Target Article

Let's face it: It's a cortical network

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Face perception elicits activation within a distributed cortical network in the human brain. The network includes visual ("core") regions, which process invariant facial features, as well as limbic and prefrontal ("extended") regions that process changeable aspects of faces. Analysis of effective connectivity reveals that the major entry node in the "face network" is the lateral fusiform gyrus and that the functional coupling between the core and the extended systems is content-dependent. A model for face perception is proposed, in which the flow of information through the network is shaped by cognitive demands.
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In a memorable scene from "Casablanca," Rick (Humphrey Bogart) looks at Ilsa (Ingrid Bergman) and says: "Here's looking at you, kid." Sixty years later, with the advent of modern functional brain imaging techniques, we have a new understanding of the neural mechanisms that mediate the "looking at you" effect. Face recognition is a highly developed skill in primates and the cognitive development of face perception suggests a special status for face processing. Shortly after birth, infants prefer to look at faces longer than at other objects (Morton and Johnson, 1991). The predilection of infants to imitate facial expressions at a very early age (Meltzoff and Moore, 1977) further suggests that face perception plays a central role in developing social interaction skills and language. It is therefore no surprise to discover that face perception is mediated by a specialized neural system in the brain.

In many fMRI studies of face perception, a localizer is used to identify the face-selective region in the fusiform gyrus, the "FFA," based on stronger response to faces than to assorted common objects (Kanwisher et al., 1997). Although the FFA also responds significantly to other objects (Ishai et al., 1999, 2000a; Haxby et al., 2001), it is commonly believed that the FFA is a face-selective "module," namely, a cortical region dedicated for the visual analysis of face stimuli. But is the FFA sufficient or even necessary for face perception? Functional MRI studies in which neural activity is not manifested by perceptual awareness provide evidence against *sufficiency*, whereas studies in which perceptual awareness is not caused by neural activity provide evidence against *necessity*. Some prosopagnosic patients, despite their profound inability to recognize faces, exhibit normal patterns of activation in the FFA (e.g., Marotta et al., 2001; Avidan et al., 2005), suggesting that activation in this region is not sufficient for face recognition, which likely depends on integration across cortical regions. Intriguingly, PS, a patient with bilateral and asymmetrical lesions in right inferior occipital gyrus (IOG) and left fusiform gyrus (FG), is prosopagnosic despite her intact left IOG and right FG (Rossion et al., 2003; Sorger et al., 2007), further suggesting that bilateral and distributed activation is necessary for face recognition. Adaptation experiments in this patient have shown that although her neural response to repeated objects in extrastriate object-selective regions was reduced, repeated and unrepeated faces evoked similar activation in the FG (Schiltz et al., 2006). It therefore seems that while activation in the FFA per se is not sufficient, adaptation in this region may be necessary for face recognition.

The recognition of facial identity is based on invariant facial features, whereas animated aspects of the face, such as speech-related movement and expression, contribute to social communication. When looking at faces, we rapidly perceive the gender, expression, age and mood. Processing information gleaned from the faces of others therefore requires the integration of activity across a network of cortical regions, and not within a single region-of-interest. Converging empirical evidence suggests that face perception is mediated by a distributed neural system (Sergent et al., 1992; Courtney et al., 1996; Haxby et al., 2000; Ishai et al., 2004, 2005). The cortical network for face perception includes the IOG and lateral FG, extrastriate regions that process the identification of individuals (Kanwisher et al., 1997; Ishai et al., 2000a; Grill-Spector et al., 2004; Rotshtein et al., 2005); the superior temporal sulcus (STS), where gaze direction and speech-related movements are processed (Calder et al., 2007; Hoffman and Haxby, 2000; Puce et al., 1998); the amygdala and insula, where facial expressions are processed (Breiter et al., 1996; Morris et al., 1996; Phillips et al., 1997; Vuilleumier et al., 2001; Ishai et al., 2004) and where a vigilant attitude toward unfamiliar people is maintained (Gobbini and Haxby, 2007); the inferior frontal gyrus (IFG), where semantic aspects are processed (Leveroni et al., 2000; Ishai et al., 2000b, 2002); and regions of the reward circuitry, including the nucleus accumbens and orbitofrontal cortex (OFC), where facial beauty and

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sexual relevance are assessed (Aharon et al., 2001; O'Doherty et al., 2003; Kranz and Ishai, 2006; Ishai, 2007). The existence of multiple face-selective regions in the human brain is also corroborated by intracranial recordings in epileptic patients undergoing brain surgery. Face-selective potentials were found in several sites along ventral occipitotemporal and lateral temporal cortices (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999), as well as the amygdala and prefrontal structures (Halgren et al., 1994a,b; Barbeau et al., in press).

