A Revised Neural Framework for Face Processing

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Abstract

Face perception relies on computations carried out in face-selective cortical areas. These areas have been intensively investigated for two decades, and this work has been guided by an influential neural model suggested by Haxby and colleagues in 2000. Here, we review new findings about face-selective areas that suggest the need for modifications and additions to the Haxby model. We suggest a revised framework based on (*a*) evidence for multiple routes from early visual areas into the face-processing system, (*b*) information about the temporal characteristics of these areas, (*c*) indications that the fusiform face area contributes to the perception of changeable aspects of faces, (*d*) the greatly elevated responses to dynamic compared with static faces in dorsal face-selective brain areas, and (*e*) the identification of three new anterior face-selective areas. Together, these findings lead us to suggest that face perception depends on two separate pathways: a ventral stream that represents form information and a dorsal stream driven by motion and form information.

INTRODUCTION

From a brief glance at a face, we are able to effortlessly assess a person's identity, emotional state, attentional focus, sex, age, physical attractiveness, and several other characteristics. The apparent ease of face perception however belies the computationally challenging nature of the task. The neurocognitive mechanisms underlying our impressive abilities have received extensive research attention for more than 40 years. This work has shown that face perception depends on the coordinated activity of a network of neural mechanisms that respond preferentially to faces. Fifteen years ago, Haxby and colleagues (2000) proposed an influential neural model that has fruitfully guided research on face processing. In this review, we reevaluate this prominent neural model in light of more recent findings. To provide context, we first discuss some general points about face processing and the face-selective brain regions. Next, we describe Haxby and colleagues' (2000) neural model of face processing and discuss recent findings that suggest modifications or additions to this model. Finally, we sketch out a new neurocognitive framework for face perception.

CENTRAL ISSUES IN FACE PERCEPTION

The Face-Specificity Hypothesis

Our review focuses on the functional roles of brain regions that show a much stronger response to faces than to other object categories in functional magnetic resonance imaging (fMRI) studies. We focus on these face-selective areas because their strong response to faces suggests they are key to understanding the neural basis of face perception. In addition, converging evidence suggests that face perception depends on different processes than those underlying other types of object perception (for an extended review, see Duchaine & Yovel 2008), and the existence of face-selective areas provides a likely neural locus for such processes.

The earliest suggestions that face processing relies on different mechanisms than other types of object recognition were prompted by reports that brain damage could selectively impair or spare face perception (Ellis & Florence 1990, Hoff & Pötzl 1937). More rigorous demonstrations of face-selective impairments in prosopagnosia, as well as the existence of object agnosia without prosopagnosia, have buttressed these claims (Busigny et al. 2010, 2014; Duchaine et al. 2006; Moscovitch et al. 1997; Rezlescu et al. 2012; Sergent & Signoret 1992). The first evidence for face specificity in the normal brain came from Yin's (1969) demonstration that turning faces upside down led to a greater decrement in performance than did inversion of other objects. Later behavioral experiments indicated this difference involves a more holistic representation than that used for object recognition (Tanaka & Farah 1993, Young et al. 1987).

The face-selective neurons first reported by Charles Gross and colleagues (Desimone et al. 1984, Gross et al. 1972) and further explored by Rolls, Perrett, and others (Perrett et al. 1982, Rolls 1984) are striking evidence for face-selective mechanisms in the nonhuman primate brain. Beginning in the 1990s, neuroimaging studies demonstrated that regions in the occipital and temporal lobes in humans and in the superior temporal sulcus of the macaque show especially strong responses to faces (Kanwisher et al. 1997, McCarthy et al. 1997, Tsao et al. 2003). By combining fMRI and single-cell recordings, Tsao et al. (2006) revealed that 97% of the neurons located within an fMRI-defined face-selective area in the macaque brain are selective for faces. Similar percentages have been found in other face-selective areas in the macaque (Freiwald & Tsao 2010), suggesting macaque face patches are composed almost entirely of face-selective neurons (but see Bell et al. 2011). Causal evidence for the face specificity of these face-selective areas has been provided by stimulation studies. Transcranial magnetic stimulation (TMS) of the right occipital face area (OFA), which resides in a region close to the surface of the brain, typically disrupts face perception,

whereas TMS of neighboring regions does not (Pitcher et al. 2007, 2009; but see Pitcher et al. 2012). Similarly, intracranial stimulation of the right OFA (Jonas et al. 2014) and face-selective regions of the right fusiform gyrus (Jonas et al. 2015, Rangarajan et al. 2014) appears to selectively disrupt face perception, although the effect on nonface perception has not been compared rigorously.

Right-Hemisphere Dominance of Face Perception

Face-selective areas are found in both the right and the left hemispheres, but the right-hemisphere areas are more important for face processing than the left-hemisphere areas (Rossion 2014). Superior behavioral performance in the left hemifield has been reported repeatedly (Levine et al. 1988, Sergent & Bindra 1981). In addition, face-selective areas in the right hemisphere are usually larger than those in the left hemisphere (Bukowski et al. 2013), as are face-selective event-related potentials over the right hemisphere (Bentin et al. 1996, Eimer 2011). The prosopagnosia literature indicates strong dominance of the right hemisphere. Unilateral lesions to the right occipital and temporal lobes are a common cause of face-perception deficits (Barton et al. 2002, Busigny et al. 2010, Dalrymple et al. 2011, De Renzi et al. 1994, Sergent & Signoret 1992, Wada & Yamamoto 2001), whereas prosopagnosia following unilateral lesions to the left hemisphere has been reported in only five patients, four of whom were left-handed (Barton 2008, Eimer & McCarthy 1999, Mattson et al. 2000, Tzavaras et al. 1973). Intracranial stimulation of face-selective fusiform regions in the right and left hemispheres has recently provided further evidence for right-hemisphere dominance (Rangarajan et al. 2014). Stimulation of the right hemisphere led to distorted face perception, whereas stimulation of the left hemisphere produced only general visual effects (e.g., perceptions of phosphenes or color changes). Intriguingly, face areas in macaques do not show right-hemisphere lateralization (Tsao et al. 2008), and stimulation of left-hemisphere face cells in these animals can affect face perception (Afraz et al. 2006, 2015).

The Bruce & Young Model

Bruce & Young (1986) proposed a comprehensive cognitive model concerned with face identity and other aspects of face processing, such as expression and lip reading, as well as with the role of semantic information in face processing. Their model was primarily based on evidence from neuropsychological and cognitive studies. As shown in **Figure 1**, the model includes processing units that work both in series and in parallel. Processing begins with the generation of a view-centered representation of the face, which is then used as input to separate processes specialized for particular tasks. Expression and lip movements are analyzed by two separate processes, regardless of whether the face is familiar or unfamiliar. Representations of face structure are compared with stored face-recognition units (FRUs), and a match between a given representation and a stored FRU results in the activation of semantic information about the person and, finally, their name. Recognition of a familiar face is based on a structural code involving an abstract facial representation that allows for recognition across changes in pose, expression, and illumination. In contrast, recognition of an unfamiliar face primarily uses pictorial codes based on information from a static image of the face and is said to depend on a different processing route that involves a module called directed visual processing.

