed results to that effect that any conclusion made is restricted to face processing in general and cannot be related to fear processing per se. Therefore, we performed additional behavioral experiments outside the scanner in order to validate the stimulus material regarding valence and emotion recognition. Subjects were asked to rate the valence of fearful and neutral face stimuli with different frequency ranges in order to account for concerns regarding differences in emotional intensity of the stimuli and emotion perception per se. The results of the ratings clearly point out that fearful faces – regardless of spatial frequency modifications – are perceived negative compared to neutral faces. Interestingly, intact faces are rated more negative than filtered images, indicating that the perception of a basic emotion like fear is influenced by spatial filtering. While a previous study (Vuilleumier et al., 2003) reported that HSF images are rated more fearful than LSF and BSF images, our data show no difference of valence ratings between HSF and LSF faces. In contrast to the earlier study (Vuilleumier et al., 2003), which asked subjects to rate the fearfulness of used images, the present study employed a valence rating from negative to positive, which could account for the different findings. The behavioral results of the valence ratings rule out the possibility that the differential signal changes in the amygdala in response to the fearful faces are the result of greater intensity of consciously perceived emotion in the LSF compared to the HSF range. First, it could be demonstrated that fearful faces in comparison to neutral ones are perceived as negative. Second, intact faces were perceived more negative than filtered faces, which is concordant with our imaging findings as BSF faces were associated with the highest signal change in the amygdala. Third, there was no difference between LSF and HSF fearful faces, indicating that the conscious negative perception of fearful stimuli was not differentially influenced or modulated by the spatial filtering of the images. This result is also reflected on a neuronal basis indicating no differential signal changes in the amygdala, arguing against the concept of a fast face processing pathway based on magnocellular inputs. Additionally to the valence rating, we tested whether fearful and happy filtered faces could be discriminated from neutral ones. Task performance in general was lower for the filtered fearful faces compared to happy and neutral ones. In a previous study (Goren & Wilson, 2006) it has been demonstrated that shifting spatial frequency bands to low peak frequencies greatly impairs performance on emotion discrimination tasks (discrimination of affect from neutral), specifically sadness, happiness and fear are affected by the lack of high peak frequencies. In the current task, fearful faces had to be recognized among happy and neutral ones. It has been shown that some emotions are easy to detect from neutral, but often confused with other emotions, whereas some emotions are hard to discriminate from neutral but rarely confused with others (Goren & Wilson, 2006). Especially fear is much harder to recognize among other emotions in brief

presentations and often confused with sadness (Goren & Wilson, 2006) or surprise (Daily et al., 2002). In the current experiment relatively brief presented fearful facial expressions (500 ms) were often mistaken for neutral faces within the LSF range. The lack of clear emotion recognition of low-pass filtered fearful faces can be explained by the fact that LSF faces represent coarse blobs which, individually, do not have sufficient resolution to provide enough information about fine scale cues such as the eye region, which is used most prominently when subjects have to discriminate fear from other expressions (Smith et al., 2005). Regarding recognition of emotion at different eccentricities of the visual field, LSF fearful faces presented in the peripheral compared to the central position were recognized more accurately. Opposed to these effects, stimulus location did not affect behavioral performance during the fMRI experiment. These discrepancies in task performance can be attributed to the fact that during the behavioral experiments the head position of the subjects was not fixed while during the fMRI experiment the head of the subjects was stably positioned in the middle of the head coil due to cushioning and the distance to the screen was fixed by using LCD goggles. Furthermore, the tasks of the two behavioral experiments are not exactly the same: outside the scanner subjects had to perform an emotion recognition task while inside the scanner they had to simply detect the spatial location of the faces in the visual field.

In summary, the behavioral results of the rating and emotion recognition experiment show that filtered fearful faces are perceived as negative when extensive processing of the visual stimuli is not restricted in terms of presentation time and that recognition of emotional facial expression is influenced by spatial frequency if the faces are displayed for a short time. The latter does not imply that the valence of the stimuli is not recognized. Although a great number of psychophysiological studies using ERPs and magnetoence-phalographic recordings demonstrated that emotional information from faces is rapidly registered and discriminated, from as early as 80 ms after stimulus onset (for a review see Palermo & Rhodes, 2007), this does not exclude the possibility that this fast detection and crude affective categorization can be influenced and/or modulated by spatial frequency modifications. Thus, LSF input drives the early detection of fearful expressions as indicated by a recent ERP study demonstrating an enhanced P1 and N170 across ventro-temporal areas for LSF only (Vlamings et al., 2009). Moreover, LSF components in faces provide a better source of information than HSF components for the correct categorization of fearful expressions in faces (Mermilloda et al., 2009). However, our amygdala fMRI findings do not ascribe a special role of LSF components of visual information within a fast face processing pathway. Thus, we propose that a flexible spatial frequency integration mechanism underlying face perception drives responses in the amygdala resulting in similar activation patterns in response to LSF and HSF information.