When activation elicited by face stimuli is compared with activation evoked by scrambled faces, a distributed neural system of multiple, bilateral regions is revealed (Fig. 1). The activation within visual, limbic and prefrontal face-responsive regions is stimulus (e.g., unfamiliar, famous, neutral and emotional faces) and task (e.g., passive viewing, attractiveness rating) independent (Ishai et al., 2005; Kranz and Ishai, 2006). These consistent and replicable distributed patterns of activation are what make faces special: The neural signature of face perception is manifested not by activation solely within the FG but rather by activation within multiple regions that comprise a network. It is therefore surprising that despite the compelling evidence in favor of a network, virtually all published studies of face perception focus on activation in the FG (or on the STS and the amygdala in studies of social cognition and emotion).

With the identification and localization of all regions that are activated by faces, the effective connectivity within this network can be quantified. In a recent study, conventional SPM analysis (Friston et al., 1995) was combined with Dynamic Causal Modeling (DCM, Friston et al., 2003) to investigate the neural coupling and functional organization between and within the core and extended

systems. It has been found that during face viewing, the core system is functionally organized in a hierarchical, feed-forward architecture, with the IOG exerting influences on both the FG and STS. Moreover, the FG, but not the STS, exerted a strong causal influence on the extended system, namely, the amygdala, IFG and OFC. Finally, content-specific alterations in functional coupling were observed within this network: Viewing emotional faces increased the coupling between the FG and the amygdala, whereas viewing famous faces increased the coupling between the FG and the OFC cortex. The FG is therefore a major entry node in the cortical network that mediates face perception (Fairhall and Ishai, 2007). Previous DCM studies of face perception have also shown that effective connectivity between regions is task-specific. For example, viewing faces was associated with an increase in bottom-up, forward connectivity from extrastriate face-selective regions to prefrontal cortex, whereas the generation of mental images of faces was associated with an increase in top-down, backward connectivity from prefrontal to extrastriate regions (Mechelli et al., 2004). Similarly, perceptual decisions about faces resulted in an increase in top-down connectivity from ventral medial frontal cortex to the fusiform gyrus (Summerfield et al., 2006).

Electrophysiological studies in non-human primates revealed face-selective neurons not only in temporal cortex (e.g., Bruce et al., 1981; Perrett et al., 1982) but also in orbitofrontal (Thorpe et al., 1983) and prefrontal (Wilson et al., 1993) cortices. Furthermore, recent fMRI studies in behaving monkeys have revealed activation in multiple face-selective regions in visual (Pinsk et al., 2005; Tsao et al., 2006) as well as limbic and prefrontal cortices (Hadj-Buzaine et al., Society for Neuroscience abstract 2006). The exciting technical development of fMRI-guided electrophysiology (e.g.,
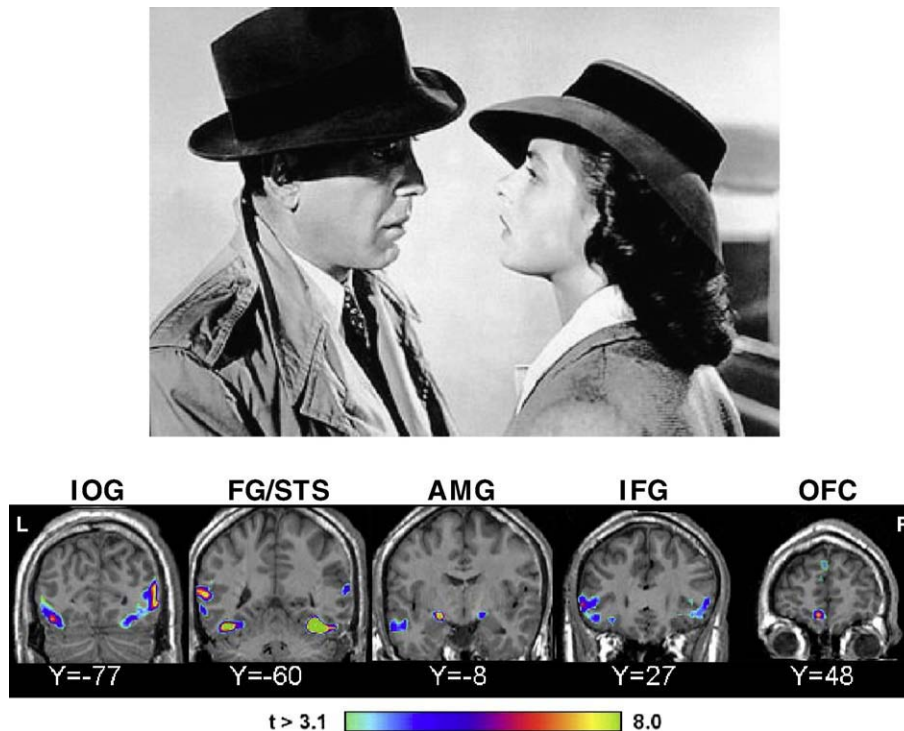