One central prediction of this model is that identity and expression are processed independently. This division was motivated by findings that prosopagnosic individuals can recognize facial expressions but not the identity of a familiar person and by data from normal individuals indicating that judgments of facial expressions do not depend on face familiarity. However, questions about these findings, together with new results, led Bruce, Young, and others (Calder & Young 2005, Young & Bruce 2011) to suggest that identity and expression may not be processed independently.
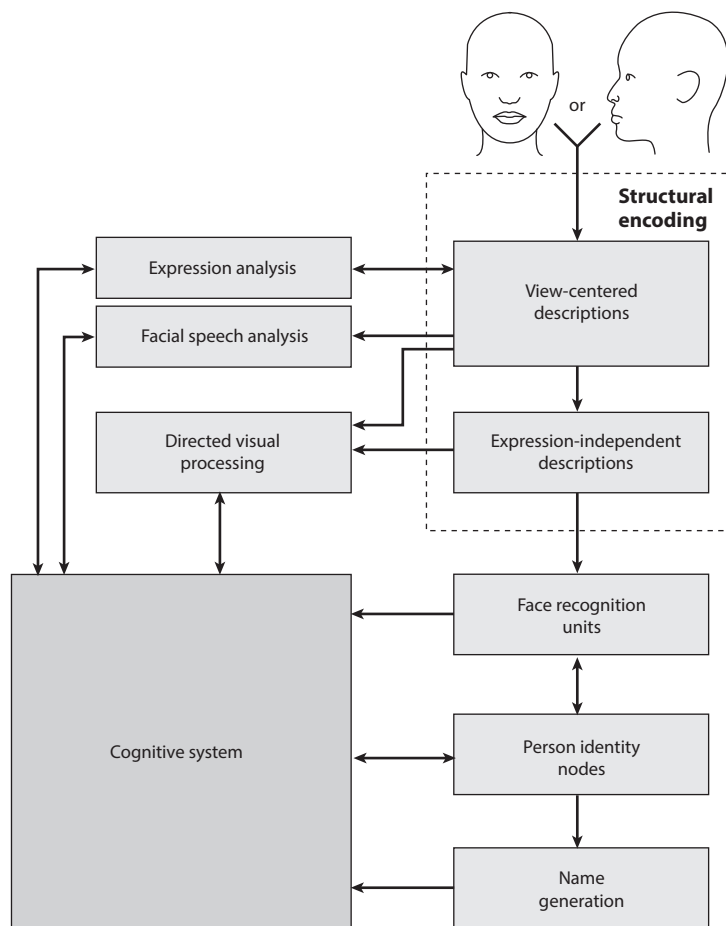
Figure 1

The Bruce & Young (1986) model of face processing.

The Bruce & Young (1986) model did not address the neuroanatomical basis for their cognitive model because the model was proposed when monkey electrophysiology and human and monkey lesion studies were the only sources of information about the neural basis of cognitive function (Young & Bruce 2011). Since the mid-1990s, however, hundreds of neuroimaging studies have dramatically increased our knowledge of the neuroanatomy underlying face processing. The next sections are devoted to introducing concepts that are central to these studies and to describing and evaluating today's leading model, proposed by Haxby et al. (2000), which integrated early cognitive and neural findings.

BACKGROUND ON FACE-SELECTIVE AREAS

Face-Selective Areas: Definition

Kanwisher et al. (1997) were the first to define face-selective brain areas as regions showing a significantly higher response to faces than to nonface objects (see also McCarthy et al. 1997).

Their pioneering study described a method for testing the selectivity and functional profile of a face-selective area. The method begins with a functional localizer in which faces and nonface objects are presented. Clusters of voxels that show a significantly higher response to faces than to the nonface objects are defined as face-selective areas. This process is done in each brain individually because the precise locations of face-selective areas vary among individuals. Group analysis is not preferable for defining a face-selective area, because group-defined areas include only the face-selective voxels that overlap across individuals, and thus many face-selective voxels in each individual are outside the region of overlap and not further analyzed (Heller et al. 2007). Once the face-selective area has been defined, the profile of its response to different types of visual stimuli is assessed using data from a different set of stimulus presentations to determine its selectivity in an independent manner (see also Baker et al. 2007a).

Face-Selective Areas: Locations

Kanwisher et al. (1997) used this method to reveal a cluster of face-selective voxels in the fusiform gyrus, which they referred to as "Area FF," although this area has since become known as the fusiform face area (FFA). The strong response to faces in the FFA however does not demonstrate that this area is specialized for face processing per se. To address alternative interpretations, Kanwisher and colleagues provided evidence that the FFA showed higher responses to intact faces than to scrambled faces, to faces than to houses, and to faces than to hands. The strong response to a wide variety of faces presented from different views, including two-tone faces, suggested that the area is indeed selective to faces, not simply to low-level visual information present in face images.

Soon after the initial report of the FFA, two other face-selective areas were found. The inferior occipital gyrus contains the OFA (Haxby et al. 1999, Gauthier et al. 2000), and the posterior part of the superior temporal sulcus houses another face-selective area (pSTS-FA) (Kanwisher et al. 1997, Hoffman & Haxby 2000) (**Figure 2**). More recent studies have revealed additional face-selective areas in more anterior parts of the brain (**Figure 2**). These additional areas are found in the anterior temporal lobe (ATL-FA) (Rajimehr et al. 2009, Tsao et al. 2008), the anterior

FFA: fusiform face area

pSTS-FA: face-selective area in the posterior superior temporal sulcus

ATL-FA: face-selective area in the anterior temporal lobe

aSTS-FA: face-selective area in the anterior superior temporal sulcus

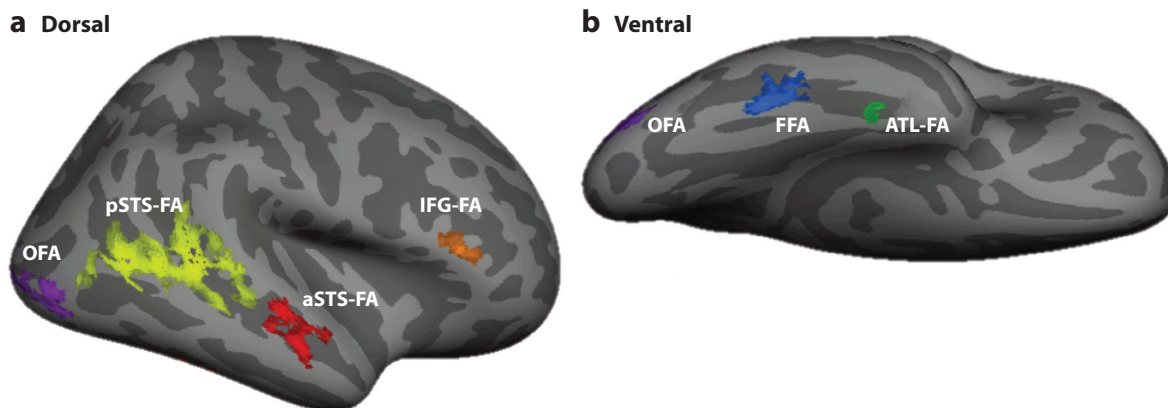**IFG-FA:** face-selective area in the inferior frontal gyrus

Figure 2

Face-selective areas. The six face-selective areas are shown in two views of the right hemisphere of a typical participant. (*a*) The dorsal face-selective areas: the posterior superior temporal sulcus face area (pSTS-FA), the anterior superior temporal sulcus face area (aSTS-FA), and inferior frontal gyrus face area (IFG-FA). (*b*) The ventral face-selective areas: the occipital face area (OFA), the fusiform face area (FFA), and the anterior temporal lobe face area (ATL-FA).

superior temporal sulcus (aSTS-FA) (Pitcher et al. 2011), and the inferior frontal gyrus (IFG-FA) (Fox et al. 2009, Chan & Downing 2011, Axelrod & Yovel 2013), and we discuss these areas in more detail below.

Do Face-Selective Areas Contribute to Other Types of Object Recognition?

