REVIEW

The role of the occipital face area in the cortical face perception network

David Pitcher · Vincent Walsh · Bradley Duchaine

Abstract Functional magnetic resonance imaging (fMRI) studies have identified spatially distinct face-selective regions in human cortex. These regions have been linked together to form the components of a cortical network specialized for face perception but the cognitive operations performed in each region are not well understood. In this paper, we review the evidence concerning one of these face-selective regions, the occipital face area (OFA), to better understand what cognitive operations it performs in the face perception network. Neuropsychological evidence and transcranial magnetic stimulation (TMS) studies demonstrate the OFA is necessary for accurate face perception. fMRI and TMS studies investigating the functional role of the OFA suggest that it preferentially represents the parts of a face, including the eyes, nose, and mouth and that it does so at an early stage of visual perception. These studies are consistent with the hypothesis that the OFA is the first stage in a hierarchical face perception network in which the OFA represents facial components prior to subsequent processing of increasingly complex facial features in higher face-selective cortical regions.

Keywords Face perception · Occipital face area (OFA) · Functional magnetic resonance imaging (fMRI) · Transcranial magnetic stimulation (TMS)

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Introduction

The ubiquitous presence of faces makes them a uniquely salient stimulus for studying the functions of human visual cortex. Functional magnetic resonance imaging (fMRI) studies graphically illustrate this saliency by identifying multiple regions distributed across cortex that exhibit a stronger neural response to faces than to other visual object categories (Puce et al. 1996; Kanwisher et al. 1997; McCarthy et al. 1997; Gauthier et al. 2000; Ishai et al. 2002). These regions have been linked together to form the components of a distributed cortical network specialized for face perception (Haxby et al. 2000; Calder and Young 2005; Ishai 2008). While the cognitive operations performed in these regions are not yet fully understood each of the regions has been shown to exhibit different functional properties (for reviews see Allison et al. 2000; Kanwisher and Yovel 2006; Ishai 2008). In this paper, we focus on what is arguably the least understood face-selective region, the occipital face area (OFA) (Puce et al. 1996; Gauthier et al. 2000) to clarify the functional role the OFA performs within the cortical face perception network.

While it has not been as extensively studied as the spatially adjacent fusiform face area (FFA) (Kanwisher et al. 1997; McCarthy et al. 1997) the OFA has been shown to perform face computations that functionally distinguish it from other face-selective cortical regions. Specifically, the OFA preferentially represents the parts of the face, such as the eyes, nose, and mouth (Pitcher et al. 2007; Liu et al. 2010; Nichols et al. 2010). This representation of face part information is consistent with the OFA acting as the first stage in a distributed network for face perception in which face computations of increasing complexity, such as identity and facial expression discrimination, are performed at higher levels of cortex (Haxby et al. 2000). Experimental techniques with high temporal resolution have further

demonstrated that the OFA processes face information approximately 100 ms after stimulus onset, an early response consistent with the OFA acting as the first face-selective cortical region (Liu et al. 2002; Pitcher et al. 2007, 2008; Sadeh et al. 2010). Neuropsychological studies of patients with acquired prosopagnosia (Rossion et al. 2003; Bouvier and Engel 2006) and transcranial magnetic stimulation (TMS) studies of healthy participants (Pitcher et al. 2007, 2008, 2009) demonstrate that the OFA is functionally necessary for some face computations, and also suggest the existence of cortical connections between early visual cortex and the FFA that bypass the OFA. This converging evidence from different experimental techniques supports the hypothesis that the OFA is an essential component of the cortical face perception network and that it represents face parts prior to subsequent processing of more complex facial aspects in higher face-selective cortical regions.

What is the OFA and where is it located?

The OFA is a functionally defined face-selective region located on the lateral surface of the occipital lobe either in,

or in the vicinity of, the inferior occipital gyrus (IOG). Early fMRI studies defined the OFA using a contrast of faces greater than scrambled images and letter strings (Puce et al. 1996), or faces greater than letter strings only (Gauthier et al. 2000) but it is now more commonly defined using a contrast of faces greater than a diverse non-face category such as objects (Yovel and Kanwisher 2005), or both objects and scenes (Large et al. 2008). The results from a conventional functional localizer in one participant using a contrast of faces greater than objects are shown in Fig. 1. We have included the OFA together with the FFA and a face-selective region in the posterior STS (pSTS) to illustrate the location of these three core face-selective regions in relation to each other.