Several methodological differences complicate a direct comparison of present and previous findings. Vuilleumier et al. (2003) demonstrated an increase in signal change in response to LSF filtered fearful versus neutral faces presented at the center of the visual field in the left amygdala using an event-related design, while in the current study the stimuli

were presented in a blocked design, which is statistically more powerful (Bandettini & Cox, 2000; Miezin, et al., 2000). However, the use of a block design may in general amplify habituation effects. To avoid such effects, task condition blocks were interleaved by fixation blocks and the design was fully counterbalanced with regard to task conditions (within runs) and location of the face stimuli (between runs). However, as previous studies reported that the amygdala response habituates (i.e., decreases over time) to repeated presentations of human facial expressions (Britton et al., 2008; Wright et al., 2001; Breiter et al., 1996; Ishai et al., 2004) we tested for habituation effects in the amygdala using an approach which has previously been applied to blocked fMRI designs and compares early versus late blocks of stimuli (Breiter et al., 1996; Feinstein et al., 2002; Phan et al., 2003; Protopopescu et al., 2005; Wright et al., 2001). Our findings differ from previously reported data (Fischer et al., 2003; Phillips et al., 2001; Williams et al., 2004) as we did not observe a rapid habituation of the amygdala to repeatedly presented emotional stimuli thereby disproving the idea that the observed effects might be biased by habituation. In line with our results, a recent study (Haas et al., 2008) also failed to find any evidence for amygdala habituation. It has been suggested that these inconsistencies likely reflect methodological differences in the temporal parameters as the studies varied in the length of blocks and experimental runs. Therefore it has been proposed that the amygdala does not exhibit habituation when shorter (e.g., 18 s) blocks are used (Haas et al., 2008), which is consistent with our data and design (one block lasted 20 s).

Further differences between our study and previous ones (Vuilleumier et al., 2003) concern the presentation time of the stimuli (500 ms vs. 200 ms), the experimental task and the low-pass cut-off value (6 vs. 8 cycles/image for LSF faces). We used a low-pass cut-off of 8 cycles/ image because it has been demonstrated in the literature (Bachmann, 1991; Costen et al., 1994, 1996) that there is enough LSF information at 8 cycles/ image to obtain more than 80% identification accuracy, and that 24 cycles/image for the HSF faces represent all the boundary edges defining important face components.

3.2. Fusiform gyrus

In the fusiform gyrus habituation effects were revealed. The initial blocks of each run elicited the greatest activation compared to late blocks indicating a gradual habituation effect in this region. This time-related differential activation in the fusiform gyrus is consistent with previous neuroimaging studies (Britton et al., 2008; Hsu & Pessoa, 2007).

The involvement of the fusiform gyrus in the processing of faces has been established by numerous imaging studies demonstrating greater activity to faces than to nonsense or non-face stimuli (Kanwisher et al., 1997; McCarthy et al., 1997; Halgren et al., 1999; Haxby et al., 1994; Haxby et al., 1999; Hoffman and Haxby, 2000; Ishai et al., 1999; Sergent et al., 1992; Puce et al., 1996). We similarly observed an increase in activity in the left and right fusiform gyrus during all tasks conditions. Responses were strongest for BSF faces, which highlights the importance of the combination of LSF and HSF cues for face detection and identification. In line with a recent study

(Rotshtein et al., 2007) LSF as well as HSF faces were associated with increased activation of the fusiform gyrus in contrast to phase-scrambled images, thereby providing visual details about faces that can be associated with specific emotional expressions. Indeed, it has been suggested that within a network of occipitotemporal regions the right fusiform gyrus combines LSF and HSF information to generate a visual representation of a face relatively independent of its spatial frequency range (Rotshtein et al., 2007). In contrast to previous studies (Levy et al., 2001; Liu & Ioannides, 2006) our results show that the spatial location of the stimuli does not influence the responses in the fusiform gyrus. Although it has to be pointed out that this central versus peripheral bias in object-related, high-order visual areas, was reported in more dorsal-posterior face-related regions compared to the more ventral-anterior part in the posterior fusiform gyrus (Levy et al., 2001). In the present study we functionally defined the fusiform gyrus, not delineating the anterior from the posterior part, which might explain why no central-field bias has been observed.

4.   Conclusion

Returning to the main hypotheses in light of our results, our findings show that spatial filtering (1) impairs emotion recognition for fearful faces, (2) affects behavioral responses (RTs and task performance), (3) influences emotion perception (ratings), (4) reduces responses in the amygdala, and that (5) the amygdala is not especially sensitive to emotional stimuli presented in the periphery. Additionally, in the fusiform gyrus no dissociation between HSF and LSF information was observed suggesting both frequency ranges are equally effective in driving responses in this brain region.