Fig. 1. "Here's looking at you." Viewing faces elicits activation within a distributed cortical network that includes visual, limbic and prefrontal regions. Coronal sections, taken from a representative subject, illustrate activation within the core (IOG, FG, STS) and extended (AMG, IFG, OFC) systems. Coordinates are in the Talairach space. L=left, R=right.
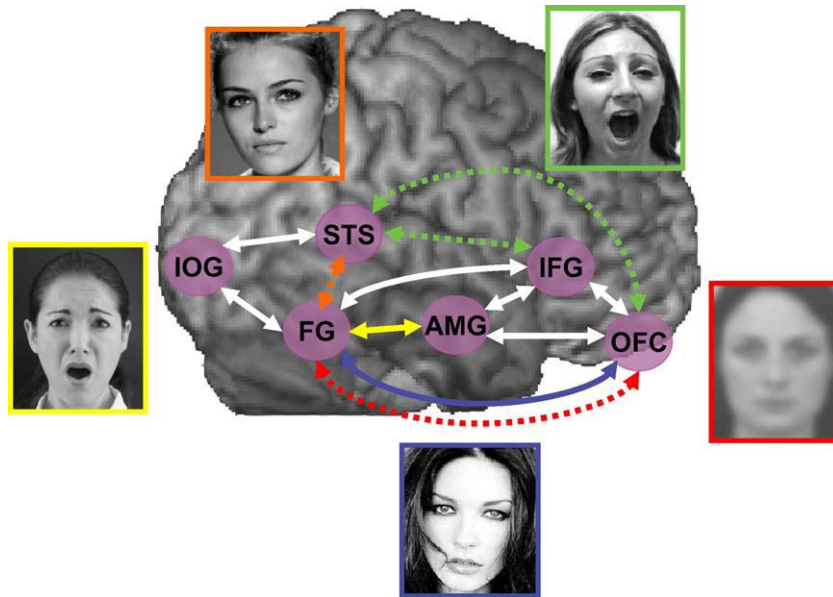
Fig. 2. Neural coupling among face-responsive regions is stimulus- and task-dependent. The model assumes reciprocal connections between all visual, limbic and prefrontal regions (although the strength of the connections may not be symmetrical). Viewing emotional faces increases the effective connectivity between the FG and the AMG (yellow), whereas viewing famous, attractive faces increases the coupling between the FG and the OFC (blue). New predictions are shown in dashed arrows: Attention to gaze direction would increase the coupling between the STS and the FG (orange); viewing animated faces would increase the coupling between the STS and the IFG/OFC (green); viewing indeterminate, low-spatial frequency faces would result in increased effective connectivity from the OFC to the FG (red).

Tsao et al., 2006) will enable not only the identification and functional characterization of all face-selective regions in the macaque brain but also the exploration of the homology between the face networks in monkey and man. Functional MRI-guided electrophysiology would provide data with superb spatial and temporal resolutions for thorough analyses of functional and effective connectivity within the cortical network for face perception. Future neuroanatomical models of face recognition will therefore have to integrate findings from human and non-human primates and from various imaging modalities.

As we currently do not have sufficient temporal information about the dynamics of face processing in the human brain, it is premature to propose a new functional model for face perception that integrates all available data. When Bruce and Young (1986) proposed their influential model for the recognition of familiar faces, they wrote: "In understanding face processing a crucial problem is to determine what uses people need to make of the information they derive from faces" (p. 306). In line with this statement and with the above mentioned DCM studies (Mechelli et al., 2004; Summerfield et al., 2006; Fairhall and Ishai, 2007), I would like to propose a working model for face perception that accounts for existing findings and from which new predictions are derived. The model depicted in Fig. 2 postulates bidirectional connections between all visual, limbic and prefrontal face-responsive regions (such large-scale integration could be mediated by synchronization of activity, as suggested by Rodriguez et al., 1999). The model further assumes that the flow of information through the face network is shaped by cognitive demands, namely, that the effective connectivity between regions depends on the nature of faces and task at hand (e.g., when we look for a friend in a crowded place, we have to match incoming visual input with faces stored in long-term memory, whereas when performing laboratory experiments such as gender discrimination, we have to focus on or

attend to specific facial features.) Consequently, several new testable predictions are suggested: Focusing attention on gaze direction would likely increase the coupling between the STS and the FG; viewing animated faces would increase the effective connectivity between the STS and the IFG/OFC; viewing disgusted faces would increase the coupling between the FG and the insula. Consistent with a recent study, which showed that the prefrontal cortex generates predictions that influence object processing in extrastriate regions (Bar et al., 2006), the model also predicts that an indeterminate facial input will increase the top-down connectivity from the OFC to the FG. Future studies will determine the extent to which various task demands are indeed associated with differential coupling among face-selective regions and the temporal dynamics of these activation patterns. Perhaps then we will understand how, when we watch Rick looking at Ilsa, our FG and STS engage limbic and prefrontal structures to create vivid memories of these immortal faces.

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