The existence of a cortical region exhibiting a strong neural response to faces in the lateral occipital cortex was demonstrated in early positron emission tomography (PET) and fMRI studies of face and object perception (Sergent et al. 1992; Clark et al. 1996; Haxby et al. 1994; Malach et al. 1995; Puce et al. 1996; Kanwisher et al. 1997; Grill-Spector et al. 1999; Haxby et al. 1999; Hoffman and Haxby 2000) but it was Gauthier et al. (2000) who named this region the occipital face area. The OFA is larger and more
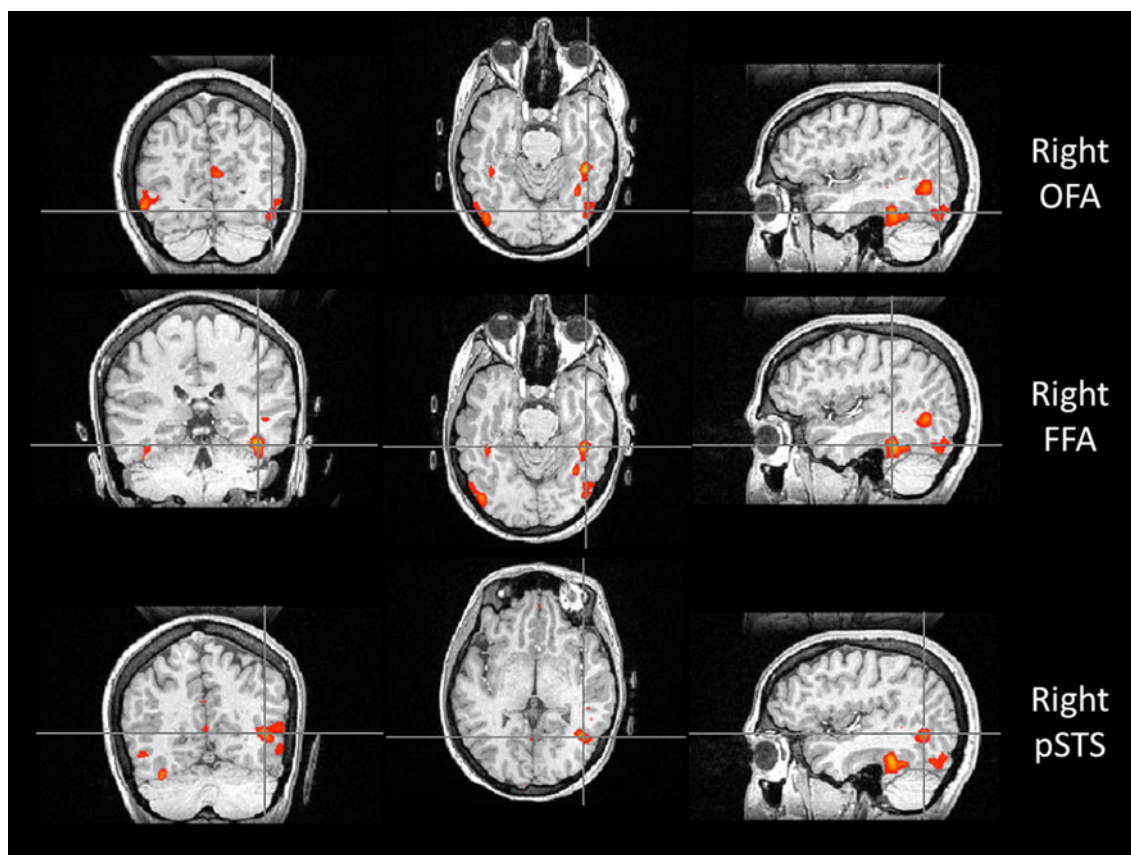

Fig. 1 The three core face-selective regions in the occipitotemporal cortex. From *top* to *bottom*: the *right* OFA, *right* FFA, and the face-selective region in the right posterior STS. The intersection of the *gray lines* identifies the region of interest (*ROI*) in each *row*. From *left* to *right*: coronal slice, horizontal slice, and sagittal slice. Face-selective ROIs identified using a contrast of faces greater than objects

Table 1 Table showing the variability of the group mean Talairach coordinates for the peak voxel in the right OFA from thirteen fMRI studies of face perception

Study	Group mean Talairach co-ordinates	fMRI contrast	N with right OFA
Fox et al. (2009)	38, −78, −12	Faces > Objects	13/15
Gauthier et al. (2000)	31, −75, 0	Faces > Letter strings	19/20
Kovács et al. (2008)	47, −71, −7	Faces > Fourier noise images	15/16
Large et al. (2008)	36, −75, −13	Faces > Places, objects, and scrambled pictures	Not reported
Liu et al. (2010)	46, −78, −7	Faces > Objects	Not reported
Nichols et al. (2010)	40, −71, −9	Faces > Houses	17/17
Pitcher et al. (2009)	45, −78, −6	Faces > Objects	15/15
Puce et al. (1996)	36, −66, −17	Faces > Letter strings	Not reported
Puce et al. (1996)	38, −62, −18	Faces > Textures	Not reported
Ramon et al. (2010a, b)	31, −85, −7	Faces > Cars and scrambled faces	13/13
Rhodes et al. (2009)	40, −78, −6	Faces > Objects	11/16
Rossion et al. (2003)	38, −80, −7	Faces > Objects	9/11
Rotshtein et al. (2005)	43, −61, −20	Faces > Houses and scrambled faces	7/8
Schiltz and Rossion (2006)	39, −77, −11	Faces > Objects and scrambled faces	11/12

frequently found in the right hemisphere (RH) than in the left hemisphere (LH), a finding consistent with other face-selective regions and with evidence from multiple experimental techniques that demonstrate face perception is preferentially lateralized in the RH (Young et al. 1985; Kanwisher et al. 1997; Barton et al. 2002; Pitcher et al. 2007). As with other functionally defined face-selective regions (including the FFA and pSTS), the OFA varies spatially between participants, with group peak Talairach coordinates placing the OFA in Brodmann area 18 or 19 depending on the study. To illustrate the range of this variability, the mean group peak Talairach coordinates for the right OFA from thirteen fMRI studies of face perception are shown in Table 1.

The lateral occipital lobe (the area of the brain in which the OFA is located) receives input from early visual cortex and is believed to represent increasingly complex object shapes prior to further analysis in higher cortical regions (Grill-Spector et al. 1998; Lerner et al. 2001; Kourtzi et al. 2003; Rotshtein et al. 2005). This hypothesis is supported by the presence of additional functionally defined category-selective regions for motion (Watson et al. 1993) objects (Malach et al. 1995) and bodies (Downing et al. 2001) that are also found in lateral occipital cortex. The intermediate position of the OFA in a cortical hierarchy between early visual cortex and the FFA was cleverly demonstrated in an fMRI study that compared the neural response across these areas to faces presented in the ipsilateral and contralateral visual field (Hemond et al. 2007). In this study, the OFA responded to faces presented in the ipsilateral visual field slightly less than two-thirds as strongly as to faces presented in the contralateral visual field. This differed from

the neural response seen in primary visual cortex that responded only to faces shown in the contralateral field and not at all to faces in the ipsilateral field. By contrast, the FFA response to faces in the contralateral and ipsilateral visual fields was almost identical. This pattern of results is consistent with the hypothesis that the OFA is positioned between early visual cortex and the FFA in the visual cortical hierarchy.

