PART 4

Social Processes

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Face Perception

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For highly social organisms like us, faces reign supreme among visual stimuli. Faces inform us not only about a person's identity, but also about his or her mood, sex, age, and direction of gaze. The ability to extract this information within a fraction of a second of viewing a face is crucial for normal social interactions and has likely played a critical role in the survival of our primate ancestors. Considerable evidence from behavioral, neuropsychological, and neurophysiological investigations supports the hypothesis that the perception of faces is conducted by specialized cognitive and neural machinery distinct from that engaged in the perception of objects (the face specificity hypothesis). This fact has important implications for social cognition. It shows that at least one aspect of social cognition is domain specific (Fodor, 1983): fundamentally different mental processes apparently go on, and different neural systems become engaged, when we think about people compared to objects (see also Downing, Jiang, Shuman, & Kanwisher, 2001; Saxe & Powell, 2006). The domain specificity of face perception invites a much broader investigation of domain specificity of other aspects of social cognition (Saxe & Powell, 2006).

In this chapter, we review the literature on the three main cortical regions engaged in face perception in humans. We begin with a broad survey of the evidence from multiple methods for the face specificity hypothesis.

SPECIALIZED MECHANISMS FOR FACE PERCEPTION: EVIDENCE FROM NEUROPSYCHOLOGY, BEHAVIOR, ELECTROPHYSIOLOGY, AND NEUROIMAGING

Evidence from neuropsychology, behavior, electrophysiology, and neuroimaging supports the hypothesis that special mechanisms are engaged for the perception of faces.

Evidence from Neuropsychology: Prosopagnosia and Agnosia

The first evidence that face perception engages specialized machinery distinct from that engaged during object perception came from the syndrome of acquired prosopagnosia, in which neurological patients lose the ability to recognize faces after brain damage. Prosopagnosia is not a general loss of the concept of the person because prosopagnosic subjects can easily identify individuals from their voice or from a verbal description of the person. Impairments in face recognition are often accompanied by deficits in other related tasks such as object recognition, as expected given the usually large size of lesions relative to functional subdivisions of the cortex. However, a few prosopagnosic patients show very selective impairments in which face recognition abilities are devastated despite the lack of discernible deficits in the recognition of nonface objects (Wada & Yamamoto, 2001). Some prosopagnosic subjects have a preserved ability to discriminate between exemplars within a category (Duchaine, Yovel, Butterworth, & Nakayama, 2004; Henke, Schweinberger, Grigo, Klos, & Sommer, 1998; McNeil & Warrington, 1993), including objects of expertise (Sergent & Signoret, 1992) arguing against the idea that mechanisms of face perception are engaged more broadly on any visual stimuli requiring fine-grained discrimination. Some cases of "developmental prosopagnosia" (Duchaine et al., 2004), a lifelong impairment in face recognition (Behrmann & Avidan, 2005) with no apparent neurological lesion, show remarkably specific deficits in face perception only (Duchaine, Yovel, Butterworth, & Nakayama, 2006).

Is face recognition merely the most difficult visual recognition task we perform, and hence the most susceptible to

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brain damage? Apparently not: the striking case of patient CK (Moscovitch, Winocur, & Behrmann, 1997; see also McMullen, Fisk, Phillips, & Maloney, 2000), who had shown deficits in object recognition but normal face recognition, indicates a double dissociation between the recognition of faces and objects. Further, patient CK, who had been a collector of toy soldiers, lost his ability to discriminate these stimuli, showing a further dissociation between face recognition (preserved) and visual expertise (impaired). Thus, taken together, these selective cases of prosopagnosia and agnosia support the face specificity hypothesis and are inconsistent with its domain-general alternatives.

Behavioral Signatures of Face-Specific Processing

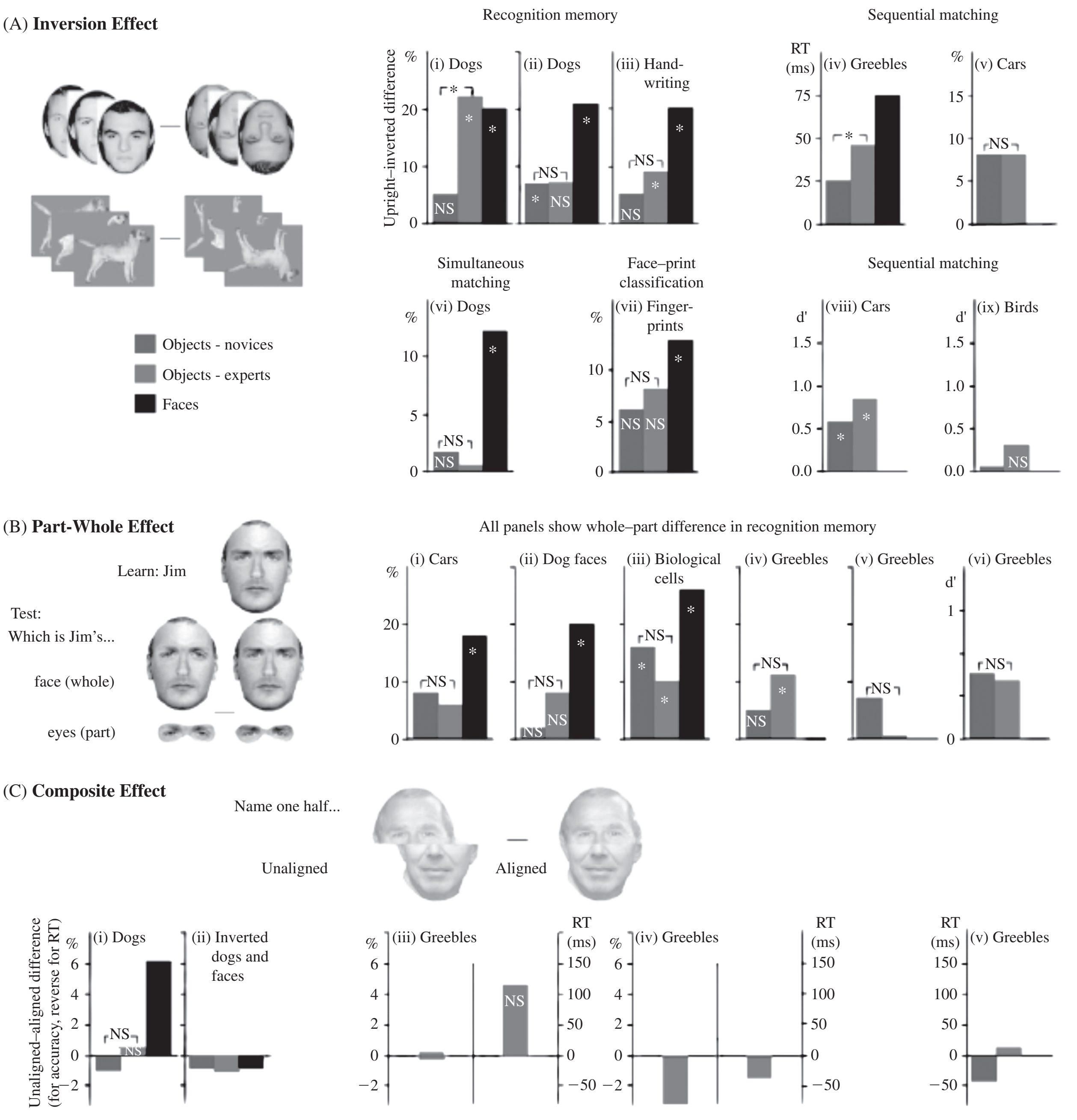
Classic behavioral work in normal subjects has also shown dissociations between the recognition of faces and objects by demonstrating a number of differences in the ways that these stimuli are processed. Best known among these signatures of face-specific processing is the face inversion effect, in which the decrement in performance that occurs when stimuli are inverted (i.e., turned upside-down) is greater for faces than for nonface stimuli (Yin, 1969). Other behavioral markers include the "part-whole" effect (Tanaka & Farah, 1993), in which subjects are better able to distinguish which of two face parts (e.g., two noses) appeared in a previously shown face when they are presented in the context of the whole face than when they are shown in isolation, and the "composite effect" (Young, Hellawell, & Hay, 1987), in which subjects are slower to identify one half of a chimeric face if it is aligned with an inconsistent other half-face than if the two half-faces are misaligned. Consistent with the holistic hypothesis, the probability of correctly identifying a whole face is greater than the sum of the probabilities of matching each of its component face halves (Yovel, Paller, & Levy, 2005). Taken together, these effects suggest that upright faces are processed in a distinctive "holistic" manner (McKone, Martini, & Nakayama, 2001; Tanaka & Farah, 2003), that is, that faces are processed as wholes rather than as sets of parts processed independently. All the holistic effects mentioned are either absent or reduced for inverted faces and nonface objects (Robbins & McKone, 2007; Tanaka & Farah, 1993), indicating that this holistic style of processing is specific to upright faces.

