

Commentary

The Face Network: Overextended? (Comment on: “Let’s face it: It’s a cortical network” by Almit Ishai)

Alison J. Wiggett and Paul E. Downing*

School of Psychology, University of Wales, Aelidat Brigantia, Penrallt Road, Bangor LL57 2AS, UK

Received 26 September 2007; revised 29 October 2007; accepted 1 November 2007
Available online 23 December 2007

We offer a critique of Ishai’s [Ishai, A., 2008. Let’s face it: it’s a cortical network. *NeuroImage*. doi:10.1016/j.neuroimage.2007.10.040] comment on the value of considering the brain areas that support face perception as a network. We emphasise that this idea is not in opposition to the notion that the fusiform gyrus plays a key role in the visual analysis of faces. More important, we argue that the definition offered of the “extended” face network – areas showing a greater fMRI response to intact than scrambled face images – is too inclusive, and present data to indicate that at least two of the proposed “nodes” of this network also respond to non-face objects (compared to scrambled controls). Finally, we consider briefly how converging methodological approaches may augment the use of fMRI alone in understanding how anatomically widespread brain areas coordinate their activity in order to make sense of the human face.
© 2007 Elsevier Inc. All rights reserved.

The human face is a source of limitless fascination to the layperson and the neuroscientist alike. In a commentary published in the current issue of *NeuroImage*, Ishai (2008) takes stock of what we know about where and how in the brain faces are processed and proposes a distributed model of face perception to encompass some of the existing evidence. While we find much in Ishai’s comments to agree with, we offer a few critiques and amplifications in the hope of making a constructive contribution to the neuroscience of face perception.

We begin on a rhetorical point. In her opening paragraphs, Ishai (2008) implies that there are proponents of a model in which face perception and the fusiform face area (FFA; Kanwisher et al., 1997) are one and the same. This is a straw man. It may be true that “it is commonly believed that the FFA is a face-selective module” (p. 2), and Ishai reviews some of the evidence in favour of this position. But we very much doubt anyone would take the position that the FFA constitutes *the* face-perception system. Even the strongest proponent of a critical role for the FFA in face perception discusses,

in a recent review of this region, the important contributions of other brain areas (Kanwisher and Yovel, 2006). For various reasons, there has been intense interest in investigating the role of the FFA relative to other face-sensitive areas and Ishai’s reminder that we must also consider those other areas is useful. But it is perfectly sensible to interpret the FFA as a critical, face-selective region, and to hold at the same time that other regions also make an important contribution, perhaps by coordinating their activity in a functional network, as Ishai and others have suggested. These are not contradictory ideas.

If there is a network for face perception, what is its structure? In common with a previous proposal (Haxby et al., 2000), Ishai (2008) distinguishes between a “core” and an “extended” network, the former focused on the invariant perceptual features of faces and the latter on their affective and semantic aspects. The nodes of this network are defined by Ishai as those which respond in fMRI more to intact than to scrambled face images, and which do so across a variety of face types (e.g. familiar, unfamiliar) and tasks (Ishai et al., 2005). These criteria, however, are insufficient to describe an area as “face-selective” (Ishai, 2008, p. 4 and elsewhere). Comparing intact and scrambled images should do a good job balancing the activation of early retinotopic visual areas (so long as the image scrambling does not introduce high spatial-frequency confounds). But there are numerous reasons why other brain areas might respond more to intact than to scrambled faces, and these may have nothing to do with face perception. Indeed any area more sensitive to a meaningful, structured stimulus, as opposed to meaningless “noise”, would be identified by this contrast. To give a more specific example, consider the recent evidence showing that (as found for faces) emotional body expressions activate the amygdala more than neutral body expressions (Hadjikhani and de Gelder, 2003; see also Peelen and Downing, 2007). If both bodies and faces (as well as emotion more generally) modulate this region, we confront the question of how informative it is to describe the amygdala as being part of a “face perception” network.

To further illustrate our point about the “extended” network, we conducted a new analysis of data we have published previously

* Corresponding author.

E-mail address: p.downing@bangor.ac.uk (P.E. Downing).

Available online on ScienceDirect (www.sciencedirect.com).

(Downing et al., 2007), contrasting the response to intact versus scrambled images of everyday objects in a block design fMRI experiment. In a random-effects group-average analysis ($N=16$), we find increased activation to the intact objects in a variety of areas throughout the brain. Two in particular are strikingly similar to the activations highlighted by Ishai (2008) as part of the face perception network (see Fig. 1, and compare with Fig. 1 of Ishai, 2008-this issue): a medial orbitofrontal activation and a bilateral response that is consistent with activation of the amygdala (although we cannot rule out that this reflects instead, or additionally, activation of nearby medial temporal cortex). Thus, there appears to be engagement of these areas by both objects and faces, although more detailed comparisons would be required to test whether face and object responses in these areas can be disentangled.