Is the OFA essential for face perception?

Neuropsychological studies of patients with category-selective visual agnosias offer the unique opportunity to investigate which cortical regions are essential for accurate perception of the impaired category. However, such patients are exceptionally rare and to date there are no reported cases of prosopagnosic patients with discrete lesions that exclusively encompass the right IOG. However, there is neuropsychological evidence from patients with more diffuse lesions to larger areas of cortex (including to the right IOG) that suggest the right OFA is a necessary component of the face perception network.

Bouvier and Engel (2006) conducted a meta-analysis of 57 patients with either achromatopsia or prosopagnosia resulting from cortical damage. The analysis included details of behavioral testing for all patients and high-resolution structural MRI scans of damaged brain areas in more than half of the reported cases. The analysis revealed that the majority of prosopagnosic patients with structural MRI scans exhibited lesions in the vicinity of the right OFA. By comparison, fewer prosopagnosic patients exhibited damage
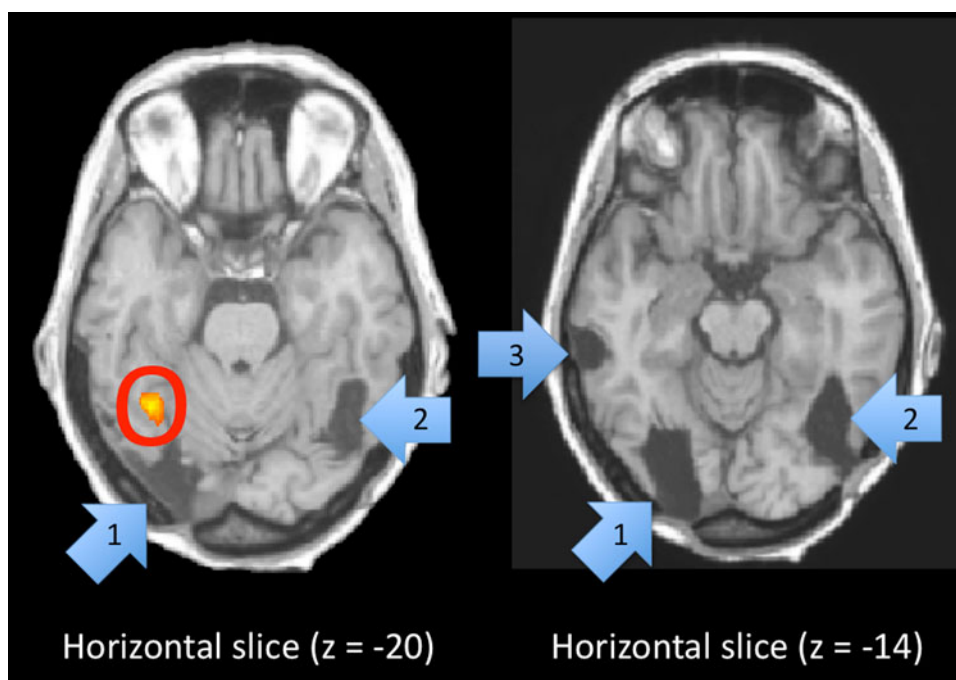
to the region usually encompassing the right FFA and very few patients exhibited damage to the right posterior STS. However, it is important to note that this type of analysis can be misleading. Averaging lesions together in an overlap analysis can highlight the borders between the location of two critical lesions rather than a single lesion hotspot, so it is important to consider this analysis with regard for evidence from single case studies of acquired prosopagnosia. The authors also noted the slices chosen for lesion illustration in the reported patients often omitted the ventral surface of the brain where the FFA is located which may have biased the results of the meta-analysis. However, despite these concerns this study still suggests the right OFA is one of the face-selective regions necessary for accurate face perception.

Single case studies of acquired prosopagnosic patients have provided more detailed examples of the functional importance of the OFA. Rossion et al. (2003) reported the case of patient P.S., a right-handed woman with a lesion extending from the posterior part of the right inferior occipital gyrus into the right posterior fusiform gyrus (see Fig. 2). This lesion leaves P.S. without a right OFA, although intriguingly she still has a right FFA. The study of P.S. has informed a number of issues, but because she exhibits additional lesions to the left fusiform gyrus (she has no left FFA) and right anterior middle temporal gyrus, the relation between her behavioral deficits and her right IOG lesion is unclear. In particular, it should be noted that cortical damage restricted to the right anterior temporal lobe has been shown to cause severe face perception impairments (Evans et al. 1995; Barton 2008). Barton (2008) also suggested that patients with bilateral lesions to face-selective regions exhibit a more severe form of prosopagnosia than patients with unilateral lesions. It is therefore important to interpret the face discrimination impairments in P.S. with respect to all her lesions and not solely with regard to the damage to her right inferior occipital gyrus.

P.S. has great difficulty with face recognition in daily life, and testing has shown she is impaired with matching unfamiliar faces seen from different viewing angles, facial gender discrimination, and facial expression matching (Rossion et al. 2003). P.S. also shows reduced holistic processing as measured by the face composite effect (Ramon et al. 2010a) and the part-whole effect (Ramon and Rossion 2010). By contrast, P.S. is unimpaired with basic-level and within-class object discrimination and recognition tasks (Rossion et al. 2003; Busigny et al. 2010). Despite her extensive cortical damage, a standard fMRI face localizer demonstrated that P.S. exhibited a normal right FFA compared with aged-matched controls (Rossion et al. 2003). Neural activity in her right FFA can still be modulated by emotionally expressive faces despite her somewhat impaired behavioral performance on a facial expression discrimination task (Peelen et al. 2009). These results demonstrate that face information can still be processed in the right FFA despite the absence of the right OFA suggesting the presence of alternate cortical routes between early visual cortex and the fusiform gyrus.

