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Selective attention modulates high-frequency activity in the face-processing network

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ABSTRACT

Face processing depends on the orchestrated activity of a large-scale neuronal network. Its activity can be modulated by attention as a function of task demands. However, it remains largely unknown whether voluntary, endogenous attention and reflexive, exogenous attention to facial expressions equally affect all regions of the face-processing network, and whether such effects primarily modify the strength of the neuronal response, the latency, the duration, or the spectral characteristics. We exploited the good temporal and spatial resolution of intracranial electroencephalography (iEEG) and recorded from depth electrodes to uncover the fast dynamics of emotional face processing. We investigated frequency-specific responses and event-related potentials (ERP) in the ventral occipito-temporal cortex (VOTC), ventral temporal cortex (VTC), anterior insula, orbitofrontal cortex (OFC), and amygdala when facial expressions were task-relevant or task-irrelevant. All investigated regions of interest (ROI) were clearly modulated by task demands and exhibited stronger changes in stimulus-induced gamma band activity (50–150 Hz) when facial expressions were task-relevant. Observed latencies demonstrate that the activation is temporally coordinated across the network, rather than serially proceeding along a processing hierarchy. Early and sustained responses to task-relevant faces in VOTC and VTC corroborate their role for the core system of face processing, but they also occurred in the anterior insula. Strong attentional modulation in the OFC and amygdala (300 msec) suggests that the extended system of the face-processing network is only recruited if the

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task demands active face processing. Contrary to our expectation, we rarely observed differences between fearful and neutral faces. Our results demonstrate that activity in the face-processing network is susceptible to the deployment of selective attention. Moreover, we show that endogenous attention operates along the whole face-processing network, and that these effects are reflected in frequency-specific changes in the gamma band.

1. Introduction

Emotionally and socially significant stimuli in our environment receive prioritized perceptual processing. This processing bias has been attributed to the engagement of reflexive, exogenous attention (Vuilleumier, 2005) and entails an adaptive advantage for the organism (Öhman & Mineka, 2001). Facial expressions are among the most emotionally and socially significant stimuli in the human environment because they signify intentions and emotional states of our conspecifics, making them essential for social communication. This has led to the hypothesis that a processing bias for emotional facial expressions is hard-wired into the human brain (Palermo & Rhodes, 2007).

Processing of faces in general and emotional facial expressions in particular depend on the orchestrated activity of large-scale neuronal networks (Gobbini & Haxby, 2007; Haxby, Hoffman, & Gobbini, 2000; Vuilleumier & Pourtois, 2007). A study using functional magnetic resonance imaging (fMRI) in humans identified a network of face-responsive regions involving the inferior occipital gyrus, the fusiform gyrus, the superior temporal sulcus, the amygdala, the hippocampus, the inferior frontal gyrus, and the orbitofrontal cortex (OFC) (Ishai, Schmidt, & Boesiger, 2005), confirming the importance of these regions for face processing. The visual perception of faces has been attributed to occipital and temporal regions including the inferior occipital, the fusiform, and the inferior temporal gyri (Kanwisher, McDermott, & Chun, 1997; Parvizi et al., 2012; Pourtois, Spinelli, Seeck, & Vuilleumier, 2010a; Tsuchiya, Kawasaki, Oya, Howard, & Adolphs, 2008). However, the face-processing network can be dynamically extended with regions recruited for the extraction of specific aspects of a face depending on the task or context at hand. Consequently, the terms “core system” and “extended system” have been coined to describe networks involved in basic visual perception and subsequent, context-related analysis of faces, respectively (Gobbini & Haxby, 2007; Haxby et al., 2000). Processing of facial expressions involves the core system and additional parts of the extended system such as the amygdala, the insula, and the OFC. Previous accounts ascribed a dominant role to the amygdala in processing especially fearful faces (Adolphs, Tranel, Damasio, & Damasio, 1994; Cornwell et al., 2008; Krolak-Salmon, Hénaff, Vighetto, Bertrand, & Mauguière, 2004; Morris et al., 1996; Pourtois, Spinelli, Seeck, & Vuilleumier, 2010b; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). More recent work showed that amygdala activity (1) is not limited to fearful facial expressions but can also be found with faces depicting neutral or happy expressions and (2) can be subsumed under processing stimulus relevance or significance (Adolphs, 2010; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002; Fusar-Poli et al., 2009; Rutishauser et al., 2011; Sander, Grafman, & Zalla, 2003). The OFC is involved in identification of facial expressions and their associated meaning (Adolphs, 2002; Rolls, 2004). The anterior portion of the insula has been associated with the perception of facial disgust (Fusar-Poli et al., 2009; Phillips et al., 1998) and salience detection (Menon & Uddin, 2010). Converging evidence comes from studies investigating non-human primates: face-selective clusters have been found in the temporal lobe, referred to as the anterior and middle face patch (Tsao, Freiwald, Tootell, & Livingstone, 2006; Tsao & Livingstone, 2008), in the frontal lobe (Tsao, Schweers, Moeller, & Freiwald, 2008), and in the amygdala (Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007; Hoffman, Gothard, Schmid, & Logothetis, 2007; Leonard, Rolls, Wilson, & Baylis, 1985). In summary, the ventral occipito-temporal cortex (VOTC), the amygdala, the OFC, and the anterior insula form a network that mediates both perceptual processing and detailed analysis of facial expressions for further guidance of behavior.

Although some studies show that emotional facial expressions capture attention automatically (Fenker et al., 2010; Vuilleumier, 2002), the activity of the face-processing network can be modulated by voluntary, endogenous attention such as task demands or the specific context at hand. For example, Monroe et al. (2013) reported larger amplitudes of the magnetic counterpart of the N170, a prominent event-related component reflecting face processing (Bentin, Allison, Puce, Perez, & McCarthy, 1996), for fearful than for happy or neutral faces in the fusiform gyrus but only when attention had to be directed to the faces' expression and not to their age. The authors concluded that a valence modulation in the fusiform gyrus is more likely under conditions of directed attention to facial expressions. Likewise, larger event-related potentials (ERP) in the amygdala were observed specifically for fearful faces in an intracranial electroencephalography (iEEG) study, but only when the patients had to pay attention to the facial expression and not to gender (Krolak-Salmon et al., 2004). Results from a meta-analysis of fMRI data further support the notion that directed attention to facial expression boosts activity within the core and extended face-processing network. Specifically, explicit compared to implicit processing of facial expressions was associated with stronger responses in the fusiform gyrus, the amygdala, and inferior frontal regions (Fusar-Poli et al., 2009). Moreover, attentional capture by emotion is not limited to visual stimuli, such as faces, and has been reported for auditory and audiovisual