According to one alternative to the face specificity hypothesis, it is our extensive experience with faces that leads us to process them in this distinctive holistic and orientation-sensitive fashion. The original impetus for this hypothesis came from Diamond and Carey's (1986) classic report that dog experts show inversion effects for dog stimuli (see Figure 43.1). Since then, claims that nonface objects of expertise exhibit facelike processing have been widespread. However, an extensive effort to replicate the original Diamond and Carey result met with total failure (Robbins & McKone, 2007). Further, McKone, Kanwisher, and Duchaine (2007) reviewed all of the relevant published behavioral experiments (including those that claim to support the expertise hypothesis) and found no evidence for facelike processing of objects of expertise (see Figure 43.1).

Electrophysiology in Humans

Face-selective electrophysiological responses occurring 170 ms after stimulus onset have also been measured in humans using scalp electrodes (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Jeffreys, 1996). These results have been replicated with both ERPs and MEG in numerous studies that show face-selective responses both as early as 100 ms after stimulus onset (Itier & Taylor, 2004; Liu, Harris, & Kanwisher, 2002), and around 170 after stimulus onset (Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Liu et al., 2002). Although it has been claimed that the face-selective N170 response is sensitive to visual expertise with nonface stimuli (Gauthier, Curran, Curby, & Collins, 2003; Rossion, Curran, & Gauthier, 2002; Tanaka & Curran, 2001), these studies are hard to interpret because none of them include all three critical conditions: faces, objects of expertise, and control objects (McKone & Kanwisher, 2005). The one published study that included all three conditions investigated the face-selective magnetic (M170) response (Halgren et al., 2000; Liu et al., 2002) and found no elevated response to cars in car experts, and no trial-by-trial correlation between the amplitude of the M170 response and successful identification of cars by car experts (Xu, 2005) . Thus, the N170 and M170 appear to be truly face-selective and at least the M170 response is not consistent with any alternative domain-general hypotheses.

What is the nature of the face representation that is manifested by the N170? Initial studies suggested that the N170 is not sensitive to identity information, but instead primarily reflects structural encoding of facial information (Bentin & Deouell, 2000). However, other studies have shown that the N170 amplitude is smaller for subsequent presentation of similar faces (within the perceptual category boundary) than different identity faces (Jacques & Rossion, 2006), which suggest that identity is processed by 170 msec after stimulus onset. (For further discussion of the logic of adaptation studies, see the discussion that follows.) Importantly, this adaptation of the N170 to identity information (i.e., the lower response for repeated compared to unrepeated face stimuli) is shown for upright faces but not inverted faces (Jacques, d'Arripe, & Rossion, 2007). Evidence for holistic processing at 170 ms after stimulus



TRENDS in Cognitive Sciences

Figure 43.1 The available data reveal no evidence for holistic processing of objects of expertise.

Note: (A) Inversion effects for homogeneous objects increase little with expertise and do not become facelike, even in a recent direct replication (aii) of the classic Diamond & Carey experiment using dogs (ai). (Instead, in most studies, experts improve relative to novices for both upright and inverted stimuli, which suggests expertise in part-based processing.) (B) The part-whole effect does not increase with expertise and does not become facelike; unlike inversion, this task is a direct measure of measures holistic processing directly. (C) The composite effect is not found for objects of expertise, despite strong effects for upright faces. The two double-panel plots in (iii) and (iv) show cases where both accuracy (% correct) and reaction time (RT) were reported. For further details and references, see McKone et al. (2007). NS = $p > .05$. From "Can Generic Expertise Explain Special Processing for Faces?" by E. McKone, N. Kanwisher, and B. C. Duchaine, 2007, *Trends in Cognitive Sciences, 11,* p. 9. Reprinted with permission.
* $p < .05$.

onset has been recently demonstrated in another adaptation study that revealed a composite effect on the N170 (Jacques et al., 2007; for more information, see Schiltz & Rossion, 2006, for similar findings with functional magnetic resonance imaging or fMRI). Taken together, these findings suggest that by 170 ms a face-specific holistic representation, which includes all aspects of facial information, is already generated.

One important unanswered question concerns the neural source of the face-selective electrophysiological responses, which could be either the fusiform face area (FFA; Halgren et al., 2000) and/or the superior temporal sulcus (STS) (Bentin et al., 1996). Although this question is difficult to answer given the relatively low spatial resolution of event related potentials (ERP) and magnetoencephalography MEG, subdural ERP measurements in epilepsy patients have shown strongly face-selective responses in discrete patches of the temporal lobe (Allison et al., 1994; Allison, Puce, Spencer, & McCarthy, 1999). Further, a powerful demonstration of the causal role of these regions in face perception comes from two studies demonstrating that electrical stimulation of these ventral temporal sites can produce a transient inability to identify faces (Mundel et al., 2003; Puce, Allison, & McCarthy, 1999).

Neurophysiology and Functional Magnetic Resonance Imaging in Monkeys

Face specificity has been demonstrated in monkeys at both the single-cell level and at the level of cortical regions. Numerous studies dating back decades have reported face-selective responses from single neurons (face cells) in the temporal lobes of macaques (Desimone, Albright, Gross, & Bruce, 1984). Face-selective regions have been reported in macaques using fMRI (Pinsk, DeSimone, Moore, Gross, & Kastner, 2005; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003) and in vervets using a novel dual-activity mapping technique based on induction of the immediate early gene zif268 (Zangenehpour & Chaudhuri, 2005).

Strong claims of face selectivity entail the prediction that no nonface stimulus will ever produce a response as strong as a face; because the set of nonface stimuli is infinite, there is always some possibility that a future study will show that a putative face-selective cell or region actually responds more to some previously untested stimulus (say, armadillos) than to faces. However, studies in neurophysiology have addressed this problem about as well as can practically be hoped for. Foldiak, Xiao, Keysers, Edwards, and Perrett (2004) used rapid serial visual presentation (RSVP) to test each cell on over 1,000 natural images, and found some cells that were truly face-selective: for some cells, the 70 stimuli producing the strongest responses all contained faces, and the next best stimuli produced less than one-fifth the maximal response.