Fig. 2 Diagram illustrating the cortical damage in P.S., a neuropsychological patient with severe acquired prosopagnosia (Rossion et al. 2003). The damaged regions are *highlighted* with *blue arrows*: *lesion 1 right* inferior occipital gyrus, *lesion 2 left* fusiform gyrus, *lesion 3 right* anterior middle temporal gyrus. Despite the extensive cortical damage P.S. still has a *right* FFA (*circled in red*). *Right* FFA defined using a contrast of faces greater than tools (peak voxel Talairach coordinates 34, −52, −20, significant $P < 0.05$, Bonferroni corrected)

Our studies that have used TMS to selectively disrupt face discrimination also suggest the right OFA is an essential component of the face perception network. TMS avoids some of the potential difficulties of patient studies that can limit their interpretation, such as individual differences in pre-morbid ability (Farah 2004) and compensatory cortical plasticity following the lesion (Robertson and Murre 1999). In our most recent study, repetitive TMS delivered over the right OFA selectively impaired a face discrimination task but had no effect on sensitive object and body discrimination tasks (Pitcher et al. 2009). This result demonstrates that TMS possesses the necessary spatial specificity to selectively impair face discrimination when delivered over the right OFA. It is important to note, however, that TMS delivered over the right OFA does not impair all face perception tasks but only tasks dependent on particular aspects of face perception. For example, TMS to the right OFA impaired the discrimination of face parts but not the spacing between these parts on a facial identity task (Pitcher et al. 2007). This study also reported that while there were no significant effects when TMS was delivered over the LH there was a trend in the data that suggested face parts might also be represented in left OFA. In a second study, TMS delivered over the right OFA impaired a discrimination task in which facial expressions were matched across different facial identities but had no effect on a matched control task in which facial identities were matched across different facial expressions (Pitcher et al. 2008). These selectively induced TMS impairments demonstrate that the right OFA is crucial for only some aspects of face perception and provide further evidence for cortical routes between early visual cortex and face-selective regions in the fusiform gyrus that bypass the OFA.

Does the OFA preferentially represent the parts of a face?

In their seminal cognitive model of face perception Bruce and Young (1986) proposed the first stage of face processing involved the structural encoding of view-centered facial descriptions. In this model, the structural encoding stage preceded all subsequent face processing operations such as those tailored for identity and expression discrimination. This hypothesis, that different aspects of face perception are performed in different components of a distributed and hierarchical network, was based on behavioral and neuropsychological studies and was later adapted to account for the emerging neuroimaging evidence (Haxby et al. 2000). Early fMRI studies suggested the IOG would be the most likely cortical locus of this initial structural encoding stage based on its location in extrastriate cortex (Haxby et al. 1999; Hoffman and Haxby 2000).

More recent studies have further characterized how this structural encoding stage may operate by demonstrating that the OFA preferentially represents the physical structure and component parts of a face (Rotshtein et al. 2005; Nichols et al. 2010). One recent fMRI study employed, a 2-by-2 blocked design with an orthogonal manipulation in which face parts (eyes, nose, and mouth) were present or absent and first order face relational configurations (the location of these parts in a face) were normal or scrambled (Liu et al. 2010). The results demonstrated that the magnitude of the BOLD response in the OFA was larger for blocks that included the face parts than for blocks without face parts. Notably, the blocks in which the parts were in a normal or a scrambled configuration produced an equivalent BOLD response in the OFA.

This preferential representation of face parts in the OFA but not the spacing between these parts is consistent with our TMS study (Pitcher et al. 2007). In the first experiment, TMS was delivered over the right OFA at a frequency of 10 Hz for 500 ms while participants performed delayed match to sample face and house discrimination tasks. Both the faces and houses varied either in the parts (the eyes and the mouth for the faces, the windows and door for the houses) or the second order spacing between these parts. TMS delivered over the right OFA selectively impaired the discrimination of the face part stimuli but had no effect on the face spacing or the house part and spacing stimuli. The similar conclusions reported in these two studies using different experimental methods provide complimentary evidence that the OFA preferentially represents the parts of a face, not the spacing between these parts.

However, it is important to note that two other fMRI adaptation studies suggest that the OFA is sensitive to the second order spacing between the component parts of a face. Rotshtein et al. (2007) reported a study in which participants were presented with face stimuli that varied the face parts (eyes, nose, and mouth) or the spacing between the parts. The results of a group average whole brain contrast (this study did not use functional localizers) revealed that the right lateral occipital sulcus (MNI co-ordinates $-39, -90, 0$) showed increased neural sensitivity (it was released from adaptation) when face parts differed across trials while neural sensitivity in the inferior occipital gyrus (MNI co-ordinates $-33, -87, -18$) increased when the spacing between face parts differed across trials. The authors concluded that face parts and the spacing between these parts were preferentially represented in two different regions of lateral occipital cortex. A more recent study directly tested what role the OFA may perform in representing the spacing between face parts (Rhodes et al. 2009). In this study, the spacing of the parts was manipulated but the face parts themselves were not, so while it does not address whether the OFA preferentially represents face

parts the results contradict the conclusion that the OFA does not represent the spacing between face parts reached by Liu et al. (2010) and Pitcher et al. (2007).

