Chapter 2

The fusiform face area

From the book:
Basingstoke, UK: Palgrave Macmillan.
Does the human brain consist of individual regions that are each specialized for a single cognitive process? The present chapter addresses this general question by considering a specific debate on the neural basis of face perception. Over a decade ago, it was reported that a region of the right fusiform cortex, within the ventral occipital-temporal visual processing stream, was specialized for processing faces and labeled the *fusiform face area* (the FFA; Kanwisher, McDermott, and Chun, 1997). The existence of a specialized brain processing region was and still is intuitively appealing, so it is not surprising that belief in the FFA has grown rapidly and is now widespread in the field of cognitive neuroscience. To illustrate, Figure 2.1 shows that the number of articles with the term *fusiform face area* in the title or abstract between 1998 and 2010 has grown exponentially (articles were identified using PubMed). The articles supporting the existence of the FFA have been published at a relatively constant rate (about 1 publication per year), so the rapid growth of studies employing the FFA illustrates an ever increasing number of cognitive neuroscientists who assume this area exists. Proponents of the minority view do not believe that the FFA is specialized for face processing and have rather proposed that face processing is mediated by numerous regions of the brain.

Figure 2.1. Number of articles with the term *fusiform face area* in the title or abstract published between 1998 and 2010.

**MAJORITY VIEW**

**FFA activation evidence**

The existence of the FFA has been based largely on fMRI evidence, where activity in the fusiform gyrus has been produced by comparing face perception to non-face object perception. Nancy
Kanwisher has been the major proponent of the FFA since its discovery.

Kanwisher et al. (1997) first identified the FFA using fMRI by presenting participants with many stimulus classes including photographs of faces, two-tone faces created by luminance thresholding the photographs, faces in ski hats that were angled (viewed from the side), common objects (Figure 2.2, upper left), hands, houses, and scrambled two-tone faces that were constructed by rearranging the internal segments of each face rendering it unrecognizable (Figure 2.2, bottom left). Participants either passively viewed items or identified whether each item matched the previous item to foster detailed stimulus processing, referred to as a 1-back task. The results did not differ as a function of task in this study or in almost any of the following studies, and thus will only be considered when relevant. In the first experiment, the contrast between photographs of faces versus photographs of common objects produced consistent activity in only 1 region, the FFA (Figure 2.2, top). In the second experiment, the FFA from the previous experiment served as a region-of-interest to further investigate the selectivity of this region. FFA activity associated with faces was greater than both objects and houses, and activity associated with two-tone faces was greater than scrambled two-tone faces (Figure 2.2, bottom). The latter comparison shows that the FFA was not driven by low-level visual features, which were matched across these stimulus classes. In a third experiment, the FFA from Experiment 1 again served as a region-of-interest. Faces in ski hats that were angled produced a greater response in the FFA than hands. Across experiments in this study, the FFA was responsive to faces (front-view, two-toned, and angled) to a greater degree than non-face stimuli (objects, hands, houses, and scrambled two-tone faces). The same year as the Kanwisher et al. study was published, McCarthy, Puce, Gore, and Allison (1997) also reported consistently greater fMRI activity in the right fusiform gyrus during face than object processing.
Figure 2.2. Top, faces as compared to objects (left) produced consistent activity in the right hemisphere fusiform face area (FFA, center, outlined in black; axial view, occipital pole at the bottom, right hemisphere on the left). This is illustrated (right) by a greater magnitude of FFA activity (percent signal change) during face (F) stimulation periods than during object (O) stimulation periods. Bottom, intact (I) faces also produced a greater FFA response than scrambled (S) faces (Kanwisher et al., 1997; The journal of neuroscience: the official journal of the Society for Neuroscience by SOCIETY FOR NEUROSCIENCE Copyright 1997 Reproduced with permission of SOCIETY FOR NEUROSCIENCE in the format Textbook via Copyright Clearance Center).