Although these data demonstrate individual cells that are strikingly face selective, they don't address the face selectivity of whole regions of the cortex. However, a more recent study demonstrates a spectacular degree of selectivity of whole regions of the cortex. Tsao, Freiwald, Tootell, and Livingstone (2006) directed eletrodes into the face-selective patches they had previously identified with fMRI (Tsao et al., 2003), and found that 97% of the visually responsive cells in these regions responded selectively (indeed, for most cells, exclusively) to faces. These stunning data suggest that the weak responses of the FFA to nonface stimuli may result from "partial voluming," that is, from the inevitable blurring of face-selective and non-face-selective regions that arise when voxel sizes are large relative to the size of the underlying functional unit. Thus, these data provide some of the strongest evidence to date on the extreme selectivity of some cortical regions for face processing (Kanwisher, 2006).

Brain Imaging in Humans

In the early 1990s, positron emission tomography (PET) studies showed activation of the ventral visual pathway, especially the fusiform gyrus, in a variety of face perception tasks (Haxby et al., 1991; Sergent, Ohta, & MacDonald, 1992). fMRI Studies of the specificity of these cortical regions for faces per se began in the mid-1990s, with demonstrations of fusiform regions that responded more strongly to faces than to letterstrings and textures (Puce, Allison, Asgari, Gore, & McCarthy, 1996), flowers (McCarthy, Luby, Gore, & Goldman-Rakic, 1997), and other stimuli, including mixed everyday objects, houses, and hands (Kanwisher, McDermott, & Chun, 1997). Although face-specific fMRI activations could also be seen in many subjects in the region of the face-selective STS (fSTS) and in the occipital lobe in a region named the occipital face area (OFA), the most consistent and robust face-selective activation was located on the lateral side of the mid-fusiform gyrus in a region we named the fusiform face area (FFA; Kanwisher et al., 1997; see Figure 43.2).

One of the most consistent finding about face-selective activations in the occipital-temporal cortex is its hemispheric asymmetry. All three face-selective regions are larger over the right than the left hemisphere. Furthermore, this asymmetry is stable across sessions (even when they take place more than 1 year apart) in particular for the FFA (Yovel, Tambini, & Bradman, 2008). This asymmetric response to faces is consistent with the finding that right hemisphere damage is necessary (though not always sufficient) for prosopagnosia (Barton, Press, Keenan, & O'Connor, 2002; Sergent & Signoret, 1992). We recently assessed whether individual differences in the asymmetric brain response to faces is associated with the behavioral left visual field superiority for face recognition. Numerous behavioral laterality studies have shown that normal individuals recognize better faces that are presented in the left visual field that projects directly to the right hemisphere than the right-visual field that projects directly to the left

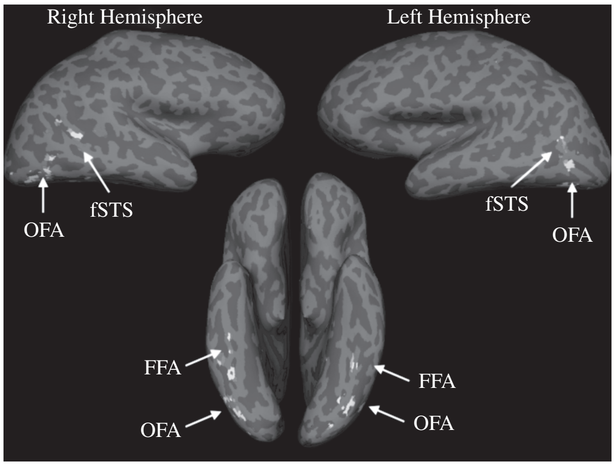


Figure 43.2 Face selective activation (faces > objects, $p < .0001$) on an inflated brain of one subject, shown from lateral and ventral views of the right and left hemispheres.

Note: Three face-selective regions are typically found: the FFA in the fusiform gyrus along the ventral part of the brain, the OFA in the lateral occipital area and the fSTS in the posterior region of the superior temporal sulcus.

hemisphere (Rhodes, 1985; Sergent & Bindra, 1981). The known right-hemisphere dominance for face processing has been suggested to account for this behavioral laterality effect. However, this association has never been demonstrated directly. We recently found that the asymmetry of the volume of the FFA was correlated across subjects with the magnitude of the behavioral asymmetry that was collected on a different session outside the scanner. That is, subjects who showed better performance for right- than left-side faces also had a larger FFA over the right than left hemisphere. This correlation was not found with the laterality of the occipital face area or with nearby object-selective regions (lateral occipital complex or LOC). These findings suggest that the asymmetric response of the brain to faces is a stable characteristic of each individual, which is manifested both at the neural and the behavioral level (Yovel et al., 2008).

The FFA region can be reliably identified in almost every normal subject in a short "localizer" fMRI scan contrasting the response to faces versus objects. In the functional region of interest (fROI) approach, the FFA is first functionally localized in each individual, then its response magnitude is measured in a new set of experimental conditions; this method enables the FFA to be studied directly despite its anatomical variability across subjects, in a statistically powerful yet unbiased fashion (Saxe, Brett, & Kanwisher, 2006). In contrast, group studies often cannot identify the FFA at all because of the variability in its precise location across subjects. Because the FFA is the most robust of the three face-selective regions (Kanwisher et al., 1997; Yovel & Kanwisher, 2004), it has been investigated most fully, more is known about it, and we focus on it in this section. We return to other face-selective regions later in the chapter.

Three lines of evidence indicate that the FFA responds specifically to faces and not to lower-level stimulus features usually present in faces (such as a pair of horizontally arranged dark regions). First, the FFA responds strongly and similarly to a wide variety of face stimuli that would appear to have few low-level features in common, including front and profile photographs of faces (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000), line drawings of faces (Spiridon & Kanwisher, 2002), cat faces (Tong et al., 2000), and two-tone stylized Mooney faces. Second, the FFA response to upright Mooney faces is almost twice as strong as the response to inverted Mooney stimuli in which the face is difficult to detect (Kanwisher, Tong, & Nakayama, 1998; Rhodes, Byatt, Michie, & Puce, 2004), even though most low-level features (such as spatial frequency composition) are identical in the two stimulus types. Finally, for bistable stimuli such as the illusory face-vase (Hasson, Hendler, Ben Bashat, & Malach, 2001), or for binocularly rivalrous stimuli in which a face is presented to one eye and a nonface is presented to the other eye (Pasley, Mayes, & Schultz, 2004; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Williams, Moss, & Bradshaw, 2004), the FFA responds more strongly when subjects perceive a face than when they do not see a face even though the retinal (Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002) stimulation is unchanged. For all these reasons, it is difficult to account for the selectivity of the FFA in terms of lower-level features that covary with faceness. Instead, these findings support the face specificity hypothesis.

However, before the specificity of the FFA can be accepted, several other alternatives must be considered. First, is the FFA engaged whenever subjects must discriminate between similar exemplars within a category, whether or not the stimulus is a face (Gauthier, Behrmann, & Tarr, 1999). No: when subjects perform within-category discrimination for faces and houses that have been matched for discriminability, the FFA still responds about three times as strongly during face discrimination as house discrimination (Yovel & Kanwisher, 2004). This experiment also rules out a second alternative to the face specificity hypothesis, according to which the FFA is involved in domain-general configural processing of any stimulus types: the FFA response was no higher when subjects discriminated faces or houses on the basis of the spacing between parts than when they discriminated faces or houses based on the appearance of the parts. Thus, the FFA is not involved in a domain-general way in either fine-grained discrimination, or configural processing, or any stimulus type; Instead, it is specific for faces per se.