Differences in experimental design between these studies may account for the discrepancy concerning whether the OFA represents the spacing of face parts. Liu et al. (2010) functionally localized the OFA using independent data so were able to measure the response to the manipulated face part and face spacing stimuli in face-selective voxels only. By contrast, Rotshtein et al. (2007) used a group average whole brain contrast and it is possible that the region that responded to face spacing changes contained voxels that were not face-selective and thus not in the OFA (note that this study reported that a nearby region in the lateral occipital sulcus was sensitive to face part changes). Note also that in the Liu study, the first order face spacing relations were scrambled while the Rotshtein study and the Rhodes study manipulated the second order relations suggesting that the OFA may compute only second order relations. However, our TMS study (Pitcher et al. 2007) also manipulated the second order relations and TMS delivered over the right OFA had no effect on the discrimination of the face spacing stimuli. Both Rotshtein et al. (2007) and Rhodes et al. (2009) used an fMRI adaptation design, which is thought to be a comparatively sensitive measure of neural activity (Grill-Spector et al. 2006). By contrast, TMS studies demonstrate which stimulus aspects are causally necessary for accurate discrimination and therefore this study provides convincing evidence that the representation of face parts in the OFA is essential for accurate face discrimination. By contrast, this result also suggests that the representation of the spacing between face parts in the OFA does not directly contribute to face discrimination. It is also possible that the spacing between face parts is represented in additional regions of visual cortex as well as in the OFA. These additional representations could have compensated for the TMS disruption of the OFA and contributed to the unimpaired performance on the face spacing task in our study.

There is evidence that supports an alternative account of the neural representation of face parts. In a PET study, Rossion et al. (2000) reported that attending to changes in face parts produced greater neural activity in the left FFA than attending to whole face changes. The opposite pattern was demonstrated in the right FFA, which showed greater activity when participants attended to changes in whole faces than to changes in face parts. This study did not examine the role of the OFA in discriminating face parts so it does not directly contradict our hypothesis but the preferential representation of face parts in face-selective regions in the LH may warrant further study (but see Schiltz and Rossion 2006; Pitcher et al. 2007).

More recently, Rossion (2008) proposed a cortical face perception model that is seemingly inconsistent with our hypothesis that the OFA preferentially represents face parts prior to subsequent processing in the FFA. This model proposed that the FFA is the first face-selective cortical region and that the FFA followed by the OFA holistically represents the percept of a whole face. The holistic face representation in the OFA, where neurons are believed to have smaller receptive fields, then refines the initially coarser holistic face representation in the FFA to facilitate identification via re-entrant processing between the two face-selective regions. Evidence in support of this model came from two neuropsychological patients (P.S. and D.F.) with face perception deficits both of whom exhibited a normal right FFA (compared with aged-matched controls) in the absence of a right OFA (Dricot et al. 2008; Steeves et al. 2009). This was interpreted as evidence that FFA activation is not dependent on prior activation in the OFA but that computations in the OFA are essential for subsequently refining the initial face representation in the FFA.

While the above case studies provide valuable information neither of the cited patients exhibit lesions exclusive to the right inferior occipital gyrus. This limits the scope of the conclusions one is able to draw regarding the functional role of the right OFA from studies of these patients. Patient P.S. exhibits lesions to her right inferior occipital gyrus, left fusiform gyrus, and right anterior middle temporal gyrus (see Fig. 2). As stated earlier, cortical damage restricted to the right anterior temporal lobe can result in severe face perception deficits (Evans et al. 1995; Barton 2008), so accounting for the impairments observed in P.S. without considering the disruptive effect of the additional lesions is potentially problematic. For example, it seems plausible that accurate face discrimination is as dependent on cortical connections between the FFA and the anterior temporal lobe (Kriegeskorte et al. 2007) as on cortical connections between the OFA and the FFA. Patient D.F has extensive bilateral damage to her lateral occipital lobes resulting in severe visual form agnosia (Milner et al. 1991; Steeves et al. 2009). This restricts the conclusions that can be made regarding face-selective regions in this patient as any performance deficits may result from her extensive wider perceptual impairments that are not limited to face perception.

Rossion (2008) also cited an fMRI study of healthy participants in support of his model. Schiltz and Rossion (2006) conducted an fMRI adaptation study of the face composite effect, a behavioral face illusion in which the top halves of faces are perceived as different faces when they are presented with the bottom half of a different face (Young et al. 1987). This effect is interpreted as evidence for the holistic processing of faces as the whole of the face, rather than just the top half, is necessary for accurate discrimination. Results demonstrated that both the FFA and the OFA were more sensitive to stimulus changes when the top halves of faces were aligned with the bottom halves of

different faces than with the original bottom halves of the same face. This demonstration that the OFA is engaged in holistic representations of the whole face is inconsistent with our hypothesis that the OFA preferentially represents face parts. More recently, the same authors reported a follow-up fMRI study (Schiltz et al. 2010) repeating the same basic design but switching to an event-related trial-by-trial adaptation design in place of the blocked adaptation design used in their earlier study. Changing the experimental design changed the pattern of the results: in this new study only the FFA was sensitive to the face composite effect but the OFA was not. This is seemingly inconsistent with Rossion's hypothesis as this proposes that the OFA constructs a holistic representation of the whole face that is refined via re-entrant processing with the FFA. We agree with Rossion's (2008) conclusion that face perception is, in part, dependent on the operation of bilateral connections between the OFA and the FFA (although such connections have yet to be demonstrated). However, we contend the hypothesis that the OFA represents face parts prior to subsequent processing in the FFA during the initial feed-forward sweep of visual perception provides a more compelling interpretation of the existing evidence.

Is the OFA the first stage of a cortical network?

Models of the cortical components of the face perception network propose that the OFA computes an early structural description of a face (Haxby et al. 2000; Calder and Young 2005) while higher-level face-selective regions such as the FFA (Hoffman and Haxby et al. 2000; Grill-Spector et al. 2004) and the anterior temporal lobe (Kriegeskorte et al. 2007) compute the invariant aspects of a face such as facial identity. This hypothesis is consistent with hierarchical models which propose that complex visual objects are recognized via a series of stages in which features of increasing complexity are extracted and analyzed at progressively higher levels of the visual processing stream (Grill-Spector et al. 1998; Lerner et al. 2001; Ullman et al. 2002; Grill-Spector and Malach 2004; Fairhall and Ishai 2007).

