

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/5785655>

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

Article in *NeuroImage* · May 2008

DOI: 10.1016/j.neuroimage.2007.10.040 · Source: PubMed

CITATIONS

336

READS

324

1 author:



Alomit Ishai

National Institutes of Health

49 PUBLICATIONS 8,284 CITATIONS

SEE PROFILE

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

Alumit Ishai*

Institute of Neuroradiology, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

Received 18 February 2007; revised 8 August 2007; accepted 27 October 2007
Available online 7 November 2007

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.

© 2007 Elsevier Inc. All rights reserved.

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

* Fax: +41 44 6353449.

E-mail address: ishai@hifo.uzh.ch.

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

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.,

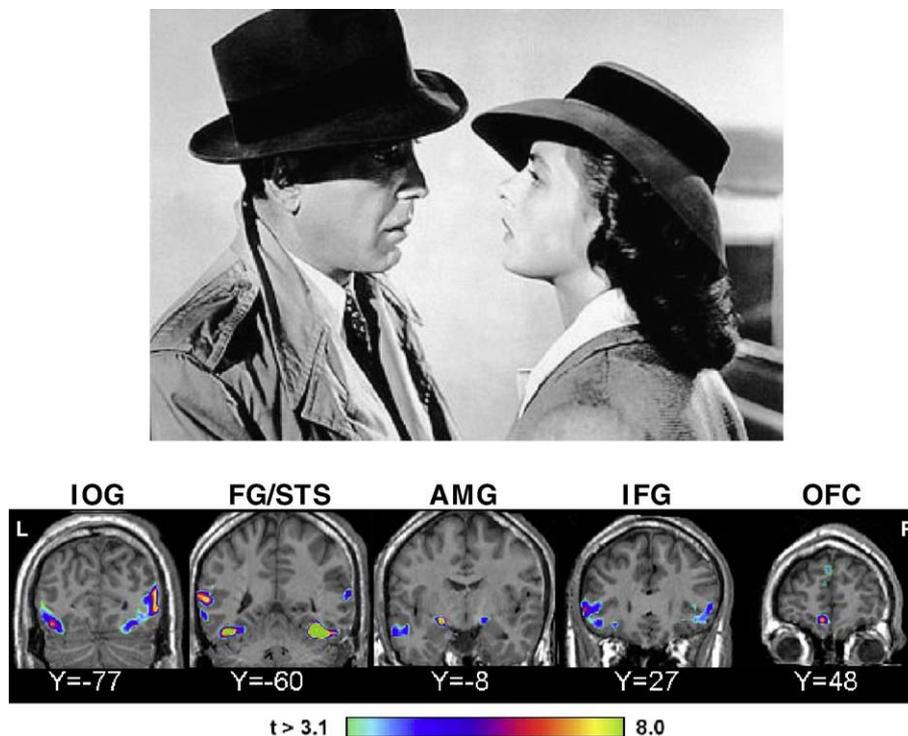


Fig. 1. “Here’s looking at you.” Viewing faces elicits activation within a distributed cortical network that includes visual, limbic and prefrontal regions. Coronal sections, taken from a representative subject, illustrate activation within the core (IOG, FG, STS) and extended (AMG, IFG, OFC) systems. Coordinates are in the Talairach space. L=left, R=right.

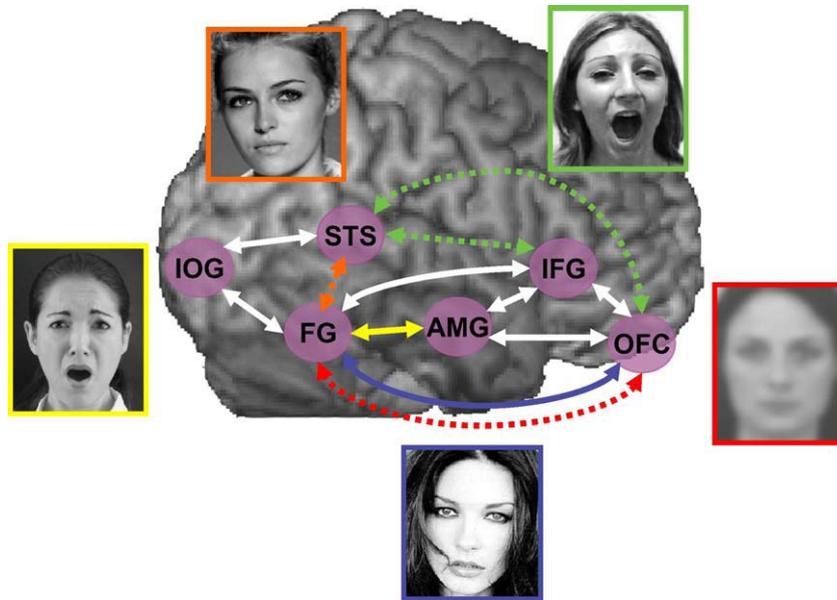


Fig. 2. Neural coupling among face-responsive regions is stimulus- and task-dependent. The model assumes reciprocal connections between all visual, limbic and prefrontal regions (although the strength of the connections may not be symmetrical). Viewing emotional faces increases the effective connectivity 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.

