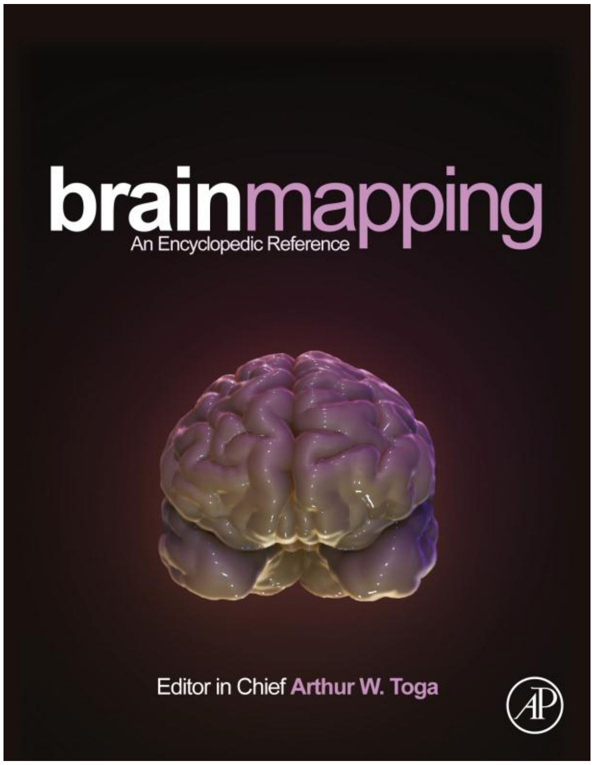

Rossion B. (2015) Face Perception. In: Arthur W. Toga, editor. *Brain Mapping: An Encyclopedic Reference*, vol. 2, pp. 515-522. Academic Press: Elsevier.

Face Perception

B Rossion, Université catholique de Louvain, Louvain-la-Neuve, Belgium

Nomenclature

FFA	Fusiform face area
IOG	Inferior occipital gyrus
IT	Inferotemporal cortex
OFA	Occipital face area
pSTS	Posterior section of the superior temporal sulcus
VOT	Ventral occipitotemporal cortex

Introduction

The human face is a familiar, complex, multidimensional visual pattern, conveying a wide variety of information about an individual (identity, sex, age, mood, ethnical origin, etc.). Understanding the neural basis of *face perception* means understanding how, from sensory information, the human brain builds a visual representation – an internal image – of a face. Face perception concerns the ability to detect a face in a visual scene (*face detection*), to discriminate a particular face from other faces (*face individualization* or *individual face discrimination*), and to associate a percept with a stored representation of a particular face in memory (*face recognition*).

The neural basis of face perception has two roots. The first source of information about the neural basis of face perception is from the study of brain-damaged patients complaining of face recognition impairments: *acquired prosopagnosia* (Bodamer, 1947). Although most patients with prosopagnosia complain of difficulties in object recognition, some patients have no difficulties in object recognition ('pure prosopagnosia'; Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). Brain damage causing prosopagnosia is variable across patients, with the lesions covering almost all the ventral surface of the occipitotemporal cortex, from the occipital pole to the temporal pole, with a right hemispheric dominance (**Figure 1**; e.g., Barton, Press, Keenan, & O'Connor, 2002).

Historically, the second source of information comes from the study of single neurons responding selectively to faces in the monkey inferotemporal cortex (IT; Gross, Rocha-Miranda, & Bender, 1972; Weiner & Grill-Spector, 2013 for review). Face-selective neurons are found in concentrations of up to 10–20% in several cytoarchitectonically defined areas of the upper and lower banks of the superior temporal sulcus (STS), in the monkey IT. Optical imaging studies have shown that these cells are organized in clusters of contiguous cortical columns (Wang, Tanaka, & Tanifuji, 1996). According to fMRI studies of the monkey brain, up to six clusters of face-selective regions can be disclosed in the monkey brain, from the posterior STS to the anterior IT cortex (Tsao, Moeller, & Freiwald, 2008). In some of these clusters, the proportion of face-selective neurons is between 40% and 70% (Bell et al., 2011) and can reach 97% for a few locations in the center of an fMRI-defined face-selective region (Tsao, Freiwald, Tootell, & Livingstone, 2006). However, the relationship between these face-selective clusters in the monkey brain and the face-selective clusters in the human brain remains unknown (Yovel & Freiwald, 2013).

A Large Set of Functional Face-Selective Clusters

The first neuroimaging studies of face perception in the healthy human brain were performed by means of positron emission tomography (PET; Sergent, Ohta, & MacDonald, 1992). They reported a right hemispheric dominance for face compared to object perception in a large set of areas of the ventral occipitotemporal (VOT) cortex, from the occipital pole to the temporal pole. These observations, as well as the involvement of the STS, were confirmed by the early fMRI studies in this field (Puce, Allison, Gore, & McCarthy, 1995). More specifically, comparing faces to pictures of nonface objects (a '*functional face localizer*'; Kanwisher, McDermott, & Chun, 1997) generally leads to at least three bilateral clusters of activation: the lateral part of the inferior occipital gyrus (IOG or 'occipital face area' (OFA); e.g., Gauthier et al., 2000a), the middle fusiform gyrus (labeled the 'fusiform face area' (FFA); Kanwisher et al., 1997), and the posterior section of the superior temporal sulcus (pSTS; e.g., Puce, Allison, Bentin, Gore, & McCarthy, 1998; **Figure 2**). These three areas would form the 'core' system for face perception, providing inputs to an extended system of temporal and prefrontal regions involved in emotional and semantic processing associated with person recognition (Atkinson & Adolphs, 2011; Haxby, Hoffman, & Gobbini, 2000; **Figure 2**).