Understanding how the hierarchical connections in the cortical face network operate will benefit from establishing when each face-selective region actively performs its functional role. Precise temporal information informs fundamental questions such as whether the extended face network operates in a predominantly feed-forward sweep or whether functionally different face-selective regions operate in parallel. In addition, demonstrating that particular face-selective areas are functionally active at multiple times will address whether the predicted feedback mechanisms are operating in the network (Haxby et al. 2000; Calder and Young 2005; Fairhall and Ishai 2007). As the OFA is the
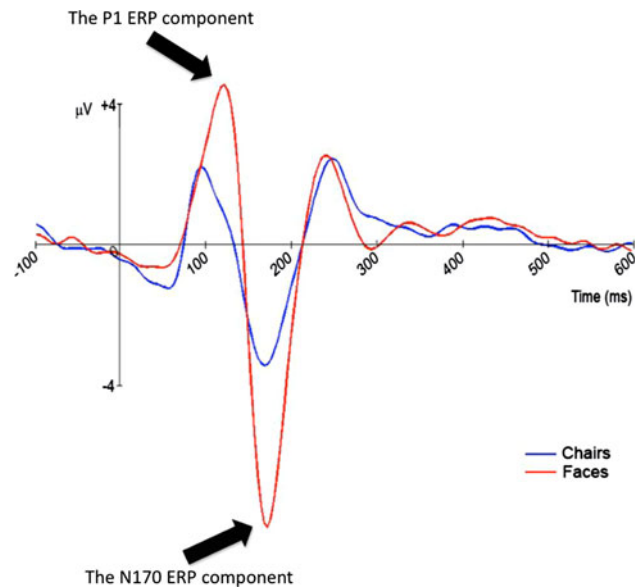

Fig. 3 The P1 and N170 ERP components. The graph shows the grand average ERP responses from ten subjects to faces (*in red*) and to chairs (*in blue*). Note that the peaks at 100 ms and at 170 ms are larger for faces. Three channels have been averaged in each subject (P8, PO8, and P10)

proposed first stage of the cortical network then any face-specific neural activity should be observed in the OFA prior to activity in all subsequent stages of the network. There is some evidence from experimental techniques with a high temporal resolution that this may be the case.

Electroencephalography (EEG) studies of face perception offer a well-established and reliable method for establishing the timing of face-specific events (Rossion and Jacques 2008). The N170 is an event-related potential (ERP) component that peaks approximately 170 ms after stimulus onset that is stronger for faces than for other categories of visual object (Bentin et al. 1996). Establishing which cortical areas generate the N170 is problematic owing to source localization issues (Slotnick 2004). Studies that have attempted to localize the N170 to face-selective regions suggest the N170 records neural activity arising from the FFA (Horovitz et al. 2004), pSTS (Henson et al. 2003), or both the FFA and pSTS (Sadeh et al. 2010) but not the OFA.

The P1 is an earlier ERP component that peaks approximately 100 ms after stimulus onset, is sometimes face-selective, and is typically recorded from electrodes over the medial occipital pole (Eimer 1998) (see Fig. 3). The earlier latency of the P1, which precedes the N170, suggests that it may, in part, be recording neural activity generated by the OFA. Although the P1 is often larger for faces than for objects (Eimer 1998; Itier and Taylor 2004; Herrmann et al. 2005; Thierry et al. 2007), this is not always the case. Modulation of the P1 also occurs in response to a variety of non-face stimuli, for example the orientation of letter strings

(Rosazza et al. 2009), and checkerboard patterns (Martinez et al. 2001). This inconsistency has led some authors to question whether the P1 actually constitutes a face-selective ERP component or whether it responds to more low-level visual characteristics (for a recent review see Rossion and Jacques 2008). However, given that some studies have shown the P1 can be modulated by face stimuli it remains possible that face-selective neurons in the OFA contribute to the P1 along with a variety of other non-face-selective sources. A recent study that looked for correlations between face-selective cortical regions and simultaneously measured face-selective ERP components demonstrated that the OFA was correlated with ERPs peaking 110 ms after stimulus onset (Sadeh et al. 2010).

Face-specific activity occurring as early as 100 ms has also been demonstrated in magnetoencephalography (MEG) studies. MEG offers a similarly precise temporal resolution to EEG but benefits from increased spatial resolution. MEG studies of face perception have identified two early face-selective components, the M100, and the M170 (Liu et al. 2002; Itier et al. 2006). The M100 occurs bilaterally approximately 100 ms after stimulus onset and exhibits a larger response amplitude to faces containing scrambled face parts (eyes, nose, and mouth) than to faces with the parts masked out but in a normal configuration (Liu et al. 2002). The M100 occurs within the same temporal window as the P1 (approximately, 80–140 ms after stimulus onset), and both are recorded from a similar scalp location. Given that the OFA and the M100 each exhibit a preference for face parts (Liu et al. 2002, 2010; Pitcher et al. 2007), it is possible that both may be recording the same underlying neural activity. However, at this stage it is difficult to draw strong conclusions as the later face-selective MEG component, the M170, also demonstrates sensitivity to face component parts (Harris and Aguirre 2008).

TMS studies can also address when a particular cortical region is engaged in a specific cognitive task with a high degree of temporal resolution. This is achieved by delivering TMS pulses over a targeted cortical region at different times from stimulus onset. Plotting the disruptive effect of the TMS demonstrates when the targeted region was crucially engaged in the task and suggests when the region is critically active. In our first TMS study, we delivered two pulses of TMS separated by 40 ms at different times from stimulus onset during different time windows while participants performed a face part discrimination task (Pitcher et al. 2007). TMS impaired discrimination when delivered 60 and 100 ms after stimulus onset but had no effect when delivered during all other time windows up to 250 ms (see Fig. 4). This 60–100 ms TMS induced impairment at the rOFA was replicated in a second study in which participants had to discriminate facial expressions (Pitcher et al. 2008). The temporal proximity of these TMS induced

impairments to the P1/M100 components reported in electrophysiological studies (Eimer 1998; Liu et al. 2002; Itier and Taylor 2004; Thierry et al. 2007) further suggests that the OFA and the P1/M100 components may reflect the same underlying neural activity. If so, then the first wave of face-specific activity in the OFA peaks approximately 100 ms after stimulus onset. OFA neural activity at 100 ms would then precede the timing of the intracranial ERP responses to faces recorded in the right fusiform gyrus of neuropsychological patients that has been shown peak at times varying from 110 to 700 ms (Allison et al. 1999; McCarthy et al. 1999; Puce et al. 1999; Barbeau et al. 2008). Face-specific neural activity in the OFA preceding face-specific neural activity in the fusiform gyrus (the cortical locus of the FFA) is consistent with the OFA being the earliest face-selective cortical region as originally proposed by Haxby et al. (2000) (but see Rossion 2008).