Acknowledgments

The author thanks Scott Fairhall, Kevan Martin and Christopher Summerfield for their helpful suggestions and the Swiss National Science Foundation grant 3200B0-105278 and Swiss National Center for Competence in Research: Neural Plasticity and Repair for their support.

References

- Aharon, I., Etcoff, N., Ariely, D., Chabris, C.F., O'Connor, E., Breiter, H.C., 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32, 537–551.
- Allison, T., Puce, A., Spencer, D.D., McCarthy, G., 1999. Electrophysiological

- studies of human face perception. I: potentials generated in occipito-temporal cortex by face and non-face stimuli. *Cereb. Cortex* 9, 415–430.
- Avidan, G., Hasson, U., Malach, R., Behrmann, M., 2005. Detailed exploration of face-related processing in congenital prosopagnosia: 2. Functional neuroimaging findings. *J. Cogn. Neurosci.* 17, 1150–1167.
- Bar, M., Kassam, K.S., Ghuman, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., Hämäläinen, M.S., Marinkovic, K., Schacter, D.L., Rosen, B.R., Halgren, E., 2006. Top-down facilitation of visual recognition. *Proc. Natl. Acad. Sci. U. S. A.* 103, 449–454.
- Barbeau, E.J., Taylor, M.J., Regis, J., Marquis, P., Chauvel, P., Liégeois-Chauvel, C., in press. Spatio temporal dynamics of face recognition. *Cereb. Cortex*. doi:10.1093/cercor/bhm140.
- Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S.E., Rosen, B.R., 1996. Response and habituation of the human amygdala during visual processing of facial expression. *Neuron* 17, 875–887.
- Bruce, V., Young, A., 1986. Understanding face recognition. *Br. J. Psychol.* 77, 305–327.
- Bruce, C.J., Desimone, R., Gross, C.G., 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J. Neurophysiol.* 46, 369–384.
- Calder, A.J., Beaver, J.D., Winston, J.S., Dolan, R.J., Jenkins, R., Eger, E., Henson, R.N.A., 2007. Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Curr. Biol.* 17, 20–25.
- Courtney, S.M., Ungerleider, L.G., Keil, K., Haxby, J.V., 1996. Object and spatial visual working memory activate separate neural systems in human cortex. *Cereb. Cortex* 6, 39–49.
- Fairhall, S.L., Ishai, A., 2007. Effective connectivity within the distributed cortical network for face perception. *Cereb. Cortex* 17, 2400–2406.
- Friston, K.J., Holmes, A.P., Poline, J.B., Grasby, P.J., Williams, S.C., Frackowiak, R.S., Turner, R., 1995. Analysis of fMRI time-series revisited. *NeuroImage* 2, 45–53.
- Friston, K.J., Harrison, L., Penny, W., 2003. Dynamic causal modelling. *NeuroImage* 19, 1273–1302.
- Gobbini, I.M., Haxby, J.V., 2007. Neural systems for recognition of familiar faces. *Neuropsychologia* 45, 32–41.
- Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within-category identification. *Nat. Neurosci.* 7, 555–562.
- Halgren, E., Baudena, P., Heit, G., Clarke, J.M., Marinkovic, K., Clarke, M., 1994a. Spatio-temporal stages in face and word processing. I. Depth-recorded potentials in the human occipital, temporal and parietal lobes. *J. Physiol. (Paris)* 88, 1–50.
- Halgren, E., Baudena, P., Heit, G., Clarke, J.M., Marinkovic, K., Chauvel, P., Clarke, M., 1994b. Spatio-temporal stages in face and word processing. 2. Depth-recorded potentials in the human frontal and Rolandic cortices. *J. Physiol. (Paris)* 88, 51–80.
- Haxby, J.V., Hoffman, E.A., Gobbini, I.M., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233.
- Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293, 2425–2430.
- Hoffman, E.A., Haxby, J.V., 2000. Distinct representation of eye gaze and identity in the distributed human neural system for face perception. *Nat. Neurosci.* 3, 80–84.
- Ishai, A., 2007. Sex, beauty and the orbitofrontal cortex. *Int. J. Psychophys.* 63, 181–185.
- Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., Haxby, J.V., 1999. Distributed representation of objects in the human ventral visual pathway. *Proc. Natl. Acad. Sci. U. S. A.* 96, 9379–9384.
- Ishai, A., Ungerleider, L.G., Martin, A., Haxby, J.V., 2000a. The representation of objects in the human occipital and temporal cortex. *J. Cogn. Neurosci.* 12, 35–51.
- Ishai, A., Ungerleider, L.G., Haxby, J.V., 2000b. Distributed neural systems for the generation of visual images. *Neuron* 28, 979–990.