These three areas present a strong right hemispheric dominance and are located outside of the retinotopic visual cortex (Halgren, Dale, Sereno, Tootell, Marinkovic, & Rosen, 1999; Weiner & Grill-Spector, 2012). Across individual brains, they vary substantially in spatial location, extent, and hemispheric dominance (Rossion, Hanseeuw, & Dricot, 2012), with the FFA being bilateral or even or larger in the left hemisphere in left-handed individuals (Bukowski, Dricot, Hanseeuw, & Rossion, 2013). Beyond these areas, face-selective responses have also been reported in the anterior section of the inferotemporal cortex, also with a right hemisphere advantage (Rajimehr, Young, & Tootell, 2009).

Even More Face-Selective Clusters

Recent fMRI studies have also reported a face-selective cluster in the posterior fusiform gyrus, more medial and anterior to the OFA: the *FFA-1* or *pFus* (Weiner & Grill-Spector, 2012, 2013; **Figure 3**), different from the anteriorly located FFA ('FFA-2' or 'midFus'). Another face-selective cluster has been identified in the anterior fusiform gyrus (*antFus*, Rossion et al., 2012, **Figure 3**). Two or even three different face-selective

Brain Mapping: An Encyclopedic Reference, (2015), vol. 2, pp. 515-522

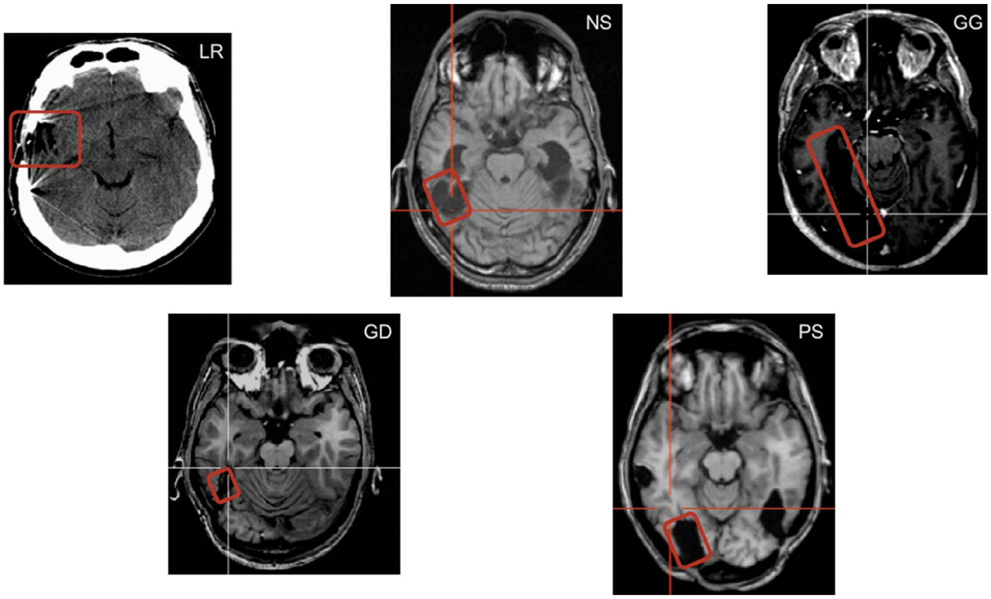

Figure 1 Variability of brain damage leading to prosopagnosia in five cases with the main, or only, lesion highlighted. PS (trauma with multiple hemorrhages; Rossion et al., 2003), GG (stroke; Busigny et al., 2010), and LR (trauma; Bukach, Bub, Gauthier, & Tarr, 2006) present with pure prosopagnosia. NS has bilateral damage following trauma and has a general form of visual agnosia, with impairment at both face and object recognition (Delvenne, Seron, Coyette, & Rossion, 2004). GD presented with a prosopagnosia and metamorphopsia following a small metastasis in the right middle fusiform gyrus (Seron et al., 1995).