Subsequent fMRI studies provided additional evidence that the FFA selectively processes faces. In all of these studies the FFA and other regions-of-interest were first identified by contrasting faces versus objects, and then the degree of face selectivity was evaluated by comparing the magnitude of activation in this region during face perception versus non-face object perception. Note that only studies that compared face to non-face object processing were considered to allow for the evaluation of the specific degree of face selectivity in the FFA. To assess whether the FFA was associated with face processing rather than low-level visual features present in faces, Kanwisher, Tong, and Nakayama (1998) employed two-tone Mooney faces (Mooney, 1957) that were only recognizable as faces when upright (Figure 2.3). These faces activated the FFA to a greater degree when they were upright as compared to when they were inverted.
It was also reported that grayscale photographs of both upright and inverted faces produced a more similar magnitude of response in the FFA, as compared to Mooney upright and inverted faces. These findings suggested that FFA is activated whenever a face is recognizable. Kanwisher, Stanley, and Harris (1999) showed that the FFA responded to grayscale photographs of both human faces and animal faces, showing that this region responded to faces more generally. The FFA also responded to a greater degree to whole humans (i.e., the head/face and body) than whole animals, arguing against the possibility that the FFA is specialized for all animate objects. Tong, Nakayama, Moscovitch, Weinrib, and Kanwisher (2000) used additional stimulus classes (Figure 2.4) to further probe the FFA and found this region was activated by human faces, cat faces, and cartoon faces (including inverted cartoon faces) to a greater degree than objects. However, the FFA was not very responsive to face schematics, suggesting that activation of this region requires detailed facial features.

Grill-Spector, Knouf, and Kanwisher (2004) presented grayscale photographs of faces, birds, flowers, houses, cars, guitars, or textures for 33 to 50 milliseconds (the duration was adjusted in an effort to
equate difficulty), so brief that they were often difficult to perceive. Stimuli from only 1 category were shown in a given sequence, and participants classified each stimulus according to whether it matched a previously learned target object (e.g., Harrison Ford for the male face category or a pigeon for the bird category), whether it was another object, or whether it was not an object (i.e., it was a texture). The right hemisphere FFA, corresponding to the face processing region in the previous studies, and the left hemisphere FFA were activated during correct identification of target faces to a greater degree than correct detection of faces, and correct detection of faces produced greater FFA activity than when a face was not detected. The same pattern of activity was observed for birds, which is not surprising given that birds have faces. This pattern of activity during face processing was not observed in the FFA for flowers, houses, guitars, or as strongly with cars, which indicated that activity in the FFA is not driven by identification of specific items within generic object categories (Jiang, Dricot, Weber, Righi, Tarr, Goebel, and Rossion, 2011, also reported a greater magnitude of activity in the right hemisphere FFA during face detection as compared to car detection).

To produce a detailed response profile of right hemisphere FFA and other categorical processing regions, Downing, Chan, Peelen, Dodds, and Kanwisher (2006) employed stimuli from 20 different object categories and found that the FFA response was highest to faces, was second highest to bodies, and was progressively weaker to stimuli from other object categories (Figure 2.5). The second most effective category is of particular relevance as it can be used to estimate the maximum FFA response to non-face objects, thus serving as a baseline measure of activity to quantify the degree of face selectivity in this region.
Figure 2.5. Activity in the right hemisphere FFA (beta is an estimate of activation magnitude) associated with each of 20 stimulus categories (Downing et al., Domain specificity in visual cortex, Cerebral Cortex, 2006, 16, 10, 1453-1461, by permission of Oxford University Press).

Table 1 illustrates the magnitude of FFA activity (percent signal change) in response to faces in addition to the magnitude of activity in response to the second most effective non-face/baseline stimulus category in 6 studies that employed objects, inverted Mooney faces, bodies, objects, cars, and bodies, respectively. The average face-to-baseline activity ratio was 2.3, which shows that the FFA produces approximately twice the response to faces as compared to non-face objects and suggests this region is specialized for processing faces.

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<th>Study</th>
<th>Faces</th>
<th>Baseline</th>
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<td>Kanwisher et al. (1997)</td>
<td>3.3</td>
<td>1.2</td>
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<td>Kanwisher et al. (1998)</td>
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<td>Tong et al. (2000)</td>
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<td>0.7</td>
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<td>Grill-Spector et al. (2004)</td>
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<td>0.9</td>
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<td>Tsao et al. (2008)</td>
<td>2.7</td>
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<td>Average activity</td>
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**FFA lesion evidence**