- Ishai, A., Haxby, J.V., Ungerleider, L.G., 2002. Visual imagery of famous faces: effects of memory and attention revealed by fMRI. *NeuroImage* 17, 1729–1741.
- Ishai, A., Pessoa, L., Bikle, P.C., Ungerleider, L.G., 2004. Repetition suppression of faces is modulated by emotion. *Proc. Natl. Acad. Sci. U. S. A.* 101, 9827–9832.
- Ishai, A., Schmidt, C.F., Boesiger, P., 2005. Face perception is mediated by a distributed cortical network. *Brain Res. Bull.* 67, 87–93.
- 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, 4302–4311.
- Kranz, F., Ishai, A., 2006. Face perception is modulated by sexual preference. *Curr. Biol.* 16, 63–68.
- Leveroni, C.L., Seidenberg, M., Mayer, A.R., Mead, L.A., Binder, J.R., Rao, S.M., 2000. Neural systems underlying the recognition of familiar and newly learned faces. *J. Neurosci.* 20, 878–886.
- Marotta, J.J., Genovese, C.R., Behrmann, M., 2001. A functional MRI study of face recognition in patients with prosopagnosia. *NeuroReport* 12, 1581–1587.
- 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, 431–444.
- Mechelli, A., Price, C.J., Friston, K.J., Ishai, A., 2004. Where bottom-up meets top-down: neuronal interactions during perception and imagery. *Cereb. Cortex* 14, 1256–1265.
- Meltzoff, A.N., Moore, M.K., 1977. Imitation of facial and manual gestures by human neonates. *Science* 198, 74–78.
- Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., Dolan, R.J., 1996. A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature* 383, 812–815.
- Morton, J., Johnson, M.H., 1991. Conspic and conlem—a 2-process theory of infant face recognition. *Psychol. Rev.* 98, 164–181.
- O’Doherty, J., Winston, J., Critchley, H.D., Perrett, D., Burt, D.M., Dolan, R.J., 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia* 41, 147–155.
- Perrett, D.I., Rolls, E.T., Caan, W., 1982. Visual neurons responsive to faces in the monkey temporal cortex. *Exp. Brain Res.* 47, 329–342.
- Phillips, M.L., Young, A.W., Senior, C., Brammer, M., Andrew, C., Calder, A.J., Bullmore, E.T., Perrett, D.I., Rowland, D., Williams, S.C.R., Gray, J.A., David, A.S., 1997. A specific neural substrate for perceiving facial expressions of disgust. *Nature* 389, 495–498.
- Pinsk, M.A., DeSimone, K., Moore, T., Gross, C.G., Kastner, S., 2005. Representations of faces and body parts in macaque temporal cortex: a functional MRI study. *Proc. Natl. Acad. Sci. U. S. A.* 102, 6996–7001.
- Puce, A., Allison, T., Bentin, S., Gore, J.C., McCarthy, G., 1998. Temporal cortex activation in humans viewing eye and mouth movements. *J. Neurosci.* 18, 2188–2199.
- Puce, A., Allison, T., McCarthy, G., 1999. Electrophysiological studies of human face perception: III. Effects of top-down processing on face-specific potentials. *Cereb. Cortex* 9, 445–458.
- Rodriguez, E., George, N., Lachaux, J.P., Martinerie, J., Renault, B., Varela, F.J., 1999. Perception’s shadow: long-distance synchronization of human brain activity. *Nature* 397, 430–433.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A.M., Lazeyras, F., Mayer, E., 2003. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain* 126, 2381–2395.
- Rotshtein, P., Henson, R.N., Treves, A., Driver, J., Dolan, R.J., 2005. Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nat. Neurosci.* 8, 107–113.
- Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain* 115, 15–36.

- Schiltz, C., Sorger, B., Caldara, R., Ahmed, F., Mayer, E., Goebel, R., Rossion, B., 2006. Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. *Cereb. Cortex* 16, 574–586.
- Sorger, B., Goebel, R., Schiltz, C., Rossion, B., 2007. Understanding the functional neuroanatomy of acquired prosopagnosia. *NeuroImage* 35, 836–852.
- Summerfield, C., Egner, T., Greene, M., Koechlin, E., Mangels, J., Hirsch, J., 2006. Predictive codes for forthcoming perception in the frontal cortex. *Science* 314, 1311–1314.
- Thorpe, S.J., Rolls, E.T., Maddison, S., 1983. Neuronal activity in the orbitofrontal cortex of the behaving monkey. *Exp. Brain Res.* 49, 93–115.
- Tsao, D.Y., Freiwald, W.A., Tootell, R.B., Livingstone, M.S., 2006. A cortical region consisting entirely of face-selective cells. *Science* 311, 670–674.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 30, 829–841.
- Wilson, F.A., Scaldie, S.P., Goldman-Rakic, P.S., 1993. Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science* 260, 1955–1958.