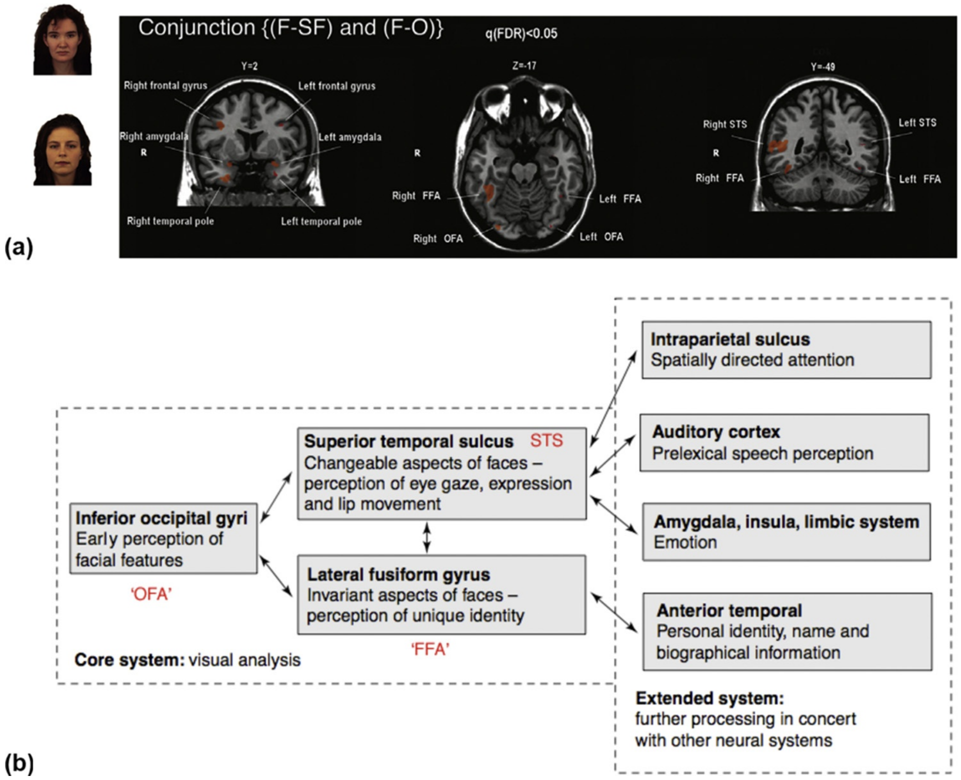

Figure 2 (a) Whole-brain (group) analysis of a large number of subjects ($N = 36$) presented with faces, scrambled faces and objects (cars; adapted from Rossion, B., Hanseeuw, B., & Dricot, L. (2012). Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis. *Brain and Cognition*, *79*, 138–157). Even though the group analysis only reveals the overlapping face-selective clusters in (normalized) individual brains, many face-selective clusters are recorded throughout the brain (here, FFA, OFA, pSTS, amygdala, temporal pole, prefrontal and cortex, all with a right hemispheric dominance). (b) Haxby et al. (2000)'s neurofunctional model of face processing, postulating a hierarchy of face-selective areas with a core system of three areas (FFA, OFA, and STS) being involved in visual analysis of faces.

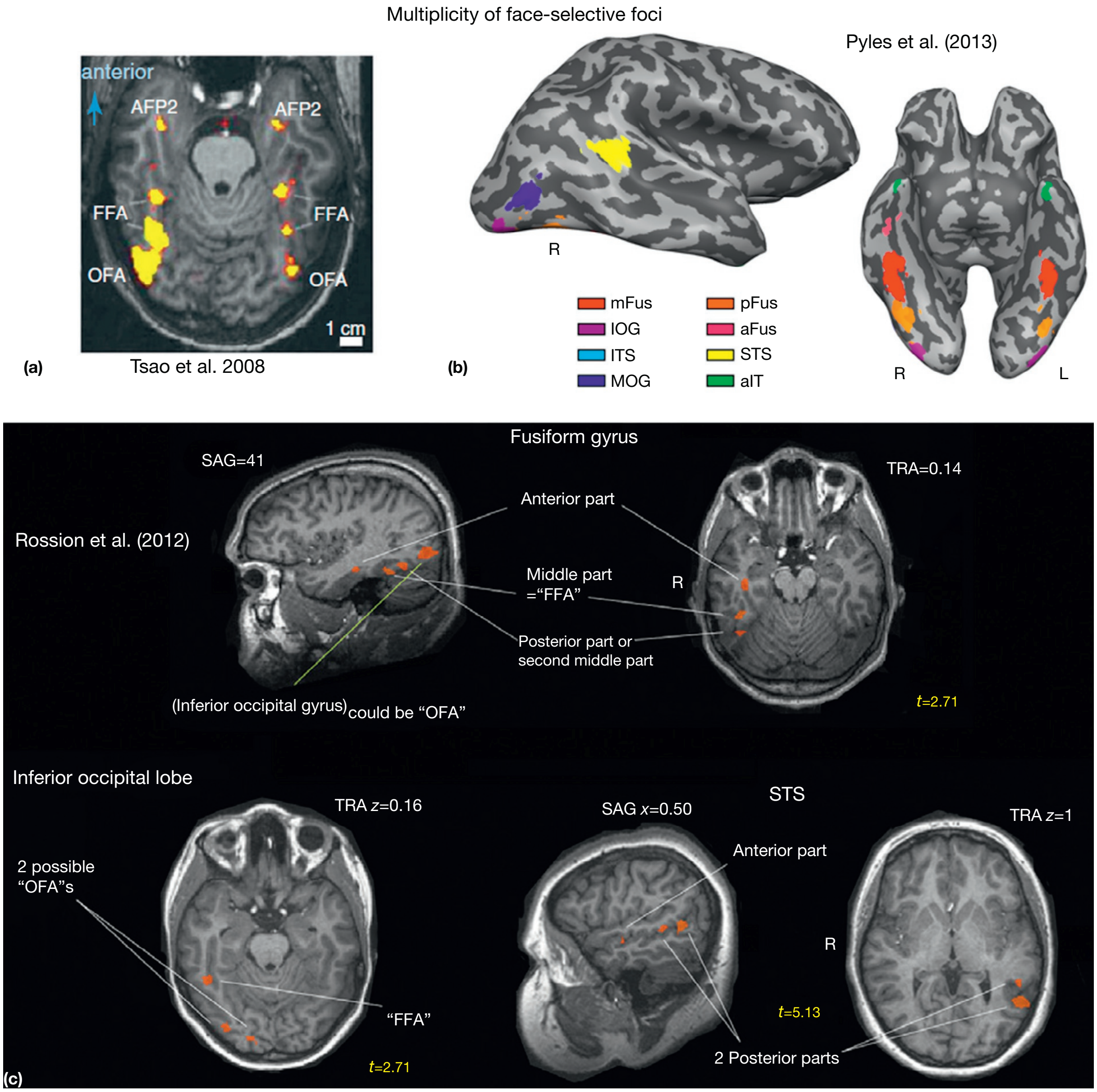

Figure 3 Showing the multiple face-selective clusters that can be observed in individual brains, from the IOG to the tip of the temporal lobe, and also along the STS. Note that when multiple clusters are found in the occipital cortex or fusiform gyrus (a, right hemisphere), researchers are faced with the difficulty of choosing between separating or lumping these clusters (see Rossion et al., 2012; Weiner & Grill-Spector, 2012). Clusters that are in fact different may be both labeled 'FFA' and 'OFA' in different individual brains, making questionable the use of such labels (Rossion et al., 2012; Weiner & Grill-Spector, 2012). Figures adapted from (a) Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 19514–19519., (b) Pyles, J. A., Verstynen, T. D., Schneider, W., & Tarr, M. J. (2013). Explicating the face perception network with white matter connectivity. *PLoS One*, *8*(4), e61611., and (c) Rossion, B., Hanseeuw, B., & Dricot, L. (2012). Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis. *Brain and Cognition*, *79*, 138–157.

clusters have also been identified in the STS (Pinsk et al., 2009), as well as two distinct face-selective clusters in the inferior occipital cortex (OFA1 and OFA2; e.g., Pyles, Verstynen, Schneider, & Tarr, 2013). Thus, considering the whole VOT cortex and the STS, numerous face-selective clusters can potentially be identified in an individual human brain.