The issue of whether face-selective areas are devoted solely to the processing of faces has been debated extensively (Tarr & Gauthier 2000, Kanwisher 2010, Haxby et al. 2001, McKone et al. 2007). One alternative to the face-specificity account is motivated by the response these areas show to nonfaces. Evidence for the representation of nonfaces in the FFA comes from studies showing above-chance decoding of the basic-level categories of nonface objects (e.g., cat, car) when the pattern of the voxels is analyzed (Haxby et al. 2001; but see Spiridon & Kanwisher 2002, O'Toole et al. 2005) and from functional magnetic resonance-adaptation (fMR-A) studies that reveal adaptation to nonfaces in the FFA (Dricot et al. 2008, Schiltz & Rossion 2006). The presence of information about a nonface stimulus in a face-selective area does not mean that the detected information contributes to the recognition of that stimulus, however. Face-selective deficits in patients with lesions to face-selective areas (Busigny et al. 2010, Rezlescu et al. 2012) and transcranial magnetic stimulation studies targeting face-selective regions (Pitcher et al. 2009, 2012) suggest that these areas make little or no contribution to recognition of nonface stimuli, although this issue needs further exploration, and the study of it will benefit from intracranial disruption techniques (Jonas et al. 2014, Rangarajan et al. 2014). A second issue to consider is the limited spatial resolution of fMRI. Each voxel contains between 500,000 and 1 million neurons. Thus, it is very likely that some neurons in an fMRI-defined face-selective area will not be face-selective, and methods such as fMR-A that may be sensitive to subvoxel neural responses may also reflect the activity of nonface-selective voxels (Grill-Spector & Malach 2001).

Another alternative to the face-specific account proposes that these areas are not specialized for faces per se but for categories for which an observer has great expertise. The neural version of the expertise hypothesis proposes that the FFA (and presumably the other face-selective areas) are specialized for representing stimulus classes with which people have extensive experience (Gauthier et al. 1999). Several studies reported increased responses in the FFA to objects of expertise in experts (Gauthier et al. 1999, 2000; Xu 2005), but many other studies have found no increase in the response of the FFA to such objects (Brants et al. 2011, Grill-Spector et al. 2004, Op de Beeck et al. 2006, Yue et al. 2006). Importantly, when responses to objects of expertise are elevated, the effects are not limited to face-selective cortex; rather, they are also found in other brain regions involved in object representation (Gauthier et al. 2000, Op de Beeck et al. 2006, Yue et al. 2006). These broad effects are consistent with accounts proposing that increased responses for objects of expertise result from increased attention (Harel et al. 2010). Further evidence inconsistent with the expertise account comes from neuropsychological cases showing a dissociation between faces and objects of expertise (Sergent & Signoret 1992, Moscovitch et al. 1997, Duchaine et al. 2006, Susilo et al. 2013, Rezlescu et al. 2014). More generally, the existence of brain areas that respond selectively to human bodies (Downing et al. 2001), places (Epstein & Kanwisher 1998), and words (Cohen et al. 2000, Baker et al. 2007b), as well as that of other face-selective areas, raises the issue of why the expertise debate has focused solely on the FFA.

HAXBY AND COLLEAGUES' MODEL OF FACE PROCESSING

In 2000, Haxby and colleagues (Haxby et al. 2000, Haxby & Gobbini 2011) proposed what has become an extremely influential neurocognitive model of face processing. The model was primarily
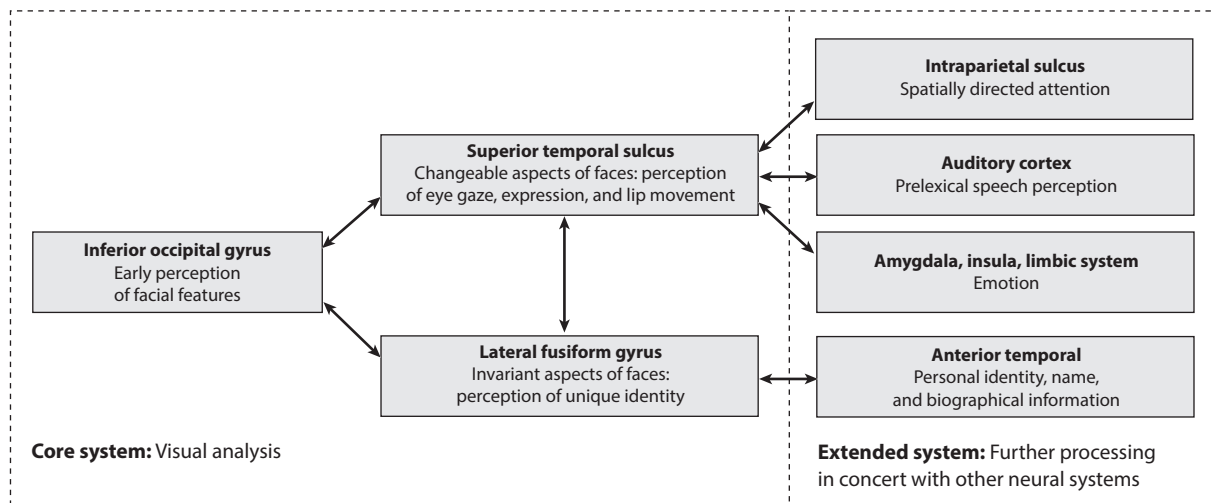
Figure 3

The model of face processing proposed by Haxby and colleagues (2000). The inferior occipital gyrus corresponds to the occipital face area (OFA), the lateral fusiform gyrus to the fusiform face area (FFA), and superior temporal sulcus to the posterior superior temporal sulcus face area (pSTS-FA).

based on findings from human neuroimaging and monkey neurophysiology studies, and elements of it were motivated by the Bruce & Young face model. Although the model was proposed when neuroimaging studies of face processing were in their early stages, it has provided an extensive and valuable framework that has dominated the field and inspired numerous studies that have tested its predictions.

As **Figure 3** shows, the Haxby model proposes that the face-processing system includes a core system, which consists of the OFA, the FFA, and the pSTS-FA, that carries out the visual analysis of faces. The OFA engages in early stages of face processing, which were not clearly defined. The OFA then sends its output to the FFA, where invariant aspects of faces such as identity and gender are represented. The OFA also provides input to the pSTS-FA, which represents changeable aspects of faces that are important for social communication, such as expression, eye-gaze, and lip movements. Back connections provide a means for recurrent processing.

The model further suggests that faces or information obtained from them is also processed by what they referred to as the extended face network. These areas are not dedicated to the processing of visual information; rather, they are connected to the core areas, and each extracts a different type of information from faces. Areas linked to the pSTS-FA include the intraparietal sulcus, which directs attention in accordance with gaze direction; the auditory cortex, which is involved with speech perception; and the amygdala and limbic system, which process emotional information from faces. The model also suggests that an area in the anterior temporal cortex is involved in the processing of semantic information of familiar faces and is linked to the FFA.

