

Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging

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Abstract

Brain imaging studies in humans have shown that face processing in several areas is modulated by the affective significance of faces, particularly with fearful expressions, but also with other social signals such gaze direction. Here we review haemodynamic and electrical neuroimaging results indicating that activity in the face-selective fusiform cortex may be enhanced by emotional (fearful) expressions, without explicit voluntary control, and presumably through direct feedback connections from the amygdala. fMRI studies show that these increased responses in fusiform cortex to fearful faces are abolished by amygdala damage in the ipsilateral hemisphere, despite preserved effects of voluntary attention on fusiform; whereas emotional increases can still arise despite deficits in attention or awareness following parietal damage, and appear relatively unaffected by pharmacological increases in cholinergic stimulation. Fear-related modulations of face processing driven by amygdala signals may implicate not only fusiform cortex, but also earlier visual areas in occipital cortex (e.g., V1) and other distant regions involved in social, cognitive, or somatic responses (e.g., superior temporal sulcus, cingulate, or parietal areas). In the temporal domain, evoked-potentials show a widespread time-course of emotional face perception, with some increases in the amplitude of responses recorded over both occipital and frontal regions for fearful relative to neutral faces (as well as in the amygdala and orbitofrontal cortex, when using intracranial recordings), but with different latencies post-stimulus onset. Early emotional responses may arise around 120 ms, prior to a full visual categorization stage indexed by the face-selective N170 component, possibly reflecting rapid emotion processing based on crude visual cues in faces. Other electrical components arise at later latencies and involve more sustained activities, probably generated in associative or supramodal brain areas, and resulting in part from the modulatory signals received from amygdala. Altogether, these fMRI and ERP results demonstrate that emotion face perception is a complex process that cannot be related to a single neural event taking place in a single brain regions, but rather implicates an interactive network with distributed activity in time and space. Moreover, although traditional models in cognitive neuropsychology have often considered that facial expression and facial identity are processed along two separate pathways, evidence from fMRI and ERPs suggests instead that emotional processing can strongly affect brain systems responsible for face recognition and memory. The functional implications of these interactions remain to be fully explored, but might play an important role in the normal development of face processing skills and in some neuropsychiatric disorders.

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1. Introduction

Faces are multi-dimensional stimuli conveying many important signals simultaneously, each with a complex social and motivational significance. Faces provide not only distinctive

information about a person's identity, gender, or age, but also more subtle signals related to emotion, trustworthiness, attractiveness, as well as gaze direction or intention of other people. However, still little is known about how these various dimensions are coded and how they are integrated into a single face percept. Results from haemodynamic and electrophysiological brain imaging in humans have begun to uncover the distributed nature of neural activity arising during the perception of faces and facial expressions, and reveal important interactions taking place between regions in this network (see Gobbini & Haxby, 2007; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007; Puce,

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Epling, Thompson, & Carrick, 2007). Here we will provide an overview of recent studies specifically concerning the interaction between face and emotion processing.

A traditional view in cognitive neuropsychology has considered that different aspects of face processing involve different specialized parallel processing routes (Bruce & Young, 1986; Burton, Young, Bruce, Johnston, & Ellis, 1991; Hancock, Bruce, & Burton, 2000). This model was primarily derived from dissociations observed in brain-damaged patients (e.g., Adolphs, Tranel, Damasio, & Damasio, 1995; Bowers, Bauer, Coslett, & Heilman, 1985; Sergent & Villemure, 1989) and behavioral measures in healthy subjects (Bruce, 1986; Bruce & Young, 1986). According to the influential cognitive model proposed by Bruce and Young (1986), facial expression and facial identity are processed along two separate pathways after an initial stage of visual structural encoding, such that expression can be processed regardless of identity, and vice versa (Bauer, 1984; Breen, Caine, & Coltheart, 2000). Indeed, in some behavioral experiments, the accuracy and speed of expression categorization tasks is unaffected by familiarity of the faces (Young, Mcweeny, Hay, & Ellis, 1986), consistent with independent processing routes for identity and expression. However, in other experiments, expression judgments can be modulated by face identity and familiarity, even though identity judgments are independent of expression (Schweinberger & Soukup, 1998), suggesting asymmetric dependencies between these processes. Similarly, learning new faces is facilitated when these unfamiliar faces are initially seen with different expressions (Baudouin, Gilibert, Sansone, & Tiberghien, 2000; Sansone & Tiberghien, 1994), again suggesting some interactions between emotion and identity processing in some circumstances. On the other hand, prosopagnosic patients with lesions in associative visual cortices can still recognize facial expressions (Damasio, Damasio, & Van Hoesen, 1982; Damasio, Tranel, & Damasio, 1990; Sergent & Villemure, 1989), whereas deficits in expression recognition can occur in patients without prosopagnosia, and often seem selective for some categories of emotion depending on the site of brain lesion, e.g., fear after amygdala lesions (Adolphs et al., 1995), disgust after insula damage (Calder, Keane, Manes, Antoun, & Young, 2000), or anger after ventral basal ganglia lesions (Calder, Keane, Lawrence, & Manes, 2004). These neuropsychological data provide compelling evidence for specialized neural systems underlying explicit recognition of facial expressions.