How Should the Cortical Face Network Be Defined?

In fMRI, the term 'selective' generally means that the cluster or area responds *more* to faces than objects, but not exclusively to faces. Few fMRI studies of face perception investigate all the face-selective clusters, focusing often solely on the FFA. Yet, there is no evidence that the FFA is more important for face perception than other face-selective areas. The FFA may be disclosed most often because of reasons that have nothing to do with its functional role (e.g., larger blood vessels in the vicinity of this area, reduced fewer magnetic susceptibility artifacts in the middle fusiform gyrus than in other areas).

This is one of the reasons why using the same statistical threshold to define all of the face-selective areas is not adequate (Rossion et al., 2012). While some studies have reported that the FFA is the most face-selective area (Tsao et al., 2008), part of the FFA selectivity may be accounted for by low-level visual cues (color and spatial frequency, Rossion et al., 2012). Lesion studies rather suggest that the lateral part of the right inferior occipital cortex is perhaps the most critical area: this is the location of the largest overlap of lesions causing prosopagnosia (Bouvier & Engel, 2006) and where electrical stimulation causes transient prosopagnosia (Jonas et al., 2012).

Since numerous face-selective clusters can be identified in the VOT cortex in some individual brains, the labeling of each of these clusters has become very subjective and open to interpretation. Anatomical constraints and spatial relationships to other functional areas will have to be used increasingly to help in defining regions such as the FFA and OFA across individual brains more objectively (Weiner & Grill-Spector, 2012). However, it is unknown whether every face-selective cluster in the VOT cortex has a specific anatomical signature, as characterized by cytoarchitectony. Rather, a face-selective cluster may concern a *subset* of an anatomical area, and there is no reason to expect that all individual human brains have the same amount of well-identified face-selective clusters in the VOT cortex. This points to analyses performed at the single subject level in future work, without forcing some arbitrary correspondence between labeled clusters across different individual brains.

Neurofunctional Decomposition

At present, the function(s) of each of the face-selective clusters of the human brain remains largely unknown. Unfortunately, the debate about the domain specificity of the neural basis of face perception has focused almost entirely on the FFA (Kanwisher, 2000; Tarr & Gauthier, 2000). FFA activation increases for nonface objects of visual expertise, such as car or bird pictures in car or bird experts, respectively (Gauthier, Skudlarski, Gore, & Anderson, 2000b). However, increases of FFA activation to nonface visual objects of expertise have not been often reported (Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Rhodes, Byatt, Michie, & Puce, 2004).

According to a hierarchical view, the OFA is the first face-selective relay of information, being associated with the '*early perception of facial features*' (**Figure 2(b)**). Processing in the OFA would be based on facial parts such as the eyes, nose, and mouth (Arcurio, Gold, & James, 2012; Haxby et al., 2000; Pitcher, Walsh, & Duchaine, 2011). This area would feed information forward to the FFA and pSTS for more elaborated processes. While the FFA would be associated with the invariant aspects of faces, in particular the perception of face identity, the pSTS would decode changeable aspects of faces such as the perception of eye gaze and expression (Haxby et al., 2000; **Figure 2(b)**). Overall, the role of the STS in changeable aspects of faces has been well supported, with studies showing its activation to changes of facial expressions and eye gaze direction (Engell & Haxby, 2007). Yet, the area showing sensitivity to changes of facial expression and gaze may be located more anteriorly in the STS, rather than in the face-selective pSTS area (Winston, Henson, Fine-Goulden, & Dolan, 2004).

The OFA is positioned closer to low-level visual areas than the FFA and shares many characteristics of retinotopic cortex, including increased position sensitivity and foveal–peripheral eccentricity maps (Levy, Hasson, Avidan, Hendler, & Malach, 2001). Hence, neurons in the OFA presumably have smaller receptive fields and show less invariance than in the FFA. However, given the low temporal resolution of fMRI, whether face selectivity emerges first in the IOG ('OFA') and triggers face selectivity in the fusiform gyrus ('FFA') remains unclear. This hierarchical view is contradicted by observations that damage to the right IOG, with no OFA, does not prevent ipsilateral FFA activation (Rossion et al., 2003; **Figure 4**).

Moreover, stimuli that are perceived as faces based on their global configuration only, such as 'Mooney' faces or Arcimboldo paintings, activate primarily the right FFA without face-selective responses in the OFA (Rossion, Dricot, Goebel, & Busigny, 2011). Also, the earliest face-selective response may appear in the FFA rather than the OFA when using a slow dynamic stimulation sequence in fMRI (Jiang et al., 2011; **Figure 5**).

Altogether, these findings suggest that the visual input could be initially categorized as a face in the fusiform gyrus ('FFA'). This initial representation would be rather coarse, sufficient for accurate detection of the stimulus as a generic face (see also Goffaux et al., 2011). In order to be discriminated from one another, faces also have to be analyzed further, at a fine-grained level.

Face Individualization Through fMR Adaptation

Both the FFA and OFA are involved in such individualization of faces, as demonstrated by fMRI adaptation, or repetition suppression, in which the neural response to a given stimulus is reduced when that stimulus is repeated (Grill-Spector & Malach, 2001). Release from adaptation to face identity (i.e., face A preceded by face B vs. face A preceded by face A) has been found in both areas but not, or only weakly, in the pSTS (Davies-Thompson, Gouws, & Andrews, 2009; **Figure 6**). fMR-adaptation studies have shown that both the FFA and OFA are sensitive to changes of a subset of the facial parts when they are inserted in whole faces or to *relative distances* between these parts in whole faces (Rhodes, Michie, Hughes, & Byatt, 2009). There is also a higher response for different than identical faces for upright but not for inverted faces in both the FFA and OFA (Yovel & Kanwisher, 2005). Both areas also show increased activation to the illusion of change of identity on the top halves of faces when these top halves are aligned with different bottom halves (Schiltz & Rossion, 2006; **Figure 6**). These observations have been taken as evidence for holistic/configural representation of individual faces in the right FFA in particular. It has also been suggested that the FFA codes individual faces relative to a norm in a face space (Loffler, Yourganov, Wilkinson, & Wilson, 2005), but these observations are controversial (Davidenko, Remus, & Grill-Spector, 2012; Kahn & Aguirre, 2012).