In the most widely discussed third alternative hypothesis, it is claimed that the FFA is not face specific because it responds more strongly to objects of expertise than to control objects. However, this effect is in fact significant in only three (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier et al., 1999; Xu, 2005) of the nine studies that have tested the hypothesis (see also Grill-Spector, Knouf, & Kanwisher, 2004; Jiang et al., 2007; Moore, Cohen, & Ranganath, 2006; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Rhodes et al., 2004; Yue, Tjan, & Biederman, 2006). A plausible alternative account of this weak and unreliable effect is that it reflects a general increase in attentional engagement for objects of expertise compared to control objects, not a special role of face regions in expertise. This alternative attentional account predicts that increased responses to objects of expertise should be found not only in the FFA but in nearby object-processing regions such as the LOC. Indeed, all four studies that have tested for effects of expertise in both the FFA and the LOC find *larger effects* of expertise in the LOC than in the FFA (Jiang et al., 2007; Moore et al., 2006; Op de Beeck et al., 2006; Yue et al., 2006). These findings are inconsistent with the expertise hypothesis, instead supporting the face specificity hypothesis (see also Kanwisher & Yovel, 2006; McKone et al., 2007).

Summary

Taken together, these lines of research make a compelling case for the existence of specialized cognitive and neural machinery for face perception per se (the face specificity hypothesis), and argue against a variety of alternative hypotheses. First, neuropsychological double dissociations exist between face recognition and visual expertise for nonface stimuli, casting doubt on the claim that these two phenomena share processing mechanisms. Second, behavioral data from normal subjects show a number of "signatures" of holistic face processing that are not observed for other stimulus classes, such as inverted faces and objects of expertise. Third, electrophysiological measurements indicate face-specific processing at or before 200 ms after stimulus onset (N170). Fourth, fMRI and physiological investigations in monkeys show strikingly selective (and often exclusive) responses to faces both within individual neurons, and more recently also within cortical regions. Finally, extensive investigation of the most robust face-selective cortical region in humans, the FFA, supports the face specificity hypothesis (see also Kanwisher & Yovel, 2006) . This strong evidence for face-specific mechanisms invites a more detailed investigation of the precise nature of the computations and representations extracted in each of the face-selective regions of the cortex, which we turn to next.

THE NATURE OF THE FACE REPRESENTATIONS IN THE FUSIFORM FACE AREA

Many experiments implicate the FFA in determining face identity, that is, in extracting the perceptual information used to distinguish between individual faces. For example, we showed a higher FFA response on trials in which subjects correctly identified a famous face than on trials in which they failed to recognize the same individual (Grill-Spector et al., 2004), implicating this region in the extraction of information about face identity. (No comparable correlation between the FFA response and performance was seen for identification of specific types of cars, guitars, buildings, etc.) Further evidence that the FFA is critical for distinguishing between individual faces comes from studies that use fMRI-adaptation, discussed later. Finally, the critical lesion site for prosopagnosia is very close to the FFA (Barton et al., 2002; Bouvier & Engel, 2006). However, these results tell us nothing about the nature of the representations extracted from faces in the FFA, which we turn to next.

Invariances of Face Representations

To understand the representations of faces extracted by the FFA, we need to determine their equivalence classes. If the FFA is involved in discriminating between individuals, then it must extract different representations for different individuals. But are these representations invariant across images of the same face that differ in size, position, view, and so on?

The best current method for approaching this problem with fMRI is fMR-adaptation (Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2001), in which the blood-oxygen-level dependent (BOLD) response to two (or more) stimuli in a given region of the brain is lower when they are the same than when they are different, indicating a sensitivity of that brain region to that stimulus difference. This sensitivity to the sameness of two stimuli enables us to ask each brain region which stimulus pairs it takes to be the same and which it takes to be different, that is, to discover equivalence classes and invariances in neural representations of faces. Several studies have found robust fMR- adaptation for faces in the FFA, that is a lower response to an identically repeated faces than to new faces (e.g., Avidan, Hasson, Malach, & Behrmann, 2005; Eger, Schweinberger, Dolan, & Henson, 2005; Gauthier & Nelson, 2001; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Yovel & Kanwisher, 2004). Does this adaptation reflect a representation of face identity that is invariant across different images of the same person? Several studies have found adaptation across repeated images of the same face even when those images differ in position (Grill-Spector et al., 1999), image size (Andrews & Schluppeck, 2004; Grill-Spector et al., 1999), and spatial scale (Eger, Schyns, & Kleinschmidt, 2004). Further, Rotshtein et al. (2005) used categorical perception of morphed faces to show adaptation across physically different images that were perceived to be the same (i.e., two faces that were on the same side of a perceptual category boundary), but not across physically different images that were perceived to be different (i.e., two faces that straddled the category boundary). A similar study with unfamiliar morphed faces also revealed a close correspondence between the perceptual boundary and the magnitude of adaptation (Gilaie-Dotan & Malach, 2007). Thus, representations in the FFA are not tied to very low-level image properties, but instead show at least partial invariance to simple image transformations.

However, representations in the FFA do not appear to be invariant to nonaffine changes such as changes in lighting direction (Bradshaw, 1968), viewpoint (Pourtois et al., 2005; Warrington, Logue, & Pratt, 1971), and combinations thereof (Avidan et al., 2005; Pourtois et al., 2005). Fang, Murray, and He (2007) found sharp view-specific tuning in the FFA and STS. View-specific tuning in the FFA was more precise after very long presentations of the adaptor (25 sec) than after shorter presentations (0.3 sec). These studies indicate that the FFA treats two images of the same face that differ in viewpoint and lighting as two different images.

In sum, studies conducted to date converge on the conclusion that neural representations of faces in the FFA discriminate between faces of different individuals and are partly tolerant to simple image transformations including size, position, and spatial scale. However, these representations are not invariant to nonaffine changes in viewpoint or lighting.

Discriminating between Familiar and Unfamiliar Faces

A finding that the FFA responds differently to familiar and unfamiliar faces would support the role of this region in face recognition (though it is not required by this hypothesis as discussed shortly). Several fMRI studies have investigated this question (George et al., 1999; Gorno-Tempini et al., 1998; Haxby et al., 1999; Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Leveroni et al., 2000; Sergent et al., 1992; Wiser et al., 2000) using as familiar faces either famous faces or faces studied in the lab.

Two studies that investigated faces learned in the lab found opposite results, one showing an increase in the response to familiar compared to unfamiliar faces in the FFA (Lehmann et al., 2004) and the other (using PET) found a decrease in the response to familiar faces (Rossion, Schiltz, & Crommelinck, 2003). Although this discrepancy may be due to the use of different tasks in the two experiments (Rossion et al., 2003; see also Henson et al., 2002), studies of famous faces, which provide a stronger manipulation of familiarity, do not give a much clearer picture. One study found a small but significant increase in the response to famous compared to nonfamous faces (Avidan et al., 2005) but two other studies found no difference in the response to famous versus nonfamous faces in the FFA (Eger et al., 2005; Pourtois et al., 2005; see also Gorno-Tempini & Price, 2001; Gorno-Tempini et al., 1998). Taken together, these studies do not show a consistently different FFA response for familiar versus unfamiliar faces. Although these studies do not strengthen the case that the FFA is important for face recognition, it is important to note that they do not provide evidence against this hypothesis either. These results may simply show that the FFA merely extracts a perceptual representation from faces in a bottom-up fashion, with actual recognition (i.e., matching to stored representations) occurring at a later stage of processing. It is also possible that information about face familiarity is represented not by an overall difference in the mean response but by the pattern of response across voxels within the FFA (Haxby et al., 2001; but see Kriegeskorte, Formisano, Sorger, & Goebel, 2007).