MAJOR FINDINGS SUGGESTING REVISIONS TO THE HAXBY MODEL

In this section, we review findings published since the Haxby model was proposed, along with the implications of these findings for our understanding of the face-selective areas. After reviewing the literature, we suggest a revised framework for face perception and mention some of the many issues that need to be addressed. Because we focus on the role of the face-selective areas in face
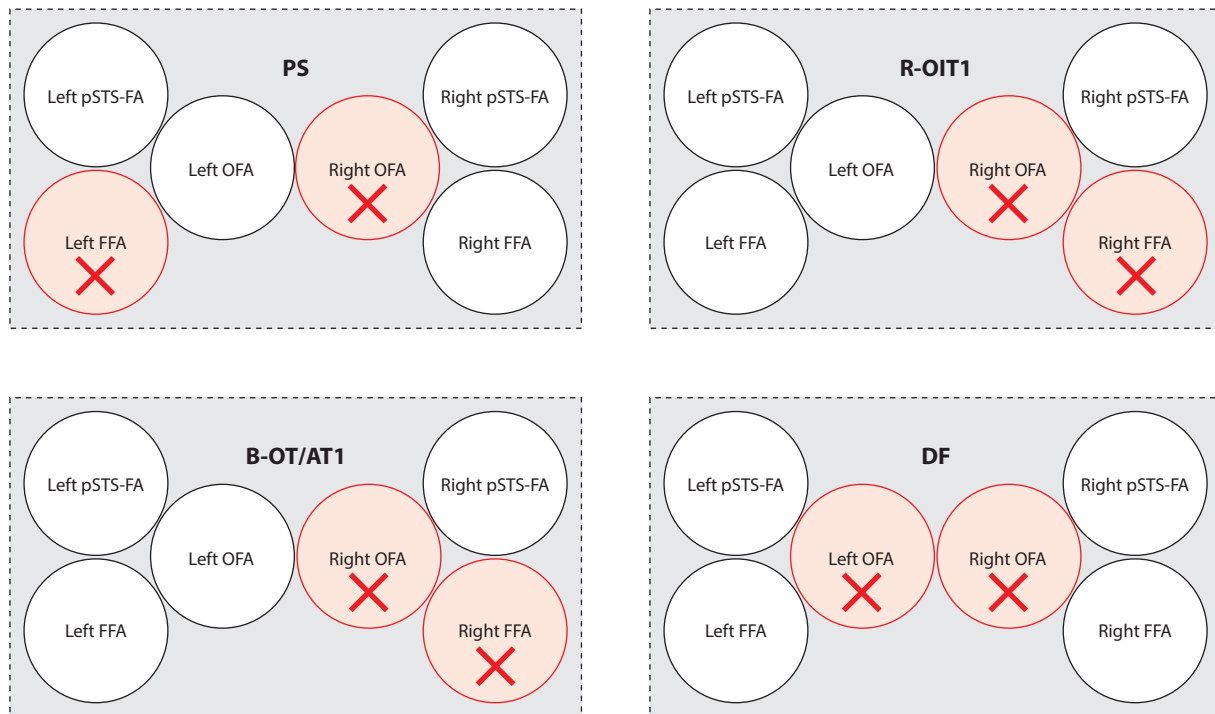
Figure 4

Schematic showing the intact and lesioned face-selective areas in four patients (PS, Sorger et al. 2007; R-IOT1 and B-OT/AT1, Dalrymple et al. 2011; DF, Steeves et al. 2006). Despite the absence of the right occipital face area (OFA), more anterior face-selective areas are present. The preservation of face-selective areas despite bilateral loss of the OFA in patient DF is especially strong evidence that the OFA is not the only entry point for the face network.

perception, our review is not concerned with many of the areas and functions of the extended system in the Haxby model.

Multiple Pathways into the Face-Processing Network

Haxby and colleagues (2000) tentatively suggested that the OFA is the entry point for information in the face-processing network, but results from several patients indicate that multiple pathways into the face system exist. For example, patient PS acquired prosopagnosia following bilateral brain damage that destroyed her right OFA, left FFA, and part of her right anterior temporal lobe (Rossion et al. 2003, Sorger et al. 2007). Despite the absence of a right OFA, PS continues to exhibit a right FFA and a right pSTS-FA that are comparable to these areas in normal participants in both size and face-selectivity (**Figure 4**) (Sorger et al. 2007). Hence, some face information is able to reach the face network in the hemisphere that is missing the OFA. Further evidence that multiple pathways convey face representations into the network is provided by three other patients with lesions to the right OFA and the right FFA who nevertheless show normal face-selectivity in the right pSTS-FA (**Figure 4**) (Dalrymple et al. 2011, Yang et al. 2015). However, the OFA could still be the gateway to the network if face information in these patients reaches the right-hemisphere face areas by way of the left OFA. Findings from patient DF, a well-studied visual form agnosic (Milner & Goodale 1995), decisively addressed this issue. DF does not exhibit

an OFA in either hemisphere, and her lesions appear to overlap the typical locations of the OFA. Notably, she still shows bilateral FFAs and pSTS-FAs (**Figure 4**) (Steeves et al. 2006).

These findings indicate that pathways directly connect early visual cortex with multiple face-selective regions. Rossion (Rossion et al. 2003, Rossion 2014) has even suggested reversing the OFA/FFA hierarchy: Information may be first processed by the FFA, then relayed to the OFA. The best evidence for this arrangement comes from patient NS, who suffered a lesion that destroyed the right fusiform regions where the right FFA is normally found. Even though the inferior occipital gyrus, which typically houses the right OFA, appeared to be intact in NS, she failed to exhibit a right OFA when examined with fMRI (Delvenne et al. 2004, Rossion 2008).

Studies examining the anatomical and functional connectivity between face-selective areas provide further support for the notion that multiple pathways into the face-processing network exist. Gschwind et al. (2012) were the first to report a fiber tracking study based on diffusion tensor imaging (DTI) between the face-selective areas. Their results suggested strong connections between the OFA and FFA, but they found no evidence for connections between either of these areas and the pSTS-FA. Furthermore, they found that early visual areas had direct connections with the FFA, although these connections were weaker than those between the early visual areas and the OFA. Similar findings were reported by Pyles et al. (2013). These findings are consistent with functional connectivity studies that examined the correlations between activations in face-selective areas during a face localizer or during rest. For example, Avidan et al. (2014) reported strong correlations between the time courses of OFA and FFA activation and much lower correlations between activation of these areas and of the pSTS-FA (see also Davies-Thompson & Andrews 2012, Fairhall & Ishai 2007).

Timing of Activity in Face-Selective Regions

The timing of neural activation in the face-selective areas has been studied with simultaneous electroencephalogram (EEG)-fMRI as well as TMS studies, and these results suggest hierarchical processing from the occipital to the temporal face-selective areas. In a simultaneous EEG-fMRI experiment, Sadeh et al. (2010) took advantage of the reliable individual differences in the magnitude of face selectivity (i.e., the difference between the response to faces and nonfaces) to examine the correlation between face-selective measures obtained with the two methods. They found that face selectivity in the OFA was correlated with face selectivity measured with EEG at 110 ms after stimulus onset, but not with face selectivity measured at 170 ms after stimulus onset (**Figure 5**). In contrast, face selectivity in the FFA and pSTS-FA were strongly correlated with face selectivity measured with EEG at 170 ms but not at 110 ms. Thus, these results indicate that the response in the OFA precedes those in the FFA and pSTS-FA by approximately 60 ms.