More recently, functional brain-imaging studies have delineated an extensive neural network of areas implicated in face processing in humans. These include not only face-selective regions in lateral fusiform gyrus (Kanwisher, McDermott, & Chun, 1997) and inferior occipital gyrus (Hoffman & Haxby, 2000), but also other regions in the superior temporal sulcus (STS) and anterior temporal pole (Haxby, Hoffman, & Gobbini, 2000; Ishai, Ungerleider, Martin, & Haxby, 2000; Sergent, Ohta, & MacDonald, 1992), as well as several areas traditionally related to the limbic system such as the amygdala, orbitofrontal cortex, and retrosplenial or posterior cingulate regions (Gorno-Tempini et al., 1998; Ishai, Pessoa, Bickle, & Ungerleider, 2004; Shah et al., 2001; Gobbini & Haxby, 2007). In this distributed network, different regions have been associated with dissocia-

ble abilities, in keeping with the traditional cognitive models. For instance, distinct cortical regions in fusiform and superior temporal cortex may subserve the recognition of invariant (e.g., identity) versus changeable aspects (e.g., expression) of faces, respectively (see Haxby et al., 2001). Likewise, in the temporal domain, electrophysiological studies using EEG or MEG have suggested that face processing activates specialized neural systems in inferior temporal cortex within 200 ms post-stimulus onset, as typically indexed by the N170 component recorded over posterior scalp electrodes (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002; George, Evans, Fiori, Davidoff, & Renault, 1996; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002; or the M170 with MEG, see Liu, Harris, & Kanwisher, 2002) as well as by the N200 measured intracranially (Allison, Ginter et al., 1994; McCarthy, Puce, Belger, & Allison, 1999; Seeck et al., 2001), whereas distinct components with different latencies and topographies seem more specifically sensitive to expressions (e.g., Krolak-Salmon, Fischer, Vighetto, & Mauguier, 2001; Munte et al., 1998).

However, the exact role and dynamics of these different brain areas and of these different cognitive processes is still far from settled, although increasing evidence from imaging studies suggests that several subregions within the distributed face network may act in concert and in fact influence each other in an interactive manner, rather than truly operate independently one from another. Yet, the functional consequences of such interactions are just beginning to be understood. Here we review the neuroanatomical systems underlying the interactions of face perception with emotion processing and attention, and will mainly focus on fearful expressions, since this emotion category has been by far the more extensively studied in recent years, and is probably the most easily corroborated by corresponding animal studies on fear processing (Davis & Whalen, 2001; LeDoux, 1996).

The case of emotion expression is also worth considering because facial expressions constitute important social and biologically meaningful incentives (Ohman & Mineka, 2001), with different content corresponding to six basic emotions (Ekman & Friesen, 1976) plus several other secondary categories (Calder, Burton, Miller, Young, & Akamatsu, 2001; Eisenberg, 2000), all playing an important role in guiding interpersonal exchanges and behavior during social interactions. Thus, emotional signals perceived from a face are likely to influence how an unknown person will be approached and later remembered, and conversely, previous familiarity with a person might certainly influence how facial expressions will be perceived and interpreted. Moreover, interactions between emotion and face perception do not only constitute a central issue to understand the architecture of social functions in the human brain (Adolphs, 2003), but also provide important insights into more general mechanisms underlying reciprocal links between emotion and cognitive processes (see Drevets & Raichle, 1998). A better understanding of how emotion can modulate perception and cognition should thus help to go beyond strict modular views of neural architecture and information processing.

In this paper, we will review recent findings showing that face processing in visual cortex and other brain regions is mod-

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