Studies of face familiarity do however enable us to address a different question about the FFA—its role in processing of nonvisual semantic information about people. Because famous faces are associated with rich semantic information about the person, but nonfamous faces are not, the lack of a consistently and robustly higher response for famous rather than nonfamous faces in the FFA casts doubt on the idea espoused by some (Martin & Chao, 2001), that this region is engaged in processing not only perceptual but also semantic information about people (Turk, Gazzaniga, & Macrae, 2005).

Face Inversion Effect and Holistic Processing

As described previously, behavioral studies have discovered distinctive “signatures” of face-like processing, including the face inversion effect (Yin, 1969) and the composite effect. Does the FFA mirror these behavioral signatures of face-specific processing?

Early studies of the face inversion effect in the FFA found little (Haxby et al., 1999; Kanwisher, Stanley, & Harris, 1999) or no (Aguirre, Singh, & D’Esposito, 1999; Leube et al., 2003) difference in the response to upright and inverted faces. However, we reported a substantially higher FFA response for upright compared to inverted faces (Yovel et al., 2004). Further, in a subsequent study, we (Yovel & Kanwisher, 2005) reported that the FFA-face inversion effect was correlated across subjects with the behavioral face inversion effect. That is, subjects who showed a large increment in performance for upright versus inverted faces also showed a large increment in the FFA response to upright versus inverted faces (see Figure 43.3). Second, we found greater fMR-adaptation for upright than inverted faces, indicating that the FFA is more sensitive to identity information in upright than in inverted faces (Yovel & Kanwisher, 2005; see also Mazard, Schiltz, & Rossion, 2006). Thus, consistent with the behavioral face inversion effect, the FFA better discriminates faces when they are upright than when they are inverted. Importantly, this pattern of response was specific to the FFA studies (see discussion of OFA and STS that follows). In summary, in contrast to previous findings that found only a weak relationship between the FFA and the face inversion effect, our findings show a close link between these behavioral and neural markers of specialized face processing.

The larger behavioral inversion effect for faces rather than objects has been taken as evidence for holistic processing of upright but not inverted faces (Farah, Tanaka, & Drain, 1995). However, more direct evidence for holistic processing comes from the composite effect (Young et al., 1987) in which subjects are not able to process the upper or lower half of a composite face independently from the other half of the face even when instructed to do so, unless the two halves are misaligned. This effect is found for upright but not inverted faces. If the FFA is engaged in holistic processing of faces, then we might expect it to show an fMRI correlate of the composite effect. One study used fMRI adaptation to show evidence for a composite face effect in the FFA (Schiltz & Rossion, 2005). In particular, the FFA only showed adaptation across two identical top halves of a face (compared to two different top halves) when the bottom half of the face was also identical, consistent with the behavioral composite face effect. As with the behavioral composite effect, the fMRI composite effect was found only for upright faces and was absent for inverted faces or misaligned faces.

Thus, fMRI measurements from the FFA show neural correlates of the classic behavioral signatures of face-like processing, including the face inversion effect and the composite effect. These findings link the behavioral evidence on face-specific processing with research on the FFA, as well as helping to characterize the operations and representations that occur in the FFA.

Representation of Configuration and Parts of Faces

Three prominent features of face stimuli are the classic frontal face configuration (the arrangement of two horizontally and symmetrically placed parts above two vertically placed parts), the presence of specific face parts (eyes, nose, mouth), and the bounding contour of a roughly oval shape with hair on the top and sides. Which of these stimulus properties are important in driving the response of the FFA? Liu and colleagues (Liu et al., 2003) created stimuli in which each of these three attributes were orthogonally varied. The face configuration was either canonical or scrambled (with face parts rearranged to occur in different positions), veridical face parts were either present or absent (i.e., replaced by black ovals), and external features were either present or absent (with a rectangular frame showing only internal features, omitting chin and hairline). This study found that the FFA responds to all three kinds of face properties.

A prominent theory (Maurer, LeGrand, & Mondloch, 2002) suggests that the spacing among face parts plays a privileged role in our representation of faces, dissociable from the representation of the shape of the parts. However, fMRI studies consistently lead to the conclusion that the FFA is involved in processing both the parts and the spacing among the parts of faces (Maurer et al., 2007; Rotshtein, Geng, Driver, & Dolan, 2007; Yovel & Kanwisher, 2004). First, Yovel and Kanwisher (2004) scanned subjects while they performed a successive discrimination task on pairs of faces that differed in either the individual parts, or in the configuration (i.e., spacing) of those parts. Subjects were informed in advance of each block which kind of discrimination they should perform. The FFA response was similar and strong in both conditions, again indicating a role of the FFA in the discrimination of both face parts and face configurations. Second, two fMRI studies that examined the brain response when subjects discriminated faces that differ in spacing or parts also support the hypothesis that the FFA is involved in processing both spacing and part information in faces. Although Maurer et al. (2007) reported some regions that were differentially sensitive to spacing information or to part-based information, these fusiform activations were located *outside* the FFA and therefore do not argue against our contention that the FFA is engaged in both processes. A close examination of the face-selective region in their study did not reveal any difference between the response to spacing and parts even when very low threshold levels were applied. Similarly, Rotshtein et al. (2007) examined repetition effects for faces that differ in spacing and parts. Several regions outside face-selective regions showed differential sensitivity to