5.   Experimental procedures

5.1.   Subjects

All subjects gave written informed consent to participate in the study, which was approved by the local ethics committee.

5.2.   Behavioral experiments

Twenty healthy adults (9 males; 28±8.8 years (mean±SD)) participated in the behavioral experiments. Six subjects of the same group also participated in the fMRI experiments.

5.3.   fMRI experiments

Twenty-one right-handed, healthy adults (6 males; 28±7.5 years (mean±SD)) with normal or corrected to normal vision were examined.

5.4.   Visual stimuli and experimental procedure

Greyscale faces with fearful, happy and neutral expressions from the Karolinska Directed Emotional Faces set (Lundqvist et al., 1998) were presented within an oval frame excluding the hair and non-facial contours. Faces were bandpass filtered using a radially symmetric filter (Goren & Wilson, 2006) and normalized in luminance (Fig. 1A). Spatial frequency content in the original stimuli (broad-band, BSF) was filtered using a high-pass cut-off that was 24 cycles/image for HSF stimuli, and a low-pass cut-off of 8 cycles/image for the LSF stimuli.

5.5.   Behavioral experiments

During the rating experiment, participants were presented with one face at a time and were asked to rate all images used in the fMRI experiment (fearful faces) and additionally all neutral faces on a scale from 1 to 9 (1=very negative; 9=very positive). Images were presented in random order and in the center of the screen. No time limit was imposed.

After the rating experiment, pairs of images, one face (LSF, HSF or BSF) and one image with unchanged amplitude spectra but scrambled phase spectra (phase-scrambled image), were presented either 1.7° (with a height of 3.8°; central location) or 9.5° (with a height of 8.2°; peripheral location) from central fixation for 500 ms. As performance declines towards the visual field periphery in most tasks when a constant stimulus size is used (Weymouth, 1958), we scaled the photographs by the human cortical magnification factor to activate an approximately equivalent portion of early visual cortex at the two eccentricities (Van Essen et al., 1984; Tolhurst & Ling, 1988; Rovamo & Virsu, 1979). We scaled our pictures based on the equation $M^{-1}=(1+aE) * M_0^{-1}$ (Rovamo & Virsu, 1979) with E referring to eccentricity in degrees and M_0 representing the value of magnification.

After face presentation subjects had to indicate via button press which emotion (happy, neutral, fearful) has been displayed (2 s) followed by a fixation cross for 2 s. Twenty images of each emotional expression either filtered (LSF, HSF) or unfiltered (BSF) were presented randomly. In one run images were presented in the central location and in the other one in the peripheral location.

5.6.   fMRI experiments

Visual stimuli were presented using LCD googles (Resonance Technology, Northridge, CA, USA) and the stimulation software Presentation (Version 9.00, Neurobehavioral Systems, Albany, CA, USA). Pairs of images, one face (LSF, HSF or BSF) and one image with unchanged amplitude spectra but scrambled phase spectra (phase-scrambled image), were presented either 1.7° (with a height of 3.8°; central location) or 9.5° (with a height of 8.2°; peripheral location) from central fixation for 500 ms, with an interstimulus interval of 1500 ms (Fig. 1B and C). Subjects had to indicate via button press on a fibre optic computer response device (Current Designs Inc., Philadelphia, PA, USA) on which side the face appeared. As control condition two phase-scrambled images were displayed, one containing a black oval-shaped circle as target. Images were scaled according to the human cortical magnification factor (see behavioral experiments for details).

The four task conditions (LSF, BSF, HSF and Control) were implemented in a blocked design and were separated from each other by a fixation condition (fixation cross in the middle of a white screen) (Fig. 1D). Experimental runs started with a fixation phase (20 s) and then alternated between task (20 s) and fixation condition (20 s) resulting in a stimulation block of

40 s, which was repeated 12 times. One experimental run lasted 8 min 20 s and was repeated six times during one scan session. Tasks were presented in a pseudo-randomized order.

Additionally, one separate functional localizer experiment was performed in order to determine the face-sensitive portion of the fusiform gyrus. This fusiform gyrus ROI was localized by presenting 18 s blocks of greyscale face (greyscale full-front images of six young males and females) or house images (greyscale full-front images of 15 different houses) interleaved with 18 s of phase-scrambled images, which were all fit behind an oval mask (7.3° of height). Each face and house block was repeated six times with stimuli presented in the center of the visual field.