Patients with prosopagnosia, a deficit in face recognition, with brain lesions that included the FFA have provided convergent evidence that this region is specialized for processing faces. It should be noted that the lesions in the large majority of patient studies have uncertain locations precluding definitive localization to the FFA, and thus were not considered (this includes brain lesions that occurred during development, where the functional organization of intact cortex is unknown due to the possibility of cortical reorganization). Barton, Press, Keenan, and O’Connor (2002) reported 4 patients with lesions to the right hemisphere FFA (Figure 2.6) that had impaired perception of the spatial configuration of face parts in a task that involved identifying spatial shifts in eye and mouth positions in altered photographs.
Figure 2.6. Lesion locations of 4 patients (key to the bottom right). Images progress from the frontal cortex at the upper left to the occipital cortex at the bottom right (coronal views, right hemisphere on the left). The overlapping lesion location (in black) included the FFA and is indicated by the arrow (Barton et al., 2002, Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia, Neurology, 58, 1, 71-78, reprinted with permission from Wolters Kluwer Health).

By comparison, a patient who also had prosopagnosia with more anterior left and right temporal lobe lesions that did not include the FFA (patient 1, the lesion is not shown) was not markedly impaired at discriminating face configuration. Wada and Yamamoto (2001) also reported a patient with a relatively restricted lesion that included the right fusiform cortex who had impaired face recognition. These lesion results complement the fMRI results and further suggest that the FFA is necessary for face processing.
Additional face processing regions

The face versus object contrast employed in the Grill-Spector et al. (2004) study described above, which is the standard method of identifying the right hemisphere FFA and the left hemisphere FFA, also revealed face activity in the left and right occipital cortex (the occipital face area, OFA), and this region had the same pattern of face activity as the FFA. In addition, face selective activity was observed in the left and right face selective superior temporal sulcus (the fSTS). These 3 face selective regions, the FFA, OFA, and fSTS, have been consistently observed in subsequent studies, and additional face selective regions have also been reported. For instance, 2 face selective regions have been reported anterior to FFA and labeled the anterior face patch 1 (AFP1) and the anterior face patch 2 (AFP2; Tsao, Moeller, and Freiwald, 2008; a face selective region anterior to the FFA has also been observed that appears to correspond to AFP1; Rajimehr, Young, and Tootell, 2009), and an additional face selective region has been observed in the right inferior frontal cortex (Chan and Downing, 2011; Jiang et al., 2011).

To better characterize the functions of the FFA, OFA, and fSTS, Liu, Harris, and Kanwisher (2010) used photographs of faces with the parts (eyes, nose, and mouth) either intact or replaced by black ovals (similar to the schematic face shown in Figure 2.4), and these parts could be in the correct or incorrect spatial locations. OFA and fSTS responded to face parts to a greater degree than black ovals regardless of spatial configuration. By comparison, the FFA was sensitive to both face parts and spatial configuration, which suggests that this region may be uniquely sensitive to the holistic processing of faces.

MINORITY VIEW

There is also evidence that the FFA processes categories of objects other than faces, which questions the degree to which the FFA is selective for processing faces. Moreover, there is evidence that face processing is distributed across numerous brain regions, which challenges the notion that the FFA is localized to a single region. If the FFA is neither selective for faces nor localized to a specific area, it would be difficult to convincingly argue for the existence of a face processing region in the brain.

Evidence described in the previous section, which was taken to support the majority view, also indicates that the FFA does not selectively process faces. Table 2.1 shows that FFA activity in 6 studies was consistently greater for faces than non-face objects, and this difference was taken to support face specificity. However, although the magnitude of activity associated with faces was about twice that of non-face objects, the magnitude of FFA activity associated with non-face
objects was also greater than the baseline level of activity, as shown by the consistently positive magnitude of non-face object activity. This indicates that the FFA responds to non-face objects, which is at odds with the view that the FFA selectively processes faces. This analysis was based on the absolute magnitude of activity associated with a single task (i.e., the magnitude of non-face object processing activity was compared to 0). By comparison, cognitive neuroscience analyses typically only consider the relative magnitudes of activity associated with 2 tasks (based on subtractive logic; Chapter 1). Desimone (1991) made the following point that is directly relevant to the interpretation of these findings when referring to the possibility that face selective cells exist in the monkey:

In some studies, a few cells classified as face selective responded only twice as well to faces as to nonface stimuli . . . . Yet, the greater the response to nonface stimuli, the more likely it is that a cell is actually tuned to some more general object feature, such as shape or texture. (p. 3)

Following this reasoning, a region that is truly face selective should respond only to faces and produce no response to non-face objects, and if there is a non-face object response this suggests the region likely processes a feature that is shared by faces and objects (such visual features are discussed below). While this could be considered a strong definition of selectivity, relaxing the requirement -- such as requiring a region to produce twice the response to faces as compared to non-face objects -- weakens the term selective such that it has little validity. For instance, under conditions of weak selectivity, it could be said that the criterion for labeling a region as selective is arbitrary, and those who aim to find a selective region need only choose the degree of selectivity that is observed in their results. Such an arbitrary procedure is clearly not good scientific practice. To make a strong case for selectivity, it would be much more compelling if a region responded to a single stimulus class and produced no response to other object classes.

Grill-Spector et al. (2004), a study discussed in the majority view section, provided further evidence that the FFA does not selectively respond to faces. Figure 2.7 shows the right hemisphere FFA and the left hemisphere FFA identified by contrasting faces versus objects (outlined in black) and the activity (in white) associated with identification versus detection of objects from 6 categories. Face processing activated 93 percent of the FFA; however, processing of all other object categories also produced activity within the FFA. Specifically, excluding birds that have faces, the other non-face categories activated 26 percent of the FFA on average. Although the authors argued that the face greater than non-face object response supported face selectivity, these results also show an object response in the FFA, which undermines the notion that this region is selective for
faces. It is also worth noting that activity associated with face identification versus detection (Figure 2.7, upper left) was not restricted to the FFA. Approximately half of the face activity was outside of this region and distributed across the ventral occipital-temporal cortex, similar to the distributed pattern of activity associated with all other object categories.

Figure 2.7. FFA in the right hemisphere and the left hemisphere (outlined in black) and activity (in white) associated with object identification in the specified categories (inferior view, occipital pole at the bottom; the arrow head at the bottom right demarcates the fusiform gyrus, fus). (Grill-Spector et al., 2004, DOI: 10.1038/nn1224; reprinted with permission of the Nature Publishing Group).

Ishai, Ungerleider, Martin, Schouten, and Haxby (1999) foreshadowed the previous findings when they reported that the FFA responded maximally to faces but also showed that this region produced robust responses to houses and chairs. Consistent with these results, Joseph and Gathers (2002) reported that objects activated the FFA, and Ewbank, Schluppeck, and Andrews (2005) found that the FFA responded less strongly to repeated objects as compared to novel objects. The latter adaptation response, referred to as repetition priming, indicates that the FFA is involved in non-face object processing (Chao, Weisberg, and Martin, 2002, reported a similar finding). In addition to casting doubt on the selectivity of the FFA, Ishai et al. (1999) reported that regions maximally responsive to houses and chairs were activated by faces in the ventral temporal cortex, indicating that face processing is mediated, to some degree, outside of the FFA. Ishai,
Ungerleider, Martin, and Haxby (2000) also reported a distributed pattern of activity in ventral temporal cortex associated with these object classes (faces, houses, and chairs) that extended into ventral occipital cortex.

Lesion evidence has further suggested that the FFA does not selectively process faces. As discussed previously, Barton et al. (2002) reported 4 patients with lesions that included the FFA and had impaired face perception (Figure 2.6). However, non-face objects were not tested in that study, leaving open the possibility that the deficit was not restricted to face processing. In a follow-up study, Barton, Cherkasova, Press, Intriligator, and O'Connor (2004) tested the same 4 participants with both face and non-face objects and found that all of the patients were impaired at face recognition, replicating the previous finding, but these patients were additionally impaired at fruit and vegetable recognition. These results suggest that the FFA mediates both face processing and non-face object processing. In the separate case study considered previously, Wada and Yamamoto (2001) reported a patient with impaired face perception following a lesion that included the right fusiform cortex. However, a very limited set of non-face objects were tested (e.g., fruit and vegetable recognition was not evaluated), such that the degree of selectivity in this patient should be treated with caution. These results indicate that a strong argument for face selectivity is not supported by the current lesion evidence.