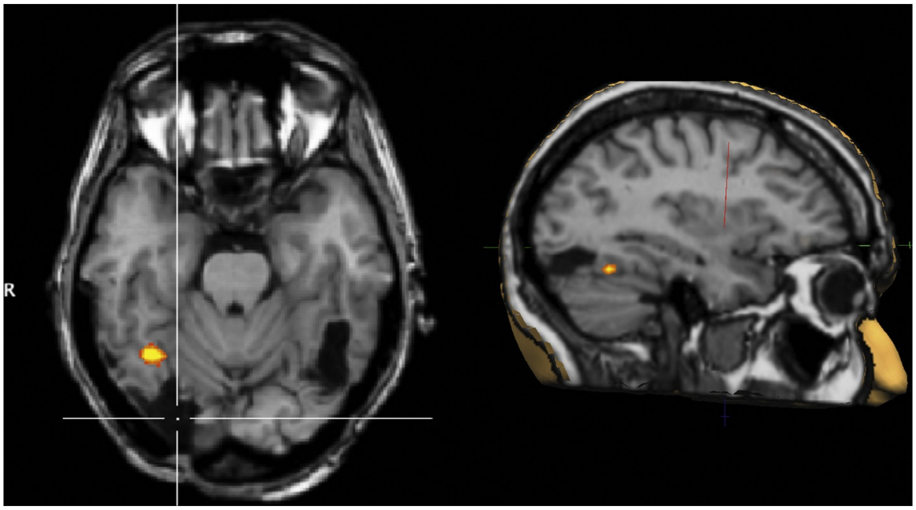

Figure 4 Face-selective response in the right middle fusiform gyrus of a prosopagnosic patient (PS, Rossion et al., 2003), despite brain damage to the ipsilateral inferior cortex and no evidence of ipsilateral posterior face-selective clusters (no right 'OFA').

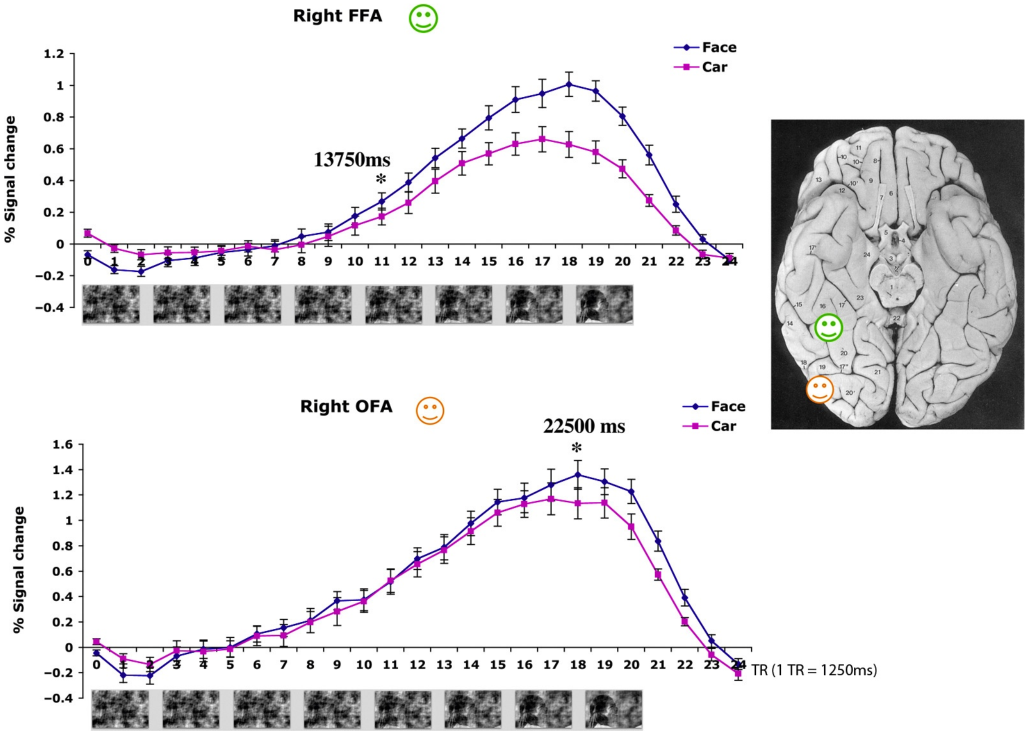

Figure 5 Slowing down the appearance of a face and keeping constant the low-level stimulation points to a temporal reverse hierarchy in the emergence of face selectivity in the human brain (Jiang et al., 2011). Note that the absolute activation starts in the OFA (volume 6, corresponding to 7500 ms for repetition times of 1250 ms) ahead of the FFA (data point 9). However, this initial activation does not differ between faces and cars. The onset of the difference between faces and cars emerges earlier in the FFA (significant at 13750 ms) than the OFA (significant at 22 500 ms).

Multivariate Pattern Analysis and the 'Decoding' of Face Identity

Over recent years, there has been a growing interest for multivariate pattern analysis (MVPA) methods in fMRI, in which the pattern of variability across voxels within a given area (or a large part of the brain; e.g., Haxby et al., 2001) is considered rather than merely the global response of the area (O'Toole et al., 2007). However, this approach may not be well suited to discriminate face exemplars, which are coded at the level of single neurons, at a level of resolution that is well below the single voxel (Rolls, 1992; Young & Yamane, 1992). Hence, MVPA analyses have generally failed to report individual face discrimination at the level of the FFA (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Natu et al., 2010) or been only able to discriminate very limited sets of highly distinctive faces just above chance level (Goesart & Op de Beeck, 2013; Nestor, Plaut, & Behrmann, 2011).