Clearly at least some of the proposed nodes of the network are implicated in other processes outside of face perception. This is likely why they are designated “extended” rather than “core” areas, but then we might ask how useful it is to call them part of a face perception network? If the aim is to give a comprehensive account of *what happens in the brain when a face is perceived, per se*, then these “extended” areas should be included, and perhaps many more as well—such as V1, which must be involved in detecting edges in the image; parts of parietal cortex to attend to or ignore the face as required; or even the superior colliculus, to help Rick hold fixation on Ilsa’s eyes! Instead it seems truer to the “faces are special” argument made by Ishai and by others (although on different grounds) to focus on brain regions that make a unique and selective

contribution to face perception, and from this point of view the utility of the extended network concept is less clear.

At least two steps are fundamental to understanding a network: describing the functional contribution of each node and describing the nature of the connections among these nodes. fMRI experiments, particularly those that capitalise on priming effects (e.g., Winston et al., 2004; Loffler et al., 2005) or on the relationship between activation and overt behaviour or conscious experience (e.g., Yovel and Kanwisher, 2005; Grill-Spector et al., 2004; Andrews et al., 2002), have made strong contributions towards the former goal. Efforts towards the latter goal have recently increased, as evidenced for example by the dynamic causal modeling study reviewed by Ishai (Fairhall and Ishai, 2007).

However, although fMRI has been an engine behind the recent intense investigation into the neural basis of face perception, it may not be the ideal approach to examine the interconnections among network “nodes”, particularly when used on its own. This is reflected in both the inherently correlational nature of the method, and in the slow and blurry time course of the BOLD signal relative to neural activity. Other tools may be better suited. Ishai (2008-this issue) discusses characterisation of focal face-selective patches in the macaque with single-unit neurophysiology. It is noteworthy that macaque studies have also produced evidence on the remote functional and anatomical connections among cell populations implicated in face perception (O Scalaidhe et al., 1997; Webster et al., 1991). In humans, the investigation of chronic lesion patients with fMRI has proved particularly powerful. For example, lesions to the amygdala, but not to nearby hippocampus, reduce or eliminate the modulation of FFA activity by emotional face expressions—demonstrating a remote interaction of two hypothesised regions of the face network (Vuilleumier et al., 2004). Additionally, two recent studies using transcranial magnetic stimulation have shown anatomically and functionally specific effects of the disruption of posterior superior temporal sulcus (Pourtois et al., 2004) and the occipital face area (Pitcher et al., 2007) on face perception. These findings open the door to future studies that could use TMS to reversibly disrupt one or more of the face-network “nodes” and measure the disruptive effects elsewhere in the network with fMRI (cf. Ruff et al., 2006; Bestmann et al., 2005). Finally, intracranial EEG recordings of epilepsy patients have been used not only to characterise the evoked response to faces in specific cortical sites (e.g. McCarthy et al., 1999) but also to shed light on the interactions among remote cortical areas (e.g. Krolak-Salmon et al., 2004; Klopp et al., 2000).

In conclusion, we agree that face perception is likely supported by activity across several widespread anatomical regions constituting an interacting network. However, it is crucial to be clear about the basis on which we include particular regions as part of this network. Some of the areas proposed as part of the “extended” network are probably involved more generally in perceiving and interpreting socially relevant stimuli. Making this distinction will be critical for future studies using fMRI and other methods if they are to advance our understanding of the neural underpinnings of face perception.

References

- Andrews, T.J., Schluppeck, D., Homfray, D., Matthews, P., Blakemore, C., 2002. Activity in the fusiform gyrus predicts conscious perception of Rubin’s vase-face illusion. *NeuroImage* 17 (2), 890–901.
- Bestmann, S., Baudewig, J., Siebner, H.R., Rothwell, J.C., Frahm, J., 2005.