5.7. MR image acquisition and analysis

MR imaging was performed at 3 T (Magnetom Trio, Siemens Healthcare, Erlangen, Germany). Initially, a high-resolution 3D T1-weighted dataset was acquired from each subject (176 sagittal sections, $1 \times 1 \times 1 mm^3$). For fMRI we used an optimized T2*-weighted MR-sequence to reduce unwanted susceptibility effects while retaining high sensitivity for activation-related signal changes in the amygdala (Morawetz et al., 2008). A gradient-echo echo planar imaging technique recording 22 sections of 2 mm thickness oriented roughly parallel to the anterior and posterior commissure at an in-plane resolution of $2 \times 2 mm^2$ was used (repetition time = 2000 ms; echo time = 36

ms; field-of-view = $192 \times 256 mm^2$). For each experimental run 250 volumes were recorded.

Data were analyzed within the framework of a random effects general linear model using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands). Preprocessing of fMRI data included 3D-motion-correction, temporal high-pass filtering (3 cycles/run), linear trend removal, spatial smoothing (Gaussian smoothing kernel, 8 mm full width half maximum), and transformation into the space of Talairach and Tournoux (1988).

ROIs were determined on a single subject level anatomically in the amygdala (mean coordinates: left: x, y, $z = -21 \pm 0.63$, -3.8 ± 1.3, -13 ± 0.2; mean size = 1084 mm^3; right: x, y, $z = 20 \pm 0.94$, -4.7 ± 0.76, -13 ± 0.27; mean size = 1078 mm^3) (Fig. 4A). The coordinates are consistent with the peaks of activation recently reported in a meta-analysis of 94 imaging studies (Costafreda et al., 2008). To test whether the differential effects of stimulus location and spatial frequency ranges are specific to the amygdala, we defined another ROI in the fusiform gyrus, an area known to be implicated in face processing (Kanwisher et al., 1997). The fusiform gyrus ROIs (Fig. 4B) were defined individually on the basis of the functional localizer experiment contrasting the face and house stimuli (q(FDR) = 0.01), which resulted in significantly activated voxels in the fusiform gyrus (mean coordinates: left: x, y, $z = -41 \pm 3.9$, -50 ± 8, -18 ± 4.1; mean size = 2923 mm^3; right: x, y, $z = 40 \pm 3$, -52 ± 8.1, -17 ± 3.2; mean size = 4508 mm^3).
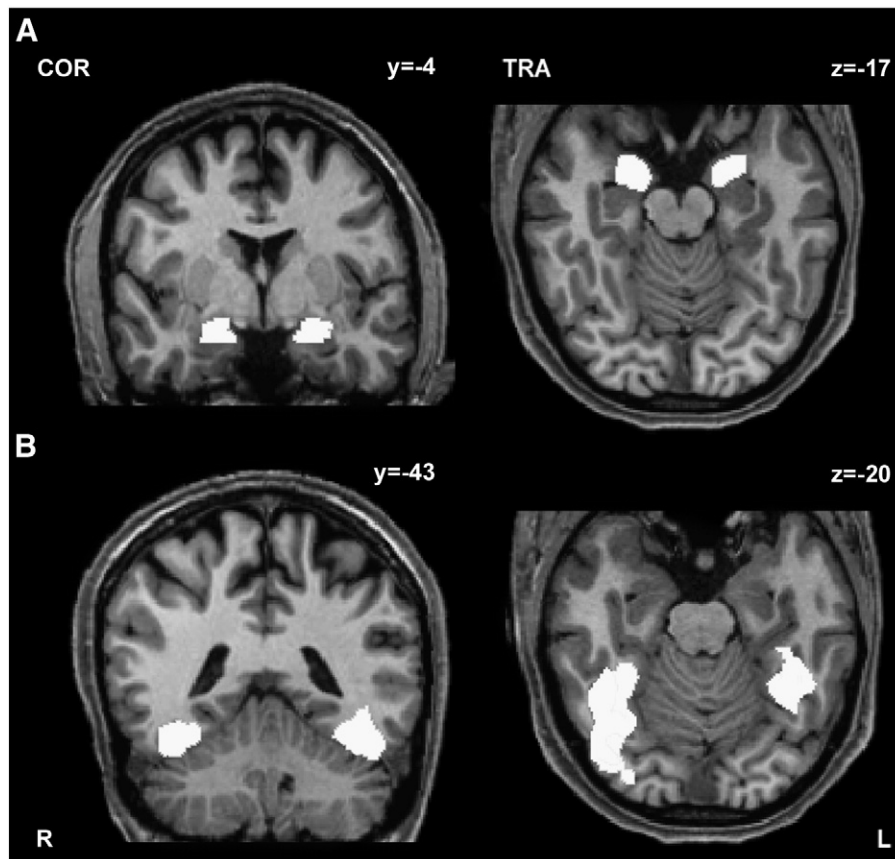
Fig. 4 – Example ROIs of one subject. (A) Coronal (left) and transversal (right) section through the amygdala. (B) Coronal (left) and transversal (right) section through the fusiform gyrus. ROIs are indicated in white. R: right; L: left.

Acknowledgments

Appendix A Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.brainres.2010.10.110.

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