The second set of revealing findings are made possible by the remarkable temporal resolution of TMS. In two early studies (Pitcher et al. 2007, 2008), behavioral performance was selectively disrupted when paired-pulse TMS was delivered to the OFA 60 and 100 ms after stimulus onset, suggesting that the OFA processes facial information within a discrete, early time window. To more precisely identify the period in which the OFA contributes to face processing, a later study used pulse pairs that were separated by only 10 ms (Pitcher et al. 2012). As **Figure 5** shows, TMS at 100/110 ms disrupted performance, whereas TMS at the neighboring time windows had no effect. This finding fits nicely with the EEG-fMRI correlations described in the previous paragraph, which found a strong correlation between face selectivity in the OFA and face selectivity measured with EEG at 110 ms after stimulus onset (Sadeh et al. 2010). An earlier time window was also implicated by disruption following pulses at 50/60 ms after stimulus onset. Unlike the 100/110 ms disruption, this effect was not face selective (Pitcher et al.
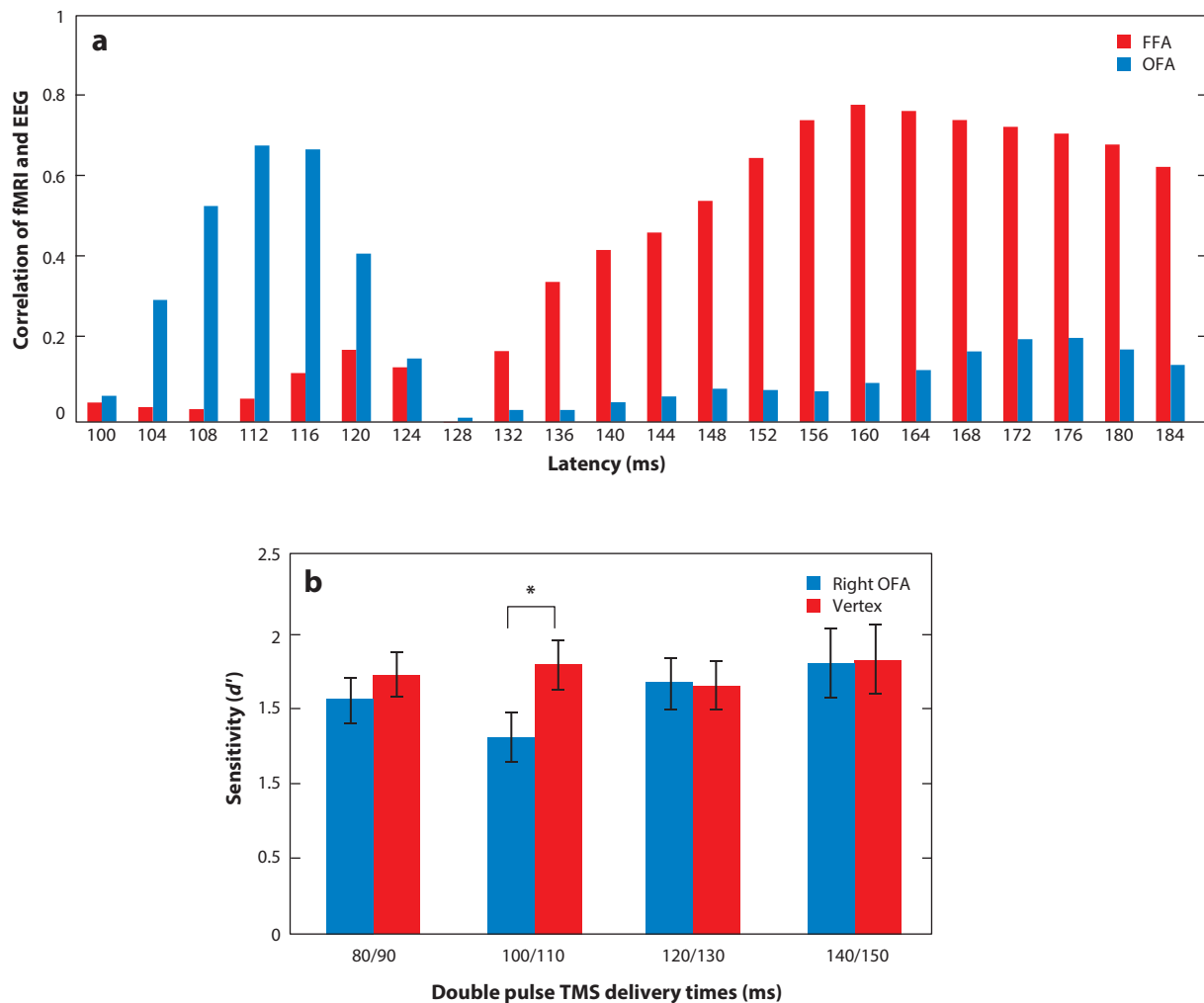
Figure 5

Temporal characteristics of face-selective areas. (*a*) Correlations between the magnitude of face selectivity in the occipital face area (OFA) and fusiform face area (FFA) with the magnitude of face-selectivity measured with event-related potentials (ERPs) at latencies ranging from 100 to 184 ms after stimulus onset (Sadeh et al. 2010). Face-selectivity in the OFA, but not the FFA, is highly correlated with the ERP face-selectivity at 110–120 ms, whereas face selectivity in the FFA, but not the OFA, is highly correlated with the ERP face-selectivity at 150–180 ms. Findings for the posterior superior temporal sulcus face area (pSTS-FA) are not shown here, but were similar to FFA. (*b*) Paired-pulse transcranial magnetic stimulation (TMS) to the right OFA disrupts face discrimination when delivered at 100–110 ms, but not when delivered at neighboring time windows (Pitcher et al. 2012). Note the correspondence between the functional magnetic resonance imaging (fMRI)-ERP results and the TMS results.

2012). A recent study delivered pulses separated by 40 ms to the pSTS-FA and OFA during an expression-discrimination task (Pitcher et al. 2014). Pairs at 60/100 ms disrupted performance in both areas, but 100/140 ms pairs affected performance only in the pSTS-FA. These results indicate that the pSTS-FA begins processing face information at a time window roughly similar to the OFA, but it also contributes to face processing later than the OFA does.

Consistent with findings in humans, single-unit recording studies also reveal evidence for hierarchical processing by showing earlier latencies in posterior face patches than in anterior

patches. Recent work in macaques has compared the timing of multiple face patches using the same set of stimuli (Freiwald & Tsao 2010). Recordings were made in four areas: the middle fundus (MF), middle lateral (ML), anterior lateral (AL), and anterior medial (AM) areas. These areas showed qualitatively different responses to face view and face identity. The more posterior areas, MF and ML, responded to specific views and were broadly tuned to identity. Cells in AL tended to respond to mirror-symmetric views and were more narrowly tuned to identity than MF and ML cells were. Neurons in AM were even more narrowly tuned to identity and exhibited nearly complete viewpoint invariance. The profiles of these patches indicate that the ventral stream progressively codes a viewpoint-invariant representation of face identity. Despite having different representational properties, these areas show similar temporal characteristics. Activity began only slightly earlier in the posterior areas than in the anterior areas (average onset times occurred at 88, 104, and 124 ms ML/MF, AL, and AM, respectively), the timing of their peak responses differed by only 19 ms (average times were 126, 133, and 145 ms for ML/MF, AL, and AM, respectively), and spiking was nearly complete in all three areas by 400 ms (Freiwald & Tsao 2010). Analysis of the responses in AL and AM found that both areas showed peak view-invariant identity selectivity at approximately 335 ms. The synchronicity of the peak responses and the substantial temporal difference between the peak responses and the peak identity selectivities in these patches suggest recurrent processing. Slightly earlier latencies with a similar pattern were found in a recent study (Issa & DiCarlo 2012). Issa & DiCarlo (2012) also made recordings in the posterior lateral (PL) area, the most posterior patch. PL had the shortest latency of all (median latencies were 74, 79, and 80 ms for PL, MF, and AL/AM, respectively).

The Fusiform Face Area May Contribute to Perception of Changeable Aspects

In the Haxby model, the FFA is involved in the processing of invariant information, including face identity, but it plays little role in the processing of changeable face aspects such as expression and gaze. Since the Haxby model was proposed, the contribution of the FFA to identity recognition has received further support from neuropsychology (Barton et al. 2002, Wada & Yamamoto 2001) and experiments using fMR-A (Gilaie-Dotan & Malach 2007, Rotshtein et al. 2005, Winston et al. 2003, Yovel & Kanwisher 2005). fMR-A studies can determine the extent to which the representation of face identity is view specific or view invariant by comparing the response of the FFA to two same-identity/same-view faces with the response to two same-identity/different-view faces. A higher response to same-identity/different-view faces indicates that these faces are represented as different faces, suggesting that the representation of identity is view specific rather than view invariant. Studies that have used this method indicate that the FFA codes a view-specific representation of face shape (Davies-Thompson et al. 2009, Ewbank & Andrews 2008, Xu & Biederman 2010).