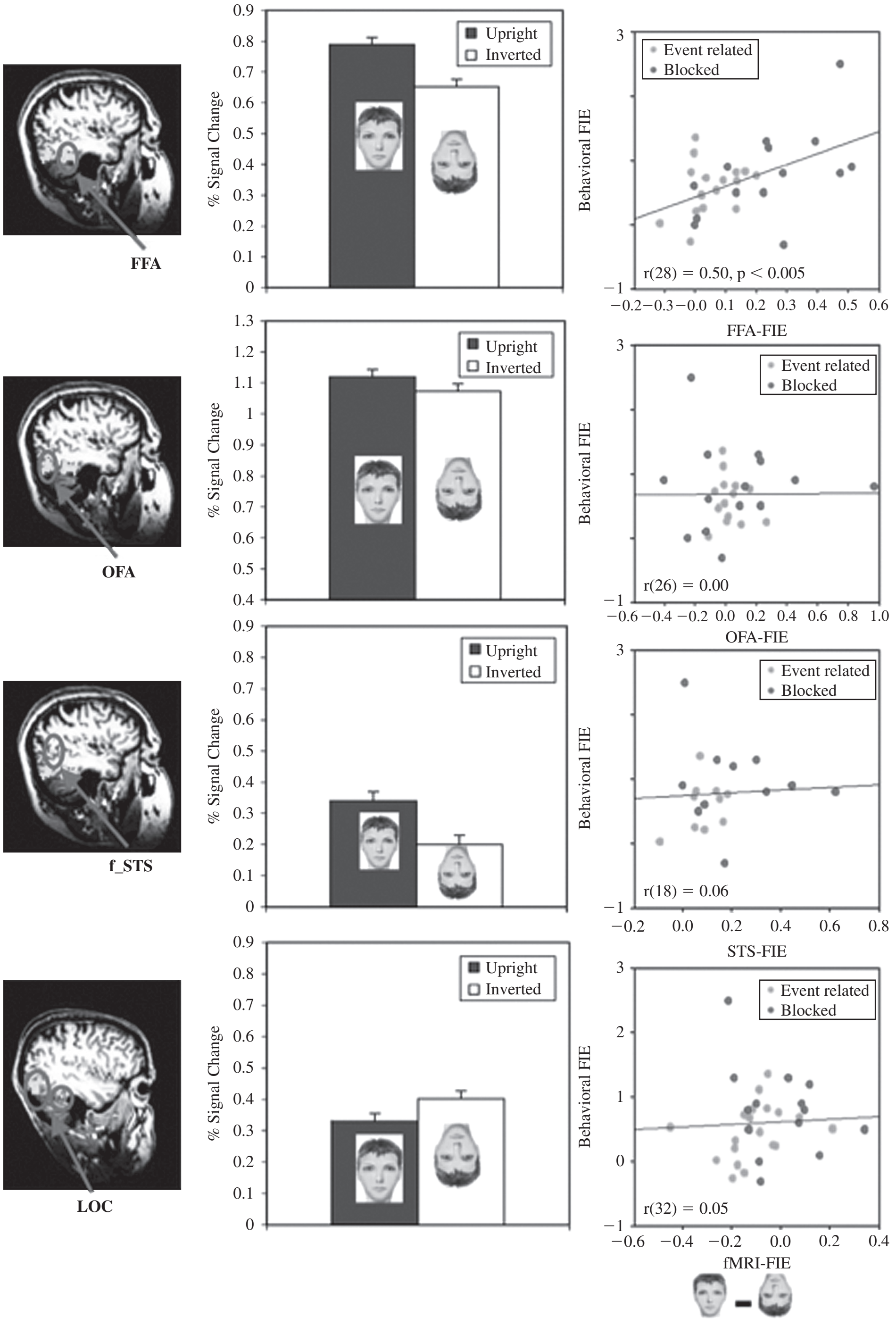


Figure 43.3 The magnitude of the face inversion effect in the FFA (but not the OFA, fSTS, or LOC) is correlated across subjects with the magnitude of the behavioral face inversion effect.

Note: From "A Whole Face Is More Than the Sum of Its Halves: Interactive Processing in Face Perception," by Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology, 15,* 2256–2262, Figure 2.

spacing versus parts, whereas an area that overlapped with the face-selective fusiform area was sensitive to repetition of parts and was correlated with performance on the spacing discrimination task. The authors concluded that information about spacing and parts may converge in the FFA.

Taken together, these studies show that the FFA is not sensitive to only a few specific face features, but instead seems to respond generally to a wide range of features spanning the whole face. Whereas several brain regions do show dissociated responses to information about spacing or parts, the FFA seems instead to generate an integrated representation that includes all aspects of face information. These findings are consistent with a recent behavioral study that found a positive correlation across subjects between performance on discrimination of spacing and discrimination of parts only for upright faces, not for inverted faces or houses (Yovel & Kanwisher, 2008). Thus, although spacing and part-based information about objects are processed by distinct mechanisms, information about the spacing and parts of upright faces are integrated into a common, holistic representation.

Norm-Based Coding of Faces

The power of caricatures to capture the likeness of a face suggests that face identity is coded in terms of deviation from the norm or average face, a hypothesis supported by behavioral studies (Leopold, O' Toole, Vetter, & Blanz, 2001; Rhodes, Brennan, & Carey, 1987). One fMRI study found higher FFA responses to atypical compared to average faces, implicating the FFA in such norm-based coding of face identity (Loffler, Yourganov, Wilkinson, & Wilson, 2005). However, efforts in this study to unconfound such face typicality effects from the greater adaptation effects expected between highly similar faces (in the average-face condition) versus very different faces (in the atypical face condition) were not entirely satisfactory. Therefore, the interesting hypothesis that the FFA codes faces in terms of deviation from the average face remains to be fully tested and explored.

Top-Heavy Figures

Although several studies have found that newborns look preferentially at facelike images (Johnson, Dziurawiec, Ellis, & Morton, 1991), this preference may reflect a more general preference for top-heavy figures (Cassia, Turati, & Simion, 2004). Top-heavy figures are similar to faces in that they contain more information in their upper half. To assess whether the FFA shows a similar preference to such figures, Caldara and colleagues (2006) presented head-shape and square-shape figures that included more information in their upper or lower halves. The right FFA showed the highest response to head-shape top-heavy stimuli. The response of the right FFA to a top-heavy square and bottom-heavy stimuli was similar and lower. This pattern is consistent with behavioral ratings of faceness on these stimuli. The left FFA and the OFA showed similar responses to top and bottom-heavy stimuli. Thus, only the right FFA shows a higher sensitivity to the type of stimuli that elicit longer looking time during the first 24 hours of life.

Fusiform Face Area and Facial Expression Information

fMRI studies of face expression have primarily focused on the amygdala (e.g., Glascher, Tuscher, Weiller, & Buchel, 2004; Williams et al., 2004). However, studies that have investigated the response of the temporal cortex have also found higher responses to emotional rather than neutral faces in the fusiform gyrus (Breiter et al., 1996; Dolan, Morris, & de Gelder, 2001; Vuilleumier, Armony, Driver, & Dolan, 2001, 2003; Williams et al., 2004). It has been suggested that this effect is modulated by connections from the amygdala (Dolan et al., 2001). Consistent with this hypothesis, effects of facial expression (in contrast to face identity) are not specific to the FFA. Given the higher arousal generated by emotional faces, the higher response to expressive than neutral faces in the FFA may reflect a general arousal effect rather than specific representation of facial expression. Indeed, one fMRI-adaptation study (Winston, Vuilleumier, & Dolan, 2003), in which expression and identity were manipulated in a factorial manner, did not find significant fMR-adaptation to expression information in the fusiform gyrus, but did find fMR-adaptation to face expression in regions in the STS. These findings are consistent with the idea that the FFA is involved in the extraction of identity but not expression information, whereas the STS shows the opposite pattern of response (Haxby, Hoffman, & Gobbini, 2000). However, another study found a higher FFA response during expression judgments and identity judgments that were done on separate blocks on the same face stimuli (Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005), casting some doubt on the simple idea that the FFA is involved exclusively in processing face identity information.

Further evidence for the possible role of the FFA in expression processing comes from a recent developmental fMRI study in which adults, teenagers (13 to 17 years), and children (8 to 11 years) were asked to classify facial expressions for upright or inverted faces (Passarotti, Smith, DeLano, & Huang, 2007) Just as for face identity findings (Yovel & Kanwisher, 2005), adults showed higher responses to upright than inverted stimuli in regions that overlap with face-selective regions in the fusiform gyrus and the STS (a face localizer was not included in Passarotti et al., 2007). In contrast, teenagers and children showed weaker or absent fMRI-face inversion effects in these regions. Finally, only in adults and only in the area that overlapped with the right FFA, a correlation across subjects was found between the fMRI and behavioral inversion effects. This finding suggests that the FFA may play some role in extracting information about emotional expressions in faces.

Summary

The results reviewed in this section provide the beginnings of a characterization of the computations and representations that occur in the FFA. The FFA is implicated in face detection and face discrimination, but evidence on the role of the FFA in discriminating familiar from unfamiliar faces or in discriminating emotional expressions in faces is inconsistent. Representations of faces in the FFA are partly invariant to simple image transformations such as changes in size, position, and spatial scale, but largely noninvariant to changes in most viewpoints and lighting direction of the face image. The FFA shows both a face inversion effect (i.e., a higher response for upright than inverted faces) and holistic processing of faces, as expected if this region plays a major role in face-processing phenomena established in previous behavioral work.