Does the OFA contribute to facial identity discrimination?

Evidence that the OFA is involved in facial identity computations comes from fMRI studies (Hoffman and Haxby 2000; Yovel and Kanwisher 2004) but the exact nature of how the OFA contributes to identification is not fully understood. While FFA activation has been shown to correlate with facial identity discrimination (Grill-Spector et al. 2004), the role of the OFA for facial identification is believed to involve the structural description of a face prior to further analysis in the FFA (Haxby et al. 1999; 2000; Hoffman and Haxby 2000). Rotshtein et al. (2005) reported an fMRI adaptation study that elegantly demonstrates how this process may function. Face stimuli were drawn from a series morphed at different gradations between images of two famous people (for example, Margaret Thatcher and Marilyn Monroe). In the scanner, participants were presented with two successive faces that were either same or different, faces in the different trials varied by 30% along the physical morphing dimension. In half of the different trials, the two faces were both perceived as the same identity (for example, both Marilyn or both Margaret), while in the other half of the different trials the two faces were perceived to be different identities (e.g., first Marilyn then Margaret or vice versa). Results showed that the OFA exhibited increased neural sensitivity (it was released from adaptation) during the different trials regardless of whether the faces were perceived as a different identity. By contrast, the FFA showed increased neural sensitivity (it was released from adaptation) only during the different trials that presented a different identity and not during different trials that presented the same identity. This evidence that the OFA is sensitive to physical changes in a face regard-

A Participants performed a delay match to sample task face part discrimination task. Double pulse TMS (40ms apart) was delivered at different times after stimulus onset of the probe face over the right OFA and the vertex control site.
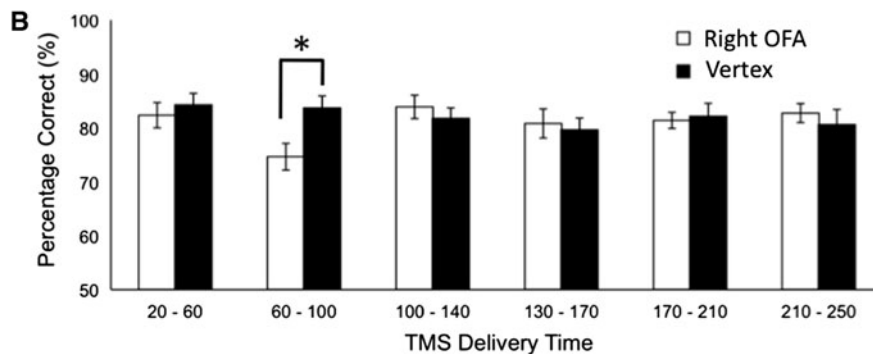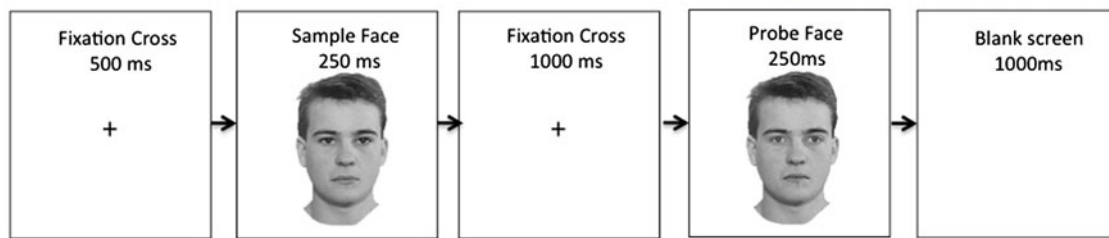
Fig. 4 a Figure illustrating the TMS trial procedure from Experiment 3 in Pitcher et al. (2007). **b** Graph illustrating that double pulse TMS delivered 60 and 100 ms after stimulus onset over the *right* OFA impairs face part discrimination (Pitcher et al. 2007). This result suggests that the OFA is critically active at an early stage of visual perception and is consistent with the OFA being the earliest face-selective cortical region

less of whether these changes contribute to the perception of a different identity is consistent with the OFA being an earlier face-selective cortical region than the FFA (see also Fox et al. 2009). By contrast, the neural response in the FFA was only sensitive to changes in the identity of the face suggesting that the region primarily computes identity and that it is not sensitive to more subtle physical changes in a face (but see Ramon et al. 2010b).

The hypothesis that the OFA is not directly sensitive to identity changes but rather to physical changes in a face is also supported by our study that demonstrated that TMS delivered over the right OFA impaired facial expression, but not facial identity discrimination (Pitcher et al. 2008). In this study, the two faces used in the expression matching task always displayed a different facial identity and thus the shape of the face parts always differed between the sample and probe stimuli regardless of whether the face displayed the same expression or not. By contrast, the faces used for the identity matching task always differed in facial expression and so participants were likely to have relied on cues other than face parts. These cues (e.g. the relative spacing of the parts, surface skin reflectance) may not have been susceptible to TMS disruption at the right OFA. In our more recent study (Pitcher et al. 2009), the face stimuli

impaired by TMS delivered over the right OFA were selected from a series morphed between two different computer generated faces making the stimuli similar in design to the morphed face stimuli reported by Rotshtein et al. (2005). The TMS induced impairment is then seemingly incongruent with the earlier finding that TMS to right OFA did not disrupt facial identity (Pitcher et al. 2008). As stated above, we argued that the identity task in this study (Pitcher et al. 2008) was not susceptible to face part discrimination impairment because of facial expression changes between the sample and probe faces. However, in the later study (Pitcher et al. 2009) the faces all had neutral expressions so face part shape differences could contribute to the discrimination task and were thus susceptible to TMS disruption of the right OFA.

