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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.

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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Abbreviations: BSF, broad-band-spatial frequency; EEG, electroencephalographic; ERP, event-related potential; fMRI, functional magnetic resonance imaging; HSF, high-spatial frequency; LSF, low-spatial frequency; M, magnocellular; P, parvocellular; ROI, region of interest; RTs, reaction times

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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