Connectivity and Functional Dynamics

Diffusion tensor imaging studies have suggested strong white-matter connections between the OFA and FFA with connections up to a face-selective cluster in the right temporal pole and between the FFA and several clusters in the lateral occipital cortex (Pyles et al., 2013). No connectivity has been disclosed between STS and FFA and other face-selective regions. The face-selective areas appear to be highly correlated with one another, especially within the same hemisphere (Davies-Thompson & Andrews, 2012). The strength of the correlation at rest between the OFA and FFA is also related to face but not object perception tasks (Zhu, Zhang, Luo, Dilks, & Liu, 2011). Although dynamic causal modeling analysis has suggested a simple feedforward relationship between face-selective regions of occipitotemporal cortex (i.e., input entering OFA and then modulating FFA; Fairhall & Ishai, 2007), these studies assumed that driving input enters OFA only and did not test alternative models in which input enters other visual regions. Moreover, the regions tested were not face-selective. Other studies have reported intrinsic bilateral connections between the right IOG and middle fusiform gyrus during face perception (Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007), these interactions being weighted differently according to the kind of repetition suppression effects observed (Ewbank, Henson, Rowe, Stoyanova, & Calder, 2013). A fundamental problem remains the low temporal resolution of fMRI. It is very likely that both feedforward and feedback connections exist between these areas and they may be involved differentially depending on the kind of task performed. Given that individual face perception, and even face recognition, is a process that takes place essentially within the first 200 ms following stimulus onset (Caharel, Ramon, & Rossion, 2014; Jacques, d'Arripe, & Rossion, 2007), a dynamic model of face perception cannot rest on fMRI evidence of the normal brain, in which

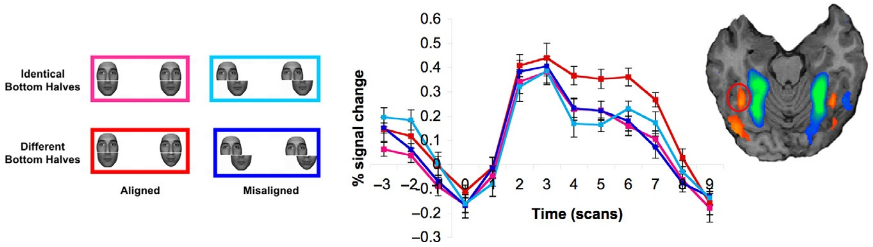

Figure 6 Blood oxygen level dependent (BOLD) response in the right FFA to the presentation of composite faces. The exact same top half is repeated in all conditions and attended. When the top halves are aligned with different bottom halves, they are perceived as different, leading to a release from fMR adaptation. This effect is not found for misaligned faces, or when aligned faces are presented upside down (Schiltz & Rossion, 2006). Similar but weaker effects are observed in the other face-selective areas such as the OFA.

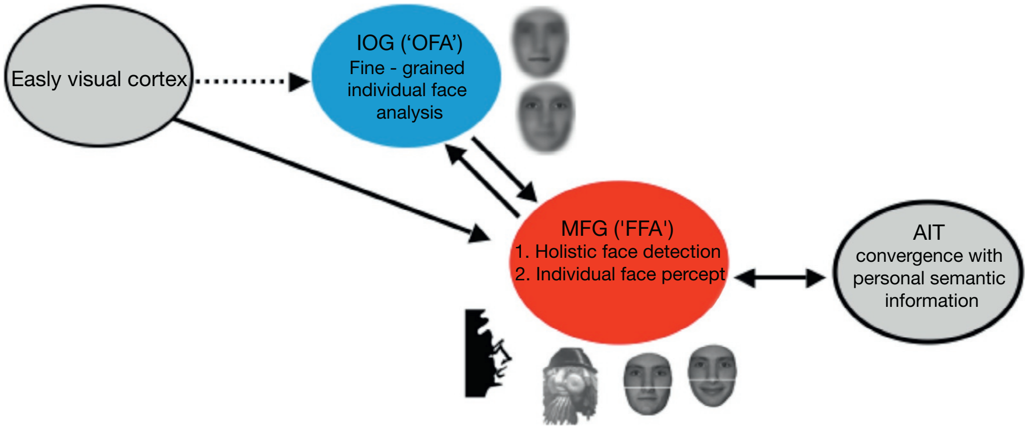

Figure 7 A reverse hierarchical neurofunctional model of face perception (adapted from Rossion, B. (2008). Constraining the cortical face network by neuroimaging studies of acquired prosopagnosia. *Neuroimage*, *40*, 423–426). Following early visual processes, input is sent to the middle fusiform gyrus, both through the IOG and independently from it. If the input matches a face representation in this region, even coarsely (template-based matching), face selectivity emerges ('FFA'; 1. holistic face detection, illustrated by Mooney and Arcimboldo faces). The representation is then refined through reentrant interactions between this higher-order area and lower-level visual areas, where face selectivity emerges later. Through this reentrant interaction, a full holistic representation of an individual face is built (2. individual face percept, illustrated by composite faces). The whole process takes no more than 200 ms.

information can flow almost freely in multiple directions of a network over several seconds.

A Reserve Hierarchy of Face Perception?

According to a reverse hierarchical view, supported by several observations (Figures 4 and 5), lower-level visual areas such as the OFA may be called upon later than the FFA, because neurons in the OFA with smaller receptive fields may be fine-tuned to subserve fine-grained analysis of faces, which is critical in real-life situations (e.g., recognizing the same identity across age differences and changes in lighting). Dynamic reentrant connectivity between these two areas would then support the full extraction of individual face representations (Figure 7).