Future questions and conclusion

To date, the OFA has been relatively understudied compared with the spatially adjacent FFA (Kanwisher and Yovel 2006), and the number of studies that address the functions of the OFA is limited. We propose that addressing the following questions concerning the functional role

of the OFA will inform our understanding of the human face perception cortical network.

1. *How face-selective is the OFA?*—Face-selective cortical regions show a greater neural response to faces than to any other category of visual stimuli, but whether these regions only represent faces is disputed (Haxby et al. 2001; Spiridon and Kanwisher 2002). The face-selectivity of the right OFA was recently demonstrated by our study that reported that TMS delivered over the right OFA impaired face discrimination but not object and body discrimination (Pitcher et al. 2009). However, more recent evidence has suggested that the OFA may also represent the orientation of two-dimensional shapes (Silvanto et al. 2010) and that the IOG may contain overlapping neuronal populations that respond to both faces and limbs (Weiner and Grill-Spector 2010).

2. *Are there feedback connections to the OFA?*—The mammalian visual system contains an extensive network of feedback connections from higher cortical areas to lower cortical areas and feedback connections are predicted in cortical face perception networks (Haxby et al. 2000; Fairhall and Ishai 2007). The OFA should be the subject of feedback signals from higher face-selective cortical regions but such connections have not yet been demonstrated.

3. *Is there a non-human primate homolog of the OFA?*—The most compelling evidence that face perception is performed in a network of face-selective cortical regions comes from recent studies that have combined fMRI and microstimulation in macaques (Tsao et al. 2006; Moeller et al. 2008). Evidence from a recent paper that aimed to establish homologies between face-selective cortical regions across species suggests that the posterior lateral face patch (PL), the most posterior of six patches reported in the macaque, is the most likely candidate for the primate homolog of the OFA (Tsao et al. 2008). However, the functions of these regions in humans and macaques will need to be better understood before exact homologies can be made.

4. *Is the OFA a face detector?*—Gauthier et al. (2000) hypothesized that a possible functional role for the OFA might involve face detection. Evidence that the OFA represents faces and the location of faces in the visual field is consistent with this hypothesis (Kovács et al. 2008; Nestor et al. 2008; Schwarzlose et al. 2008). However, more recent evidence that the OFA is sensitive to changes in face stimuli even when the subject is behaviorally unaware of the change runs contrary to the hypothesis that the OFA operates as face detector (Large et al. 2008; Fox et al. 2009).
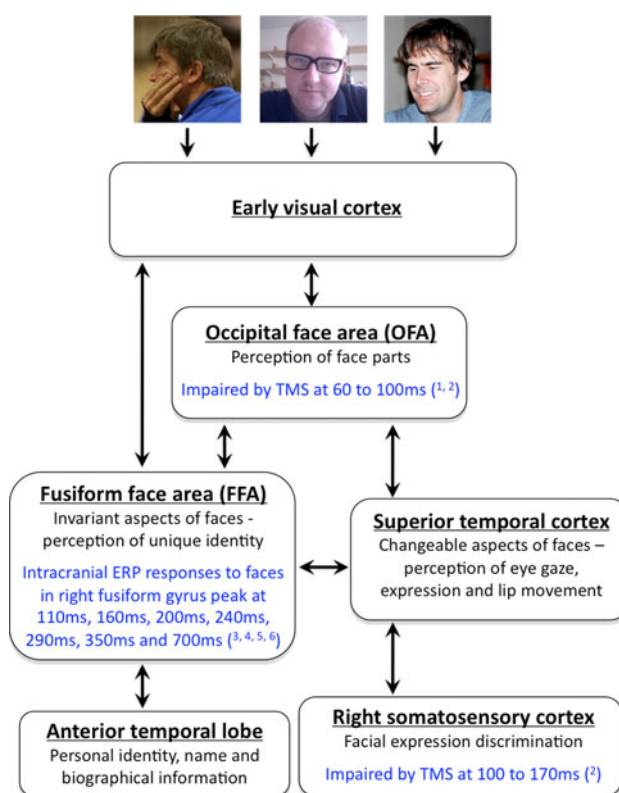
Fig. 5 A cortical model of the face-processing network (adapted from Haxby et al. 2000) with temporal information added from intracranial ERP and TMS studies (*1* Pitcher et al. 2007; *2* Pitcher et al. 2008; *3* Allison et al. 1999; *4* McCarthy et al. 1999; *5* Puce et al. 1999; *6* Barbeau et al. 2008). The model and the connections between the functional areas are hypothetical

If the OFA is the first stage of a distributed cortical network specialized for face perception (Haxby et al. 2000; Calder and Young 2005; Ishai 2008), then a better understanding of the functional role the OFA performs will be essential in establishing how this network operates. In this paper, we have presented evidence consistent with the hypothesis that the OFA represents the parts of a face and that it does so prior to more detailed analyses performed at higher face-selective cortical regions. Our conclusions are, in part, based on adding temporal information to the existing cortical model of face perception proposed by Haxby et al. (2000), and we contend that experimental techniques with high temporal resolution add essential information in the study of cortical networks. To further illustrate this point, we have included a model adapted from Haxby et al. (2000) that includes information concerning when some of the face-selective cortical regions are functionally active (see Fig. 5).

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