Although the results discussed above provide strong evidence that the FFA plays a role in face identity computations, several studies that have been conducted since the Haxby model was proposed have indicated that the FFA may also be involved in expression processing (for a review, see Calder 2011, Bernstein & Yovel 2015). The FFA responds strongly to facial expression both when it is attended and when it is unattended (Ganel et al. 2005), and its response is modulated by the intensity of the facial expression (Surguladze et al. 2003, Winston et al. 2003). This area is also sensitive to differences in facial expressions across faces, as measured with fMR-A (Fox et al. 2009, Kadosh et al. 2010, Xu & Biederman 2010). In addition, poor expression recognition in a patient with brain damage that destroyed the right FFA but spared the right OFA and right pSTS-FA suggests that FFA representations contribute to expression recognition, at least for static faces (Dalrymple et al. 2011). Although these results indicate that both the FFA and the pSTS-FA play a role in expression processing, these two areas may extract different types of information about facial expression.

Evidence for this distinction comes from a study by Said et al. (2011), who presented observers with computer-generated faces that differed from an average face in two ways. In one dimension, the faces varied in expression, whereas in the other, they varied in terms of typicality relative to the average face shape, without varying in expression. The FFA was sensitive to deviations from the average face along both dimensions. In contrast, the pSTS-FA was sensitive only to faces that differ in expression, not to face typicality per se. These findings suggest that the response of the FFA to facial expression may reflect a broad sensitivity to shape information, whereas the pSTS-FA may be responsive only to face shapes that convey emotional information.

The Dorsal Face-Selective Areas Show Much Stronger Responses to Dynamic Faces than to Static Faces

Most fMRI and behavioral studies of face processing used static faces, so little is known about how dynamic faces are processed. However, recent studies that use videos of moving faces suggest that the ventral and dorsal face pathways substantially differ in their sensitivity to dynamic information (see also O'Toole et al. 2002). In contrast to the OFA and the FFA, which showed modest increases in response to dynamic compared with static stimuli, the response of the right STS-FA to dynamic faces was almost twice that to static faces (Fox et al. 2009). Dynamic faces also differentially affected cluster size. Whereas the OFA and the FFA tended to be approximately twice as large when localized with dynamic versus static stimuli, the pSTS-FA was five times larger. Importantly, increased face selectivity in the pSTS-FA primarily resulted from its much stronger response to dynamic faces, whereas the FFA and OFA had similar responses to dynamic and static faces but lower responses to dynamic versus to static objects (Fox et al. 2009).

Similar findings were reported in a later study that also used a dynamic localizer to identify face-selective areas and that then examined the selectivity for dynamic and static images with an independent data set (Pitcher et al. 2011). Consistent with the results reported by Fox et al. (2009), the response to dynamic faces was only slightly higher than the response to static faces in the OFA and FFA, whereas the response of the pSTS-FA was significantly larger for dynamic faces than for static faces (**Figure 6**). In addition, the dynamic localizers in the studies by Pitcher et al. (2011) and Fox et al. (2009) revealed additional face-selective areas in the anterior STS (aSTS-FA) and
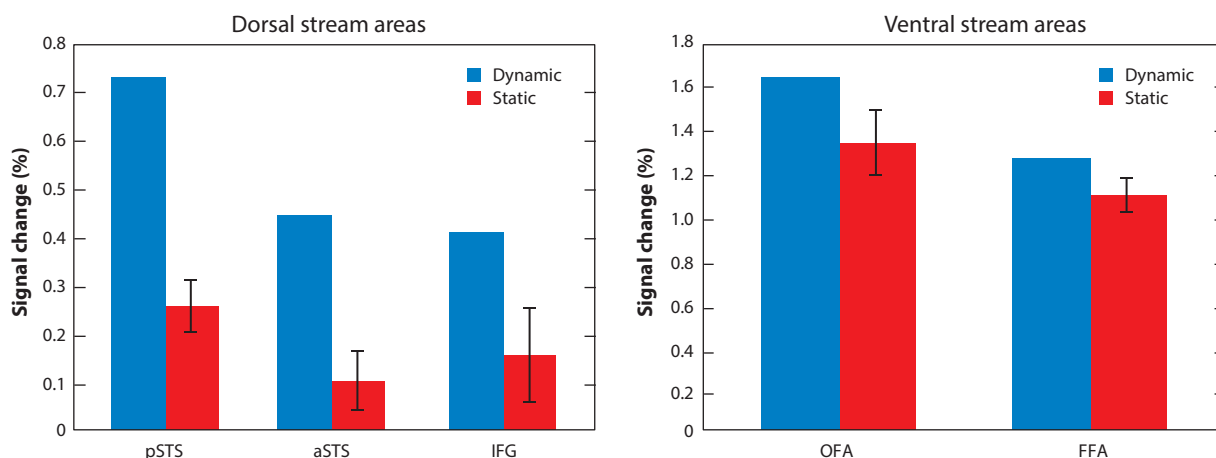

Figure 6

Responses to dynamic and static faces in five face-selective areas. (Pitcher et al. 2011). Error bars indicate the standard error of the difference between the responses to dynamic and static faces.

inferior frontal gyrus (IFG-FA) (see below), and the relative responses to dynamic and static faces seen in these areas were similar to those seen in the pSTS-FA. These studies suggest that the dorsal face-selective areas are specifically tuned to face motion, a finding consistent with results from previous studies showing that this area plays a role in biological motion (Grossman et al. 2000, Puce et al. 1998), whereas the FFA and OFA extract similar information from dynamic and static faces.

Further evidence for a static versus dynamic dissociation between the pSTS-FA and the ventral face pathways has been recently reported in a combined TMS-fMRI study (Pitcher et al. 2014). Participants underwent face localizer scans prior to and after offline delivery of TMS to the right OFA or the right pSTS-FA. TMS to the OFA decreased the pSTS-FA response to static faces but did not affect its response to dynamic faces. In contrast, stimulation of the pSTS-FA lessened its response to dynamic faces but did not affect its response to static faces. These findings suggest that dynamic facial information is processed primarily by a dorsal pathway along the STS.

Additional Face-Selective Areas in the Temporal and Frontal Lobes

The three core face-selective areas featured in the Haxby model have received extensive research attention. In recent years, however, additional areas that show face selectivity comparable to that of the core areas have been reported.

A face-selective area in the anterior temporal lobe.
Positron emission tomography (PET) studies that reported an area responsive to faces in the anterior temporal lobe (ATL) (Sergent et al. 1992), as well as those that reported prosopagnosia resulting from lesions to the ATL (Barton et al. 2002, Busigny et al. 2014), suggested the existence of a critical area for face processing in the ATL. Localizing and investigating such an area with fMRI is challenging, owing to the low signal-to-noise ratio in this part of the brain. The few studies that did find a face-selective area in the ATL found it in only about half of their subjects, and found that the volume of the area was relatively small (Nasr & Tootell 2012, Pinsk et al. 2009, Rajimehr et al. 2009, Tsao et al. 2008). However, several recent studies revealed an anterior temporal face-selective area in the right hemisphere in nearly all of their participants. These studies have done so using localizers involving familiar and emotional faces (Avidan et al. 2014); coronal scanning (Axelrod & Yovel 2013); and dynamic, emotional faces (Yang et al. 2015).

Yang et al. (2015) found that the right ATL-FA showed a weaker response to pairs of different images of the same celebrity (e.g., two different images of Natalie Portman) than to pairs showing different celebrities (e.g., Natalie Portman and Uma Thurman). In contrast, the FFA and all of the other face-selective areas responded similarly to pairs showing different images of same identity and to pairs showing different identities. Further support for the role of the ATL-FA in identity processing comes from human fMRI studies that have used multivoxel pattern analysis (MVPA) to decode face identity across different face appearances (Anzellotti et al. 2013), although it is not clear whether the clusters reported in some papers were actually face selective (Goesaert & Op de Beeck 2013, Kriegeskorte et al. 2007, Nestor et al. 2011). In contrast, a recent study, which localized the ATL face-selective area in all participants, did not reveal identity decoding of famous faces in the face-selective area of the ATL but did find evidence of above-chance decoding in the FFA (Axelrod & Yovel 2015). Thus, more research on the ATL-FA needs to be done in order to shed light on its role in face recognition and on its relationship with its probable monkey homolog, the macaque anterior medial (AM) area (Tsao et al. 2008, Yovel & Freiwald 2013). Dubois et al. (2015) recently provided evidence suggesting that the distribution of identity-selective neurons in the ATL-FA may play a role in the inconsistent conclusions drawn from studies using different methods. They recorded from view-independent, identity-specific neurons in macaque anterior

face patches but were unable to decode identity in these regions using fMRI-based MVPA. Analysis of the location of the neurons showed that they were weakly clustered by identity, making MVPA an ineffective method for probing whether the macaque anterior patches contain identity-specific neurons. In contrast, a lack of clustering by identity would not be expected to affect the sensitivity of studies measuring fMR-A.

Face-selective area in the anterior superior temporal sulcus. A face-selective area in the anterior STS (aSTS-FA) has been described in one study that used a static localizer (Pinsk et al. 2009) and in two studies that used a dynamic localizer (Fox et al. 2009, Pitcher et al. 2011). It is not surprising this area has rarely been identified with localizers using static images of faces and objects because its response to static faces in one study was as low as its response to objects (Pitcher et al. 2011). Despite its weak response to static faces, however, an adaptation experiment and an MVPA study using static faces found that an area close to the aSTS-FA codes the direction of eye gaze (Calder et al. 2007, Carlin et al. 2011). The gaze findings were consistent with the results of studies that recorded from neurons in macaque aSTS that were responsive to particular gaze directions (Perrett et al. 1985). The strong response of both the anterior and posterior STS to dynamic faces suggests that previous studies investigating STS activity in response to static faces might have produced a limited and maybe even inaccurate view of its role in face processing. Finally, a recent study showed overlap between the response to faces and voices in the STS, suggesting that it may carry a multimodal representations of people (Watson et al. 2014).

Prefrontal face areas. The first reports of face-selective neural responses in the prefrontal cortex were published in a single-unit recording study in monkeys (Ó Scalaidhe et al. 1997). Similar to face-selective neurons in IT, these neurons showed little response to objects or to scrambled faces, but did appear to show face-selective responses when monkeys were not performing a working memory task. The authors concluded that these responses were stimulus dependent, not task dependent. About a decade later, neuroimaging studies of the macaque brain revealed three face areas in the prefrontal cortex (Tsao et al. 2008). However, a systematic investigation of the selectivity profile of the neurons located within these fMRI-defined face areas has not yet been reported.

Face-selective activation in the lateral prefrontal cortex in humans has been reported in several articles (Chan & Downing 2011, Rajimehr et al. 2009; for review, see Chan 2013). Pitcher et al. (2011) and Fox et al. (2009) found that the prefrontal face area could be identified in a larger number of subjects using a dynamic face localizer rather than a static one, suggesting that this area may be associated with the network that processes dynamic faces in the STS. Further evidence for a frontal contribution to human face processing comes from the demonstration that direct electrical stimulation of the right anterior lateral prefrontal cortex in a patient produced face-specific visual hallucinations and illusions (Vignal et al. 2000), as well as from the selective deficit for fearful face recognition that the same patient exhibited following resection of right anterior lateral prefrontal cortex (Marinkovic et al. 2000). Despite these findings, only one study has attempted to study the functional profile of the anterior lateral prefrontal cortex in a systematic way. Chan & Downing (2011) have found that unlike the FFA, the IFG-FA showed a higher response to eyes alone and a lower response to faces without eyes than to faces with eyes. They therefore speculated that the IFG-FA may be associated with the processing of gaze information and possibly with eye movements, given its proximity to the frontal eye fields.

Face-selective subdivisions of the fusiform gyrus. Weiner & Grill-Spector (2012) have suggested that the FFA is not a single area but instead contains two separate regions (see also Engell & McCarthy 2013, Kietzmann et al. 2012, Pinsk et al. 2009). One region is in the posterior fusiform
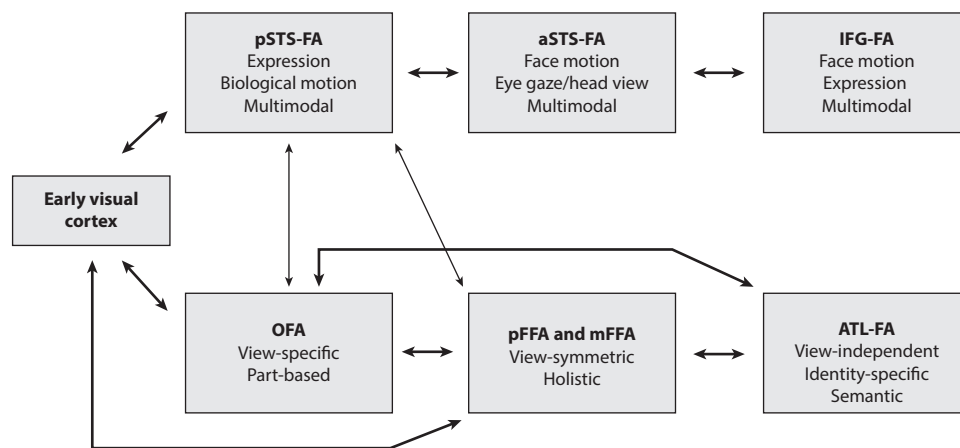
Figure 7

Revised framework for the roles and connections between face-selective areas. The ventral face-processing pathway consists of the occipital face area (OFA), the fusiform face area (FFA), and the anterior temporal lobe face area (ATL-FA), whereas the dorsal face-processing pathway comprises the posterior superior temporal sulcus face area (pSTS-FA), the anterior superior temporal sulcus face area (aSTS-FA), and the inferior frontal gyrus face area (IFG-FA).

gyrus (pFus), and the other is in the middle fusiform gyrus (mFus). These areas are separated by 10–15 mm, and a body-selective area lies between them (Weiner & Grill-Spector 2012). It is not clear whether these two areas have different functional roles in face processing. Notably, most studies conducted so far have treated the FFA as one area and, when two areas are found, either lump the two areas together or report on only one of them. A third, more anterior face-selective area located in the fusiform gyrus between mFus and the ATL-FA was reported by Rossion et al. (2012). Signal dropoff makes this a challenging area to identify using fMRI, but intracerebral recordings in a patient indicate that the region is highly selective for faces (Jonas et al. 2015), and intracranial stimulation of it severely disrupted the patient's ability to recognize famous faces (Jonas et al. 2015).

A REVISED NEURAL FRAMEWORK FOR FACE PROCESSING

Taken together, the findings discussed above suggest that a revised neural framework for face processing is needed [see Collins & Olson (2014) for a related framework]. **Figure 7** illustrates this framework, which consists of three extensively studied regions, the OFA, the FFA, and the pSTS-FA, and three more recently identified areas, the ATL-FA, aSTS-FA, and IFG-FA. Connectivity studies (Ethofer et al. 2011, Pyles et al. 2013) and studies showing the functional responses of these areas to dynamic and static faces (Fox et al. 2009, Pitcher et al. 2011) suggest that they can be divided into two separate but interacting pathways (Pitcher et al. 2014, Turk-Browne et al. 2010). The ventral pathway includes the OFA, FFA, and ATL-FA, whereas the dorsal pathway consists of the pSTS-FA, aSTS-FA, and IFG-FA.

Ventral Stream Face-Selective Areas

In the framework we have sketched out, ventral stream areas preferentially represent form information, providing the primary means to represent invariant features such as identity, sex, and age,

but also contributing to facial expression recognition. The OFA is the most posterior ventral area and represents face information starting approximately 100 ms after stimulus onset, only slightly before the other face-selective areas (Pitcher et al. 2007, Sadeh et al. 2010). OFA neurons have small receptive fields (Hemond et al. 2007, Schwarzlose et al. 2008); represent face parts in a view-specific manner (Pitcher et al. 2007); and are not sensitive to faces with poorly defined face parts, such as Mooney faces (Rossion et al. 2011). The OFA is tightly linked to the FFA and is connected to the ATL-FA, but the nature of its connections to the pSTS-FA and to other dorsal stream areas remains unclear (Gschwind et al. 2012, Pitcher et al. 2014, Pyles et al. 2013).

Multiple face-selective areas are present in the fusiform gyrus (Jonas et al. 2015, Weiner & Grill-Spector 2012). In our framework, these areas receive input not only from the OFA but also from early visual areas (Steeves et al. 2006), beginning approximately 100 ms after stimulus onset (Parvizi et al. 2012) and showing maximum face-selectivity approximately 170 ms after onset (Sadeh et al. 2010). The FFAs contain representations, which have larger receptive fields (Hemond et al. 2007, Rossion et al. 2011) and are more holistically integrated (Axelrod & Yovel 2010; Harris & Aguirre 2008, 2010; Rossion et al. 2011; Schiltz & Rossion 2006) than representations in the OFA. In contrast to the OFA, which is view specific, the FFA representations are mirror-symmetric, consistent with its higher location in the hierarchy (Axelrod & Yovel 2012, Kietzmann et al. 2012). The FFA represents information used for computing face identity (Gilaie-Dotan & Malach 2007, Grill-Spector et al. 2004, Hoffman & Haxby 2000, Rotshtein et al. 2005, Winston et al. 2003, Yovel & Kanwisher 2005), and its general role in representing form information also contributes to the recognition of facial expressions (Dalrymple et al. 2011, Fox et al. 2009, Furl et al. 2007, Ganel et al. 2005, Ishai et al. 2004, Kadosh et al. 2010, Vuilleumier et al. 2001, Xu & Biederman 2010).

The ATL-FA is the most anterior area in the ventral stream and appears to receive form information from both the OFA and the FFA (Gschwind et al. 2012, Pyles et al. 2013). Little is known about the functional role of the ATL-FA, but our framework tentatively proposes that it contains relatively image-invariant representations of face identity (Anzellotti et al. 2013, Yang et al. 2015; for a review, see Collins & Olson 2014). Such a role would fit well with findings from its likely macaque homolog, AM, which codes identity across a wide range of views (Freiwald & Tsao 2010). Activity in the ATL-FA begins shortly after the onset of activity in the OFA and FFA (Marinkovic et al. 2000), and representations of face identity and possibly other invariant aspects are sharpened over the course of several hundred milliseconds through recurrent processing with the OFA and FFA.

In summary, the ventral face pathway processes faces in a hierarchical manner, starting with parallel interactive processing of view-dependent representation in the OFA and view-symmetric representation in the FFA. These processing streams roughly correspond to the early stages of the Bruce & Young (1986) model. Notably, the FFA does not appear to represent face familiarity and therefore probably is not the neural locus of the face-recognition units in the Bruce & Young (1986) model. Image invariance in the ATL-FA suggests that this area is the most likely locus for the face-recognition units used to recognize familiar faces. Invariance in the ATL is also consistent with a large body of behavioral findings showing that the representation of familiar faces does not vary with changes in pose and illumination, whereas the representation of unfamiliar faces is more view selective (Burton 2013). The ATL-FA may also integrate visual representations with semantic representations.

Dorsal Stream Face-Selective Areas

The dorsal stream in our framework comprises the pSTS-FA, the aSTS-FA, and the IFG-FA. These areas show a much stronger response to dynamic faces than to static faces, and this characteristic fits well with their role in representing aspects of faces that change rapidly such as expression,

gaze, and mouth movements (Haxby et al. 2000). However, this property may not exclude it from responding to identity information conveyed by dynamic faces (O'Toole et al. 2002).

The pSTS-FA receives motion and form information from early visual areas (Dalrymple et al. 2011, Steeves et al. 2006). Based on EEG-fMRI correlational data, activity in pSTS-FA begins to respond at approximately the same time as the FFA and peaks at a similar point, 170 ms after stimulus onset (Sadeh et al. 2010). In a functional connectivity study, Davies-Thompson & Andrews (2012) reported strong connections between the STS and IFG, consistent with DTI results reported by Ethofer and colleagues (2011). Although these studies were done without face localizers, and thus may have recorded from areas outside the face-selective areas, recordings in IFG found somewhat later responses, with latencies of approximately 150 ms and peaks at approximately 250 ms after stimulus onset (Marinkovic et al. 2000). MT+/V5, which represents motion in early visual cortex, may be an important source of this information, although we note that perception of biological motion, which also relies on regions in the STS (Grossman et al. 2000), is not affected by disruptions in MT+/V5 (Grossman et al. 2005, Vaina et al. 1990). Future investigation is needed to obtain a greater understanding of the connectivity between the pSTS-FA and MT, the aSTS-FA, and the IFG-FA, as is more detailed examination of the functional roles these areas play in face processing. Finally, the recently reported sensitivity of the STS to both dynamic faces and human voices suggests that this area may be the locus of multimodal processing of person-related information (Watson et al. 2014).

In conclusion, we suggest that the network of face-selective areas can be divided into two streams: a ventral stream, which extracts form information from faces, and a dorsal stream, which is specialized for processing dynamic information from faces. The ventral stream represents the structure and surface properties of a face in the posterior face-selective areas and matches these representations with stored representations of familiar faces in the anterior temporal face-selective area. The dorsal stream plays a role in ongoing social interactions, which require the extraction of constantly changing information from moving faces (Haxby et al. 2000). We hope future research will benefit from this framework. Below we list some of the issues most in need of investigation to advance our understanding of the neural basis of face processing.

FUTURE ISSUES

1. We still have much to learn about the functional roles of and interactions among face-selective areas, particularly the anterior areas.

2. Given that in real life we primarily encounter moving faces, more studies are needed that explore face processing with dynamic faces.

3. What is the relationship between human face areas and macaque face patches? The identification of homologies would be a major step forward because it would provide a tighter link between human areas and the revealing single-cell findings in macaque face patches.

4. Are particular types of face-processing deficits associated with damage or developmental abnormalities in specific face-selective areas?

5. Do subdivisions within face-selective areas exist that support representation of specific invariant and changeable aspects of face perception such as identification, sex, age, gaze, or expression, among others?

6. What are the functional roles of face-selective areas in the left hemisphere?

DISCLOSURE STATEMENT

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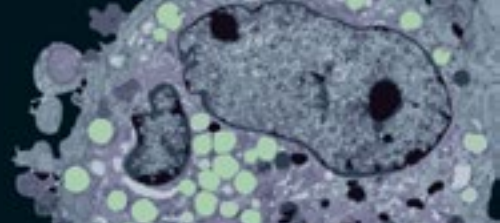
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