The preceding results indicate that the FFA is not particularly selective for faces, given that this region has also been shown to process non-face objects. A related line of evidence, touched on above, has indicated that face processing is not primarily localized to the FFA but is rather distributed across ventral temporal cortex. Haxby, Gobbini, Furey, Ishai, Shouten, and Pietrini (2001) investigated the pattern of fMRI activity in ventral temporal cortex produced by many different object categories including faces, houses, chairs, and shoes. Figure 2.8 shows the regions of ventral temporal cortex that were activated (in red/orange/yellow) or deactivated (in purple/blue/cyan) by each object category. The analysis was conducted separately for even runs and odd runs, in part to test whether the pattern of activation associated with each category was consistently produced across runs. The high within category correlations across even and odd runs show that these patterns of activation were robust (Figure 2.8; an r value of 1 indicates maximum correlation, an r value of 0 indicates no correlation, and an r value of -1 indicates maximum anti-correlation). In direct opposition to the view that face processing is localized to the fusiform gyrus, face activity was not restricted to this region but was rather distributed across ventral temporal cortex, like the other object categories. The overall pattern of activity associated with each object was distinct, as indicated by the negative between category correlations (shown adjacent to slanted arrowheads in Figure 2.8). An analysis was also
conducted where each stimulus in half of the entire stimulus set was identified based on comparing the pattern of ventral temporal activity produced by that stimulus with the pattern of ventral temporal activity produced by each of the separate stimulus categories generated from the other half of the stimulus set. The category of each stimulus was taken to be the category with the highest correlation with that stimulus. This analysis procedure identified the category of individual stimuli with a remarkably high accuracy of 96 percent. The same analysis was conducted after excluding the activity that responded maximally to faces, which included the FFA, and this had no effect on the perfect face identification accuracy. These results suggest the FFA does not have a privileged role in face processing, and rather indicates that face processing is distributed across the ventral temporal cortex and, based on the findings of Ishai et al. (2000), the processing of this object category is distributed across the ventral occipital cortex as well.
Figure 2.8. Face, house, chair, and shoe patterns of activity in ventral temporal cortex (axial views, occipital pole at the bottom of each image). Red/orange/yellow and purple/blue/cyan illustrate progressively greater positive and negative activation magnitudes, respectively. Within and between-category correlations (r values) are shown adjacent to the corresponding vertical and diagonal arrows, respectively (From Haxby et al., 2001, Distributed and overlapping representations of faces and objects in ventral temporal cortex, Science, 293, 2425-2430. Reprinted with permission from AAAS).

The evidence that face processing is distributed across ventral temporal cortex may at first seem at odds with the evidence supporting the majority view that the FFA is specialized for face processing, but the findings taken to support both views are actually consistent. As described above, while Kanwisher et al. (1997) originally defined the FFA as being localized to a single region within the right hemisphere, subsequent studies by proponents of the FFA have reported increasing numbers of face processing regions including left and right FFA, OFA, and fSTS (Grill-Spector, Knouf, Kanwisher, 2004; Liu, Harris, and Kanwisher, 2010), left and right AFP1 and AFP2 (Tsao Moeller, and Freiwald, 2008; Rajimehr, Young, and Tootell, 2009), and the right inferior frontal cortex (Chan and Downing, 2011; Jiang et al., 2011). This puts the current face processing region tally from FFA proponents at a minimum of 6 (and up to 12 if counted separately in each hemisphere), and new face processing regions appear to be discovered on a regular basis (e.g., Jiang et al., 2011, reported face selective activity in left and right amygdala, and Ku, Tolias, Logothetis, and Goense, 2011, observed many other face selective regions using fMRI in monkeys). This substantial number of face processing regions is inconsistent with the notion of a single or even a few localized face processing regions, and rather supports the distributed model of face processing. Related to this, ERP evidence was not considered in this chapter because face processing has been associated with many regions making the localization of the underlying neural sources inherently uncertain.

The evidence that face processing is distributed across ventral occipital-temporal cortex leads to the question of what type of processing is occurring in each of these islands of activation (Figure 2.8). What is the neural code? The answer is currently unknown, but Tanaka’s (1993) study of visual object processing in monkey inferior temporal cortex has provided important clues. Tanaka found that the inferior temporal cortex is organized in columns of cells that respond to complex visual features (Figure 2.9), much more complex than the simple features such as line orientation or color that are coded in earlier visual regions of the occipital cortex.
Figure 2.9. Left, illustration of the procedure used to isolate the complex visual features that activated individual cells in the monkey inferior temporal cortex. In this example, a cell was similarly activated by a tiger head at the object level of processing (the top stimulus), stimuli at intermediate levels of processing (the next 3 stimuli), and 2 black rectangles overlapping a white square (the 2nd stimulus from the bottom), the complex features that can be assumed to have produced the object response as further decomposition (the bottom stimulus) produced a weaker response. Right, schematic of cell columns in the monkey inferior temporal cortex that respond to complex visual features (From Tanaka, 1993, Neuronal mechanisms of object recognition, Science, 262, 685-688. Reprinted with permission from AAAS).

These results suggest that the distributed pattern of activity in ventral temporal cortex associated with a particular object, such as a face or a house, reflects processing in regions that code the complex visual features that comprise the object. Again, exactly which complex visual feature is coded by each specific region of ventral temporal cortex has yet to be delineated. To make headway toward understanding the neural basis of object processing, future research will need to focus on deciphering the visual feature processing code in the ventral occipital-temporal cortex.
COUNTERPOINTS

Rather than the FFA being selective for face processing, it has been proposed that this region processes objects of expertise given that we are all face experts. Gauthier, Tarr, Anderson, Skudlarski, and Gore (1999) trained participants for approximately 7 hours on novel object stimuli they called greebles (Figure 2.10), and found that greeble processing produced a larger FFA response for greeble experts than greeble novices (as expected, faces produced an FFA response for both greeble experts and novices).

Figure 2.10. Novel objects (greebles) used to test whether the FFA responds to stimuli of expertise (Gauthier et al., 1999, DOI: 10.1038/9224; reprinted with permission of the Nature Publishing Group).

In a related study, Gauthier, Skudlarski, Gore, and Anderson (2000) reported that pictures of birds produced greater activity in the right FFA of bird experts but not car experts (i.e., there was a bird expertise effect in the right FFA); however, a standard analysis did not reveal a corresponding car expertise effect. Using a similar paradigm, Xu (2005) reported the opposite pattern of findings, a car expertise effect in the right FFA but little if any bird expertise effect. Employing a different class of stimuli, Harley, Pope, Villablanca, Mumford, Suh, Mazziotta, Enzmann, and Engel (2009) presented lung radiographs to radiology experts or novices. A standard analysis did not produce any activation difference in the right FFA for experts versus novices; however, an expertise effect was revealed by correlating FFA activity as a function of each individual participant’s level of expertise. The expertise explanation of FFA activation is widely considered viable; however, this view has many serious limitations. First, it assumes the FFA exists, which may be incorrect. Second, an expertise explanation of FFA
activation is not a hypothesis about how information is processed in the brain -- which is of primary interest in cognitive neuroscience -- but is simply a potential confound associated with faces. By comparison, the distributed processing view is a viable alternative to the existence of an FFA. Third, almost all of the stimuli that have been used to study expertise have face-like properties, including greebles (Figure 2.10), birds, and even the front of cars can be mapped onto a face (e.g., the windshield could be processed like eyes as in the movie Cars). As such, experts of a given object class may be allocating greater attention to the face-like properties of their objects of expertise. That is, expertise effects might actually reflect attention effects as it is known that attention to faces can increase activity in the FFA (Serences, Schwarzbach, Courtney, Golay, and Yantis, 2004). For instance, if a car expert processes a car and attends to its face-like features, it follows that the magnitude of FFA activity will increase due to attentional amplification of neural activity in this region (Chapter 3), as opposed to activity reflecting expertise processing. Fourth, expertise effects are inherently weak, sometimes they occur in the FFA, but just as often they are not observed. By comparison, face responses in the FFA are extremely robust, therefore it is highly unlikely that weak expertise effects are driving the strong face responses observed in the FFA. McKone, Kanwisher, and Duchaine (2006) pointed out the 2 latter limitations, but also incorrectly claimed that faces and objects of expertise should produce the same pattern of results. This could be considered a straw man -- a misrepresentation of an opponent's position -- as face processing effects would actually be expected to produce more robust effects given that this object class is arguably of greater potential relevance to everyