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Research Report

Attention inhibition of early cortical activation to fearful faces

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ABSTRACT

Several lines of evidence demonstrate that processing facial expression can occur in the first 130 ms following a face presentation, but it remains unclear how this is modulated by attention. We presented neutral, fearful and happy faces to subjects who attended either to repeated identity or to repeated emotions. Brain activity was recorded using magnetoencephalography (MEG) and analyzed with event-related beamforming, providing both temporal and spatial information of processing in the brain. The first MEG component, at 90 ms (M90), was sensitive to facial expression, but only when attention was not directed to expression; non-attended fearful faces increased activation in occipital and right middle frontal gyri. Around 150 ms, activity in several brain regions, regardless of the direction of attention, was larger to emotional compared to neutral faces; attention directed to facial expressions increased activity in the right fusiform gyrus and the anterior insula bilaterally. M220 was not modulated by individual facial expressions; however, attention directed to facial expressions enhanced activity in the right inferior parietal lobe and precuneus, while attention directed to identity enhanced posterior cingulate activity. These data demonstrate that facial expression processing involves frontal brain areas as early as 90 ms. Attention directed to emotional expressions obscured this early automatic processing but increased the M170 activity. The M220 sources varied with the direction of attention. Thus, the pattern of neural activation to faces varied with attention to emotions or to identity, demonstrating separate and only partially overlapping networks for these two facets of information contained in faces.

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1. Introduction

We extract considerable information critical for social interactions, rapidly and effectively from faces, including identity and emotions. A recent focus in the neurosciences has been the perception and processing of facial expressions, with

studies implicating a large distributed neural network. This affect-sensitive network includes regions in the visual-ventral stream as well as the superior temporal sulcus and dorso-frontal and orbito-frontal regions (Adolphs, 2002; Phan et al., 2002), but the timing of their involvement and their modulation by attention are only beginning to emerge.

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The classic view is that after occipital activity around 100 ms, face processing continues along the ventral visual pathways arriving at the fusiform gyrus at around 170 ms (Allison et al., 1994; Bentin et al., 1996), before reaching anterior regions (Haxby et al., 2000). However, event-related potential (ERP/EEG) and event-related field magnetoencephalography (ERF/MEG) studies have shown more rapid processing of facial expressions, with components between 90 and 130 ms indexing differences between emotional and neutral faces, seen anteriorly in fronto-medial and orbito-frontal regions (Eimer and Holmes, 2002; Holmes et al., 2003; Streit et al., 2003) and occipitally (Batty et al., 2003; Eger et al., 2003; Halgren et al., 2000; Pizzagalli et al., 1999).

The question of the neural pathways allowing this rapid frontal activation is still posed but the implication of a subcortical route is increasingly hypothesized. As suggested first by several fMRI and PET studies, this route would bypass the visual cortex and involve the superior colliculus, pulvinar and amygdala. It would effect a rapid and coarse visual analysis, notably of aversive stimuli such as fearful or angry faces (Das et al., 2005; de Gelder et al., 1999; de Marco et al., 2006; Liddell et al., 2005; Morris et al., 2001; Morris et al., 1999; Ohman and Mineka, 2001). However, neither fMRI nor PET can determine the time course of such pathways. The most direct evidence of a subcortical pathway comes from MEG studies which have shown very rapid activation of the amygdala following presentation of stimuli including fearful faces (Cornwell et al., 2008; Ioannides, 2006; Liu et al., 1999; Luo et al., 2007, 2009). The role of such a pathway in processing aversive stimuli is reinforced by the fact that the majority of the data showing frontal activation for facial expression, at latencies inferior to 130 ms were using fearful faces stimuli (Eimer and Holmes, 2002; Holmes et al., 2003; Kawasaki et al., 2001; Liu et al., 1999; Streit et al., 2003; Williams et al., 2004), and that amygdala activation has been largely associated with fear perception (Adolphs et al., 2005; Adolphs et al., 1995; Anderson and Phelps, 2000; Broks et al., 1998; Calder et al., 2001; Krolak-Salmon et al., 2004; Morris et al., 1996).

Thus, the very rapid processing of fearful faces has been demonstrated by a range of electromagnetic studies, yet the modulation of this processing by attention is still not fully characterized. Although Pessoa et al. (2002) reported activation to emotional expressions only if subjects attended to the emotions, suggesting that attention is necessary for this process, most authors report that fear processing occurs without directed attention (Batty et al., 2003; Bradley, 1997; Vuilleumier and Schwartz, 2001) or unconsciously (de Gelder et al., 1999; Morris et al., 2001; Morris et al., 1999; Whalen et al., 1998), and that a fast neural network is activated automatically for the unconscious capture of attention by aversive faces (Bradley, 1997; de Gelder et al., 1999; Pourtois et al., 2004; Pourtois et al., 2005; Vuilleumier and Schwartz, 2001). Whether attention is or is not necessary for the early fear processing, it could nevertheless play a modulating role. Williams et al. (2005) compared neutral and fearful faces using fMRI in two attentional conditions: attend-face and attend-house. When subjects attended to houses, amygdala activation for fearful faces was greater than when subjects attended to faces; i.e., amygdala sensitivity to potentially threatening stimuli was greater under conditions of inattention. Likewise, Batty et al.,

(2003) found the ERP P1 (at 100 ms) sensitive to facial expressions, but only in the implicit emotion discrimination task. In fact, the neurophysiological studies that report a sensitivity for facial expression in the first 130 ms were mostly implicit emotional perception tasks (Eger et al., 2003; Eimer and Holmes, 2002; Halgren et al., 2000; Holmes et al., 2003; Kawasaki et al., 2001; Pizzagalli et al., 1999; Streit et al., 2003), while contrarily, the response to attended fearful faces was recorded only after 250 ms (Krolak-Salmon et al., 2001, 2003). Taken together, these results suggest that attention directed to the emotional content of faces could inhibit the fast network.

To determine whether the early frontal neural response to emotional faces can be modulated by emotion-specific attention, we used two tasks – an emotion and an identity discrimination task – in which subjects attended either to facial emotion or to facial identity. The use of MEG and beamformer source analyses provided the means to assess both the timing of face processing, with superior temporal resolution than fMRI, and spatial localization of face processing, with superior resolution than ERPs. We expected that evidence of a fast emotion-detection pathway would be more apparent when emotional expression was processed implicitly. As the early cortical emotional response has been reported primarily with fearful faces, we used happy and fearful faces to determine if this activation is triggered by facial expression more generally or only by threat-related stimuli.

2. Results

2.1. Behavioural performance

We measured accuracy and reaction times (RTs) for each participant (Fig. 1). Subjects made more errors in the emotion than the identity task (mean accuracy 78 and 84%, respectively; $F_{2,26}=4.951$; $p<0.05$) and responded more slowly in the emotion than the identity task (mean 678 and 549 ms, respectively; $F_{2,26}=19.79$; $p<0.001$). There was a significant interaction between task and facial expressions for both RT ($F_{4,52}=7.018$; $p<0.01$) and accuracy ($F_{4,48}=11.418$; $p<0.01$). Post-hoc tests indicated that in the emotion discrimination task, neutral faces were recognised more slowly than fearful ($p<0.05$) and happy faces (Fig. 1, top; $p<0.001$), and accuracy was higher (i.e., subjects correctly identified that an emotion that repeated) for happy faces (91%) than for neutral or fearful faces (Fig. 1, bottom; mean 71% and 74%, respectively; $p<0.001$). In the identity discrimination task, no differences were observed between emotions in accuracy or reaction time.

2.2. MEG data

The following results are given as the brain area location and the point of maximum activity in the Talairach coordinates. However, the coordinates should be used only as an approximation of the centroid of the clusters, as the MEG spatial resolution can be affected by the orientation or the depth of the source (Hillebrand and Barnes, 2002). Recent findings have shown that MEG can accurately localize both shallow, cortical

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