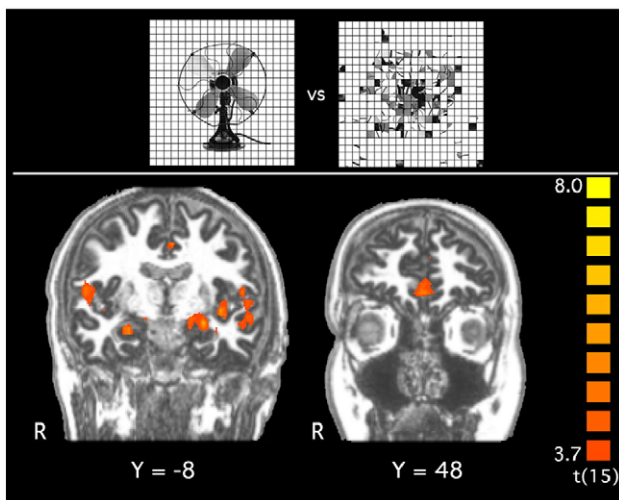


Fig. 1. Are all of the “extended” nodes of the proposed network face-selective? We compared the activation produced by intact minus scrambled images of assorted ordinary objects (examples at top) in a blocked-design fMRI experiment (see Downing et al., 2007, for a description of the procedural details). A random-effects, group average ($N=16$) contrast showed activations that are similar to some of the “extended network” areas proposed by Ishai (2008; see Fig. 1). In the lower panel, the left image shows increased activation to intact objects in a bilateral region, possibly the amygdala. The right image shows increased activity in the medial orbitofrontal cortex. Data are shown over an anatomical image taken from a single participant and are normalised to Talairach space. The Y coordinates indicate slice positions and match those from the third and fifth panel of Ishai (2008; Fig. 1, bottom).

- BOLD MRI responses to repetitive TMS over human dorsal premotor cortex. *NeuroImage* 28 (1), 22–29.
- Downing, P.E., Wiggett, A.J., Peelen, M.V., 2007. Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *J. Neurosci.* 27 (1), 226–233.
- Fairhall, S.L., Ishai, A., 2007. Effective connectivity within the distributed cortical network for face perception. *Cereb. Cortex* 17, 2400–2406.
- Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within-category identification. *Nat. Neurosci.* 7 (5), 555–562.
- Hadjikhani, N., de Gelder, B., 2003. Seeing fearful body expressions activates the fusiform cortex and amygdala. *Curr. Biol.* 13 (24), 2201–2205.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4 (6), 223–233.
- Ishai, A., 2008. Let's face it: it's a cortical network. *NeuroImage* 40 (2), 415–419.
- Ishai, A., Schmidt, C.F., Boesiger, P., 2005. Face perception is mediated by a distributed cortical network. *Brain Res. Bull.* 67 (1–2), 87–93.
- Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 361 (1476), 2109–2128.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.
- Klopp, J., Marinkovic, K., Chauvel, P., Nenov, V., Halgren, E., 2000. Early widespread cortical distribution of coherent fusiform face selective activity. *Hum. Brain Mapp.* 11 (4), 286–293.
- Krolak-Salmon, P., Hénaff, M.A., Vighetto, A., Bertrand, O., Mauguière, F., 2004. Early amygdala reaction to fear spreading in occipital, temporal, and frontal cortex: a depth electrode ERP study in human. *Neuron* 42 (4), 665–676.
- Loffler, G., Yourganov, G., Wilkinson, F., Wilson, H.R., 2005. fMRI evidence for the neural representation of faces. *Nat. Neurosci.* 8 (10), 1386–1390.
- McCarthy, G., Puce, A., Belger, A., Allison, T., 1999. Electrophysiological studies of human face perception. II: response properties of face-specific potentials generated in occipitotemporal cortex. *Cereb. Cortex* 9 (5), 431–444.
- O Scailaidhe, S.P., Wilson, F.A., Goldman-Rakic, P.S., 1997. Areal segregation of face-processing neurons in prefrontal cortex. *Science* 278 (5340), 1135–1138.
- Peelen, M.V., Downing, P.E., 2007. The neural basis of visual body perception. *Nat. Rev., Neurosci.* 8 (8), 636–648.
- Pitcher, D., Walsh, V., Yovel, G., Duchaine, B., 2007. TMS evidence for the involvement of the right occipital face area in early face processing. *Curr. Biol.* 17, 1568–1573.
- Pourtois, G., Sander, D., Andres, M., Grandjean, D., Reveret, L., et al., 2004. Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals. *Eur. J. Neurosci.* 20 (12), 3507–3515.
- Ruff, C.C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., et al., 2006. Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. *Curr. Biol.* 16 (15), 1479–1488.
- Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nat. Neurosci.* 7 (11), 1271–1278.
- Webster, M.J., Ungerleider, L.G., Bachevalier, J., 1991. Connections of inferior temporal areas TE and TEO with medial temporal-lobe structures in infant and adult monkeys. *J. Neurosci.* 11 (4), 1095–1116.
- Winston, J.S., Henson, R.N., Fine-Goulden, M.R., Dolan, R.J., 2004. fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *J. Neurophysiol.* 92 (3), 1830–1839.
- Yovel, G., Kanwisher, N., 2005. The neural basis of the behavioral face-inversion effect. *Curr. Biol.* 15 (24), 2256–2262.