Conclusions and Future Challenges

Functional neuroimaging studies of the human brain have shown that there are multiple clusters of voxels in the STS and in the VOT cortex, which respond more, sometimes almost exclusively, to faces than other visual object categories. The challenges for future research in this field will be to understand the reason why there are so many face-selective clusters in the human brain, define how they differ in size and number across individual brains, relate these clusters to anatomy, define their spatiotemporal connectivity, and associate the dynamics of this network to behavioral performance at face recognition.

Acknowledgements

Bruno Rossion is supported by the Belgian National Fund for Scientific Research (FNRS).

See also: **INTRODUCTION TO ACQUISITION METHODS**: Obtaining Quantitative Information from fMRI; Temporal Resolution and Spatial Resolution of fMRI; **INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE**: Face Perception: Extracting Social Information from Faces: The Role of Static and Dynamic Face Information; **INTRODUCTION TO SYSTEMS**: Expertise and Object Recognition; Neural Codes for Shape Perception.

References

Andrews, T. J., Davies-Thompson, J., Kingstone, A., & Young, A. W. (2010). Internal and external features of the face are represented holistically in face-selective regions of visual cortex. *Journal of Neuroscience*, *30*, 3544–3552.

Arcurio, L. R., Gold, J. M., & James, T. W. (2012). The response of face-selective cortex with single face parts and part combinations. *Neuropsychologia*, *50*, 2454–2459.

Atkinson, A. P., & Adolphs, R. (2011). The neuropsychology of face perception: Beyond simple dissociations and functional selectivity. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *366*(1571), 1726–1738.

Barton, J. J., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology*, *58*, 71–78.

Bell, A. H., Malecek, N. J., Morin, E. L., Hadj-Bouziane, F., Tootell, R. B., & Ungerleider, L. G. (2011). Relationship between functional magnetic resonance imaging-identified regions and neuronal category selectivity. *Journal of Neuroscience*, *31*, 12229–12240.

Bodamer, J. (1947). Die-prosop-agnosie. *Archives of Psychiatry Nervenkrankh*, *179*, 6–54, English translation by. Ellis, H. D., & Florence, M. (1990). *Cognitive Neuropsychology*, *7*, 81–105.

Bouvier, S. E., & Engel, S. A. (2006). Behavioral deficits and cortical damage loci in cerebral achromatopsia. *Cerebral Cortex*, *16*, 183–191.

Bukach, C. M., Bub, D. M., Gauthier, I., & Tarr, M. J. (2006). Perceptual expertise effects are not all or none: Local perceptual expertise for faces in a case of prosopagnosia. *Journal of Cognitive Neuroscience*, *18*, 48–63.

Bukowski, H., Dricot, L., Hanseeuw, B., & Rossion, B. (2013). Cerebral lateralization of face-sensitive areas in left-handers: Only the FFA does not get in right. *Cortex*, *49*(9), 2583–2589.

Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., & Rossion, B. (2010). Holistic perception of the individual face is specific and necessary: Evidence from an extensive case study of acquired prosopagnosia. *Neuropsychologia*, *48*, 4057–4092.

Caharel, S., Ramon, M., & Rossion, B. (2014). Face familiarity decisions take 200 ms in the human brain: Electrophysiological evidence. *Journal of Cognitive Neuroscience*, *26*, 81–95.

Davidenko, N., Remus, D. A., & Grill-Spector, K. (2012). Face-likeness and image variability drive responses in human face-selective ventral regions. *Human Brain Mapping*, *33*(10), 2334–2349.

Davies-Thompson, J., Gouws, A., & Andrews, T. J. (2009). An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia*, *47*, 1627–1635.

Davies-Thompson, J., & Andrews, T. J. (2012). Intra- and interhemispheric connectivity between face-selective regions in the human brain. *Journal of Neurophysiology*, *108*(11), 3087–3095.

Delvenne, J. F., Seron, X., Coyette, F., & Rossion, B. (2004). Evidence for perceptual deficits in associative visual (prosop)agnosia: A single-case study. *Neuropsychologia*, *42*, 597–612.

Engell, A. D., & Haxby, J. V. (2007). Facial expression and gaze-direction in human superior temporal sulcus. *Neuropsychologia*, *45*(14), 3234–3241.

Ewbank, M. P., Henson, R. N., Rowe, J. B., Stoyanova, R. S., & Calder, A. J. (2013). Different neural mechanisms within occipitotemporal cortex underlie repetition suppression across same and different-size faces. *Cerebral Cortex*, *23*(5), 1073–1084.

Fairhall, S. L., & Ishai, A. (2007). Effective connectivity within the distributed cortical network for face perception. *Cerebral Cortex*, *17*, 2400–2406.

Gainotti, G. (2007). Face familiarity feelings, the right temporal lobe and the possible underlying neural mechanisms. *Brain Research Reviews*, *56*(1), 214–235.

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000a). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000b). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, *12*, 495–504.

Goesaert, E., & Op de Beeck, H. P. (2013). Representations of facial identity information in the ventral visual stream investigated with multivoxel pattern analyses. *The Journal of Neuroscience*, *33*(19), 8549–8558.

Goffaux, V., Peters, J., Haubrechts, J., Schiltz, C., Jansma, B., & Goebel, R. (2011). From coarse to fine? Spatial and Temporal dynamics of cortical face processing. *Cerebral Cortex*, *21*, 467–476.

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation, A tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293–321.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, *35*, 96–111.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B., Marinkovic, K., & Rosen, B. R. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping*, *7*, 29–37.

Harel, A., Gilaie-Dotan, S., Malach, R., & Bentin, S. (2010). Top-down engagement modulates the neural expressions of visual expertise. *Cerebral Cortex*, *20*, 2304–2318.

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.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.

Ishai, A. (2008). Let's face it: It's a cortical network. *NeuroImage*, *40*, 415–419.

Jacques, C., d'Arripe, O., & Rossion, B. (2007). The time course of the inversion effect during individual face discrimination. *Journal of Vision*, *7*(8), 3, 1–9.

Jiang, F., Dricot, L., Righi, G., Tarr, M. J., Goebel, R., Weber, J., et al. (2011). Face categorization in visual scenes may start in a higher order area of the right fusiform gyrus, evidence from dynamic visual stimulation in neuroimaging. *Journal of Neurophysiology*, *106*, 2720–2736.

Jonas, J., Descoins, M., Koessler, L., Colnat-Coulbois, S., Sauvee, M., Guye, M., et al. (2012). Focal electrical intracerebral stimulation of a face-sensitive area causes transient prosopagnosia. *Neuroscience*, *222*, 281–288.

Kahn, D. A., & Aguirre, G. K. (2012). Confounding of norm-based and adaptation effects in brain responses. *NeuroImage*, *60*(4), 2294–2299.

Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, *3*, 759–763.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.

Kriegeskorte, N., Formisano, E., Sorger, B., & Goebel, R. (2007). Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 20600–20605.

Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, *4*(5), 533–539.

Loffler, G., Yourganov, F., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, *8*, 1386–1390.

Natu, V. S., Jiang, F., Narvekar, A., Keshvari, S., Blanz, V., & O'Toole, A. J. (2010). Dissociable neural patterns of facial identity across changes in viewpoint. *Journal of Cognitive Neuroscience*, *22*, 1570–1582.

Nestor, A., Plaut, D. C., & Behrmann, M. (2011). Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 9998–10003.

O'Toole, A. J., Jiang, F., Abdi, H., Pénard, N., Dunlop, J. P., & Parent, M. A. (2007). Theoretical, statistical, and practical perspectives on pattern-based classification approaches to the analysis of functional neuroimaging data. *Journal of Cognitive Neuroscience*, *19*, 1735–1752.

Pinsk, M. A., Arcaro, M., Weiner, K. S., Kalkus, J. F., Inati, S. J., Gross, C. G., et al. (2009). Neural representations of faces and body parts in macaque and human cortex: A comparative fMRI study. *Journal of Neurophysiology*, *101*, 2581–2600.

Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research*, *209*, 481–493.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience*, *18*, 2188–2199.

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive areas in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, *74*, 1192–1199.

Pyles, J. A., Verstynen, T. D., Schneider, W., & Tarr, M. J. (2013). Explicating the face perception network with white matter connectivity. *PLoS ONE*, *8*(4), e61611.

Rajimehr, R., Young, J. C., & Tootell, R. B. (2009). An anterior temporal face patch in human cortex predicted by macaque maps. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 1995–2000.

Rhodes, G., Byatt, G., Michie, P. T., & Puce, A. (2004). Is the fusiform face area specialized for faces individuation or expert individuation? *Journal of Cognitive Neuroscience*, *16*, 189–203.

Rhodes, G., Michie, P. T., Hughes, M. E., & Byatt, G. (2009). The fusiform face area and occipital face area show sensitivity to spatial relations in faces. *European Journal of Neuroscience*, *30*(4), 721–733.

Rolls, E. T. (1992). Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical visual areas. *Philosophical Transactions of the Royal Society of London*, *335*, 11–21.

Rossion, B. (2008). Constraining the cortical face network by neuroimaging studies of acquired prosopagnosia. *NeuroImage*, *40*, 423–426.

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.

Rossion, B., Dricot, L., Goebel, R., & Busigny, T. (2011). Holistic face categorization in higher-level cortical visual areas of the normal and prosopagnosic brain: Towards a non-hierarchical view of face perception. *Frontiers in Human Neuroscience*, *4*, 225.

Rossion, B., Hanseeuw, B., & Dricot, L. (2012). Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis. *Brain and Cognition*, *79*, 138–157.

Rotshtein, P., Vuilleumier, P., Winston, J., Driver, J., & Dolan, R. (2007). Distinct and convergent visual processing of high and low spatial frequency information in faces. *Cerebral Cortex*, *17*(11), 2713–2724.

Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage*, *32*, 1385–1394.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, *115*, 15–36.

Seron, X., Mataigne, F., Coyette, F., Rectem, D., Bruyer, R., & Laterre, E. C. (1995). A case of metamorphopsia restricted to faces and different familiar objects. *Revue Neurologique (Paris)*, *151*(12), 691–698.

Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, *3*, 764–769.

Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical area consisting entirely of face-selective cells. *Science*, *311*, 670–674.

Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 19514–19519.

Wang, G., Tanaka, K., & Tanifuji, M. (1996). Optical imaging of functional organization in the monkey inferotemporal cortex. *Science*, *272*, 1665–1668.

Weiner, K. S., & Grill-Spector, K. (2012). The improbable simplicity of the fusiform face area. *Trends in Cognitive Sciences*, *16*(5), 251–254.

Weiner, K. S., & Grill-Spector, K. (2013). Neural representations of faces and limbs neighbor in human high-level visual cortex: Evidence for a new organization principle. *Psychological Research*, *77*(1), 74–97.

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. *Journal of Neurophysiology*, *92*, 1830–1839.

Young, M. P., & Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science*, *29*(256), 1327–1331.

Yovel, G., & Freiwald, W. A. (2013). Face recognition systems in monkey and human: Are they the same thing? *F1000 Prime Reports*, *5*, 10.

Yovel, G., & Kanwisher, N. (2005). The neural basis of the face inversion effect. *Current Biology*, *15*, 2256–2262.

Zhang, H., Tian, J., Liu, J., Li, J., & Lee, K. (2009). Intrinsically organized network for face perception during the resting state. *Neuroscience Letters*, *454*, 1–5.

Zhu, Q., Zhang, J., Luo, Y. L., Dilks, D. D., & Liu, J. (2011). Resting-state neural activity across face-selective cortical regions is behaviorally relevant. *Journal of Neuroscience*, *31*(28), 10323–10330.

*Brain Mapping: An Encyclopedic Reference, (*2015), vol. 2, pp. 515-522