Although the FFA is by far the most robust and hence most studied of the face-selective regions of the cortex, two other face-selective regions have also been investigated, the OFA in the lateral occipital cortex and what we call the fSTS (a face-selective region in the posterior part of the superior termporal gyrus). Figure 43.2 shows these face-selective activations on an inflated brain from one subject. Ongoing work has begun to reveal a functional division of labor between these three cortical regions.

FUNCTION OF THE FACE-SELECTIVE OCCIPITAL FACE AREA

Situated just posterior and lateral to the FFA, the most natural hypothesis is that the OFA is an earlier stage of the face-processing network that sends its output to the FFA. Although the responses of the OFA are in many ways similar to responses of the FFA, they do differ in some telling respects that are largely consistent with this hypothesis. First, the OFA has a stronger contralateral-field bias than the FFA (Hemond, Kanwisher, & Op de Beeck, 2007). Second, Rotshtein et al. (2005) showed that a posterior face-sensitive region in the inferior occipital gyrus, presumably the OFA, is sensitive to physical changes in the face stimulus, independent of whether those changes are perceived as a change in face identity, whereas a face-sensitive region in the right fusiform gyrus, presumably the FFA, is sensitive only to perceived changes in face identity. Third, Yovel and Kanwisher (2005) found that the OFA showed a similar response to upright and inverted faces, and there was no correlation across subjects between the magnitude of the behavioral face inversion effect and the difference in the response of the OFA to upright and inverted faces (OFA-face inversion effect). In contrast, the FFA showed higher response to upright than inverted faces and this difference was correlated across subjects with the behavioral face inversion effect. Finally, whereas the FFA responds to first-order stimulus information about both face parts and face configurations, the OFA is sensitive only to face parts (Liu et al., 2003). Consistent with these findings, a transcranial magnetic stimulation (TMS) study (Pitcher, Walsh, Yovel, & Duchaine, 2007; Pitcher, Garrido, Walsh, & Duchaine, 2008) showed that that OFA stimulation that takes place 60 to 100 ms after stimulus onset disrupts discrimination of faces that differ in parts but not in spacing among them. Taken together, these findings suggest that the OFA constitutes an earlier stage of face processing, which represents information that is more closely tied to the face stimulus, whereas the FFA represents the perceived identity of the face.

However, all of the data just summarized is based on the functional properties of the OFA and FFA. What do we know about the critical question of how these regions are connected? Efforts to answer this question using functional connectivity (Fairhall & Ishai, 2007) are suggestive but not yet conclusive, and fiber-tracing methods cannot distinguish direct connections between the OFA and FFA from other nearby fibers. However, evidence from disruption methods shows that the OFA is a necessary stage in the face-processing network. First, patient PS with no right OFA but intact right FFA was severely prosopagnosic (Rossion et al., 2003). Although this result by itself makes sense, a puzzle arises from the fact that the same patient shows a face-selective activation in the fusiform gyrus (FFA) in fMRI. One possibility is that the right FFA receives input form the left OFA. However, a study of another patient (DF) with bilateral lesions in the OFA also shows apparently intact face-selective activation in the FFA (Steeves et al., 2006). These data suggest that the FFA gets face input from early visual areas outside the OFA (Dricot, Sorger, Schiltz, Goebel, & Rossion, 2008). However, this input does not generate an intact representation of identity information in the FFA. fMRI adaptation has shown that the FFA in patient PS does not discriminate between individual faces (Schiltz, Sorger, Ahmed, Mayer, & Goebel, 2006), suggesting that interaction with the OFA is necessary for normal functioning of the FFA. In a follow-up study that tested adaptation to faces in nearby nonface selective regions, the absence of adaptation for face identity in the FFA was replicated, but intact adaptation effect to faces in nearby object processing regions was observed. These findings suggest that the OFA is associated with the FFA but not with nearby nonface selective regions that show normal adaptation response even when the OFA is damaged (Dricot et al., 2008). Finally, as mentioned previously, TMS to the OFA selectively disrupts perception of face parts (Pitcher et al., 2007; Schiltz & Rossion, 2005).

In sum, the OFA appears to constitute an early stage of face processing necessary for the perception of face parts, and most likely connecting directly to the FFA, but not processing the only input to the FFA.

FUNCTION OF THE FACE-SELECTIVE REGION IN THE SUPERIOR TEMPORAL SULCUS

Although the FFA can be found in essentially all normal subjects, the face-selective region in the STS (fSTS) is less reliable; it is found in only half (Kanwisher et al., 1997) to three quarters (Yovel & Kanwisher, 2005) of subjects scanned individually. For this reason, this region has been studied less extensively than the FFA, although numerous studies investigate responses in the STS to face stimuli. Nonetheless, evidence suggests important functional distinctions between the fSTS and other face-selective regions of the cortex, with the fSTS more involved in processing dynamic and social aspects of faces such as emotional expression and gaze (Haxby et al., 2000).

First, the fSTS does not show the same involvement in the detection of faces and the perceptual analysis of face identity that has been found in the FFA. Two studies have found that the FFA but not the fSTS is correlated with successful face detection. Andrews and Schulppeck (2004) presented ambiguous stimuli (Mooney faces) that on some trials were perceived as faces but on others were perceived as novel blobs. Whereas the FFA response was stronger for face than blob percepts (see also Kanwisher et al., 1998), the fSTS showed no difference between the two types of trials. These findings are consistent with Grill-Spector et al. (2004) who found that the response of the FFA was correlated with successful detection of faces in brief masked stimuli, but the response of the fSTS was not. The failure to find a correlation with successful face detection in the fSTS when stimuli are held constant (or are similar) is somewhat surprising given that this region by definition responds more strongly when faces are present than when they are not. In any event, the correlation with successful face detection of the FFA but not fSTS, which was found in both studies, shows a dissociation between the two regions.

Given the findings just described, it is not surprising that the fSTS shows no sensitivity to face identity information. For example, Grill-Spector et al. (2004) found no correlation of the fSTS response with successful identification of faces. Similarly, studies that used fMR-adaptation found sensitivity to face identity in the FFA but not in the fSTS (Andrews & Schluppeck, 2004; Yovel & Kanwisher, 2005). Several studies have found a robust face inversion effect (higher response to upright than inverted faces) in the fSTS (Haxby et al., 1999; Leube et al., 2003; Yovel & Kanwisher, 2005). However, in contrast to the FFA, this difference between upright and inverted faces was not correlated with the behavioral face inversion effect measured in a face identity discrimination task (Yovel & Kanwisher, 2005; see Figure 43.3). These findings are consistent with the idea that the fSTS is not involved in extracting individual identity from faces. Its higher response to upright rather than inverted faces may suggest that the computations that are done in the fSTS to extract dynamic aspects of facial information are specific to upright faces.

Several studies have provided compelling evidence that the fSTS is involved in the processing of eye gaze, emotional expression, and dynamic information about faces. First, Hoffman and Haxby (2000) showed that although the FFA responds more strongly when subjects performed a one-back task on face identity rather than gaze information, the fSTS showed a higher response for the gaze task than the identity task. Second, an fMR-adaptation study (Winston et al., 2003) in which expression and identity were manipulated in a factorial manner, found significant sensitivity to information about emotional expression in faces in the fSTS but none in the fusiform gyrus (see also Andrews & Ewbank, 2004). Other studies have shown strong responses in fSTS to dynamic face stimuli in which expression or gaze changes (Calvert & Campbell, 2003; Thompson, Hardee, Panayiotou, Crewther, & Puce, 2007).

Is an intact OFA necessary for an fSTS activation? fMRI studies of patients with unilateral (Sorger, Goebel, Schiltz, & Rossion, 2007) and bilateral OFA (Steeves et al., 2006) lesions show intact fSTS activation in these patients, which suggests that the fSTS gets face input from areas outside the OFA. It is still not known, however, whether more subtle fMRI measures of the fSTS activation during expression and gaze processing may be intact in these patients.

In sum, whereas the FFA and OFA appear to be more involved in the analysis of face identity, the STS is more involved in the analysis of social and dynamic information in faces such as gaze, expression, and movement (Haxby et al., 2000).

ORIGINS OF FACE PROCESSING

How do face-selective cortical regions and adult-like face processing arise in development? Are they constructed by a process of experience-dependent cortical self-organization (Jacobs, 1997)? Are some aspects of face processing partly innately specified? For the case of faces, these questions have been hard to answer because both experiential and evolutionary arguments are plausible. Evidence from individuals with face impairments due to developmental prosopagnosia and congenital cataracts are suggestive (for a review, see Kanwisher & Yovel, 2006; McKone et al., 2007), but do not yet provide definitive answers to these questions (but see Duchaine, Germine, & Nakayama, 2007; Grueter et al., 2007). However, clues are beginning to emerge from a number of recent studies.

Ongoing work is characterizing the developmental trajectory of face perception abilities, and the face-selective cortex, in increasing detail. Neuroimaging studies show that the FFA is still developing into the early teenage years (Aylward et al., 2005; Golarai et al., 2007; Passarotti et al., 2003; Scherf, Behrmann, Humphrey, & Luna, 2007). In contrast, behavioral work shows that all of the key behavioral signatures of adult-like face processing are qualitatively present by 4 years of age (Kanwisher & Yovel, 2006; McKone et al., 2007). A major puzzle for future research will be to understand why the FFA changes at least twofold in volume between age 7 and adulthood, after face perceptual abilities are largely in place. Whatever the ultimate answer to this question, it is important to note that late development of face perception (whether by 4 or 14 years of age) need not indicate a critical role for experience in the construction of the FFA; maturation could explain some of all of this developmental change. To understand how face-processing mechanisms arise, we must turn to other methods.

At least some aspects of face perception appear to be innately specified because infants less than 24 hours old preferentially track schematic faces compared to visually similar scrambled or inverted faces (Cassia et al., 2004; Johnson, Dziurawiec, Ellis, & Morton, 1991). Experience also affects face perception, as evidenced by the "other race effect," in which neural responses (Golby, Gabrieli, Chiao, & Eberhardt, 2001) and behavioral performance (Malpass & Kravitz, 1969; Meissner & John, 2001) and are higher for faces of a familiar than for an unfamiliar race, even if (in the latter case) the relevant experience occurs after age 3 (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005). However, these two observations leave open a vast space of possible scenarios in which genes and environment interact in the construction of a selective region of cortex such as the FFA. Two recent findings suggest a greater role for genes than many would have guessed.

First, Polk, Park, Smith, and Park (2007) compared the spatial distribution of response to various stimulus categories across the ventral visual pathway in twins. They found that for faces and places the pattern of response was more similar for monozygotic than dizygotic twins, whereas for pseudowords and chairs, it was not. This result indicates that differences between individuals in the pattern of response to faces in the ventral visual pathway are due in part to genes. However, note that this result does not argue against a role for experience in the construction of the FFA. Although genes might exert some kind of direct control over neural connectivity, another possibility is that genes that affect social behavior lead some individuals to look at faces more than others do, and this differential experience itself affects neural responses to these categories. Although this study presents some of the first evidence we know of for a genetic influence on the cortical machinery of face perception (see also Duchaine et al., 2007; Grueter et al., 2007), that evidence does not necessarily argue against a role for experience in the construction of the FFA. There are many possible causal pathways from genes to neural architecture, some of which crucially implicate experience as the key intervening variable.

Another recent study argues that experience with faces may not be necessary for the construction of face-processing machinery. Sugita (2008) raised baby monkeys without ever allowing them to see faces, from birth to the age of 6, 12, or 24 months. The monkeys lived in enriched visual environments and were cared for by human caretakers who wore hoods over their faces at all times while in the presence of the monkeys. Astonishingly, when the monkeys were first tested on face perception, even after 2 years of deprivation, they showed the standard preference to look at static photographs of faces over novel object photographs. Even more surprising, they showed adult-like sensitivity to differences between faces: given a choice between a face they had just habituated to, and a new face, they looked more at the new face, even though the differences between faces were very subtle. These findings leave little room for a role of face experience in the construction of adult face- processing performance, at least in monkeys. Crucial future work should use even more subtle tests to ask whether these monkeys have truly normal face perception abilities. Also of great interest is the question of whether these monkeys who never saw faces in the first 2 years of life nonetheless have normal face-selective cortical regions (Tsao et al., 2003), and if so, how quickly these arise after exposure to faces.

Although we still don't know how the machinery of face processing arises during development, new evidence suggests that experience with faces may not be necessary.

SUMMARY

In this chapter, we described the current state of knowledge about face-selective regions of cortex in humans and their role in face perception. Current evidence supports the hypothesis that the FFA is specifically involved in face perception per se. The division of labor between the three face-selective cortical regions is beginning to come into focus, with the OFA apparently more involved in the analysis of face parts, the FFA involved in the construction of perceptual descriptions of faces used in face identity discrimination, and the fSTS involved in discriminating social/dynamic information in faces such as eye gaze direction and perhaps also emotional expression. Further work is characterizing the representations of faces extracted in each of these regions, though much remains to be done. Finally, although the FFA is clearly influenced both by experience and by genes, very recent work opens up the surprising possibility that experience with faces may not be necessary for the construction of adult-like face-processing abilities.

Despite the wealth of knowledge accrued from the past decade of research into the cortical regions involved in face perception, fundamental questions remain unanswered. First, we have only begun to scratch the surface in understanding what information is represented in each of these regions, and we have no idea at all about the neural circuits that give rise to these representations. Second, virtually nothing is known about the connections between each of these regions, or between these regions and the rest of the brain. Third, although current methods of human cognitive neuroscience can tell us about time (via ERPs and MEG) or about space (via fMRI), we have almost no data that can tell us about the precise time course of response in specific spatially resolved regions of the brain (for powerful but rare data on this question, see Mundel et al., 2003; Puce et al., 1999). For example, despite the many fMRI studies of the FFA using fMRI, it is unknown which of its response properties arise during the initial feedforward response to a stimulus, and which may arise hundreds of milliseconds later. Fourth, with few exceptions (Afraz, Kiani, & Esteky, 2006; Pitcher et al., 2007; Puce et al., 1999), we know very little about the causal structure of the face-processing system: which regions play a necessary role in which aspects of face perception. Finally, we know next to nothing about why face-selective regions land so systematically where they do in the cortex, or about the mechanisms that wire this system up during development.

These questions remain largely unanswered because current methods of human cognitive neuroscience cannot answer them. However, the bright light on the horizon is the fact that monkeys too have face-selective regions of the cortex and methods exist to tackle most of these questions in macaques. Indeed, the combination of behavioral, neuroimaging, and physiological studies in monkeys (Tsao & Livingstone, 2008) is likely to prove very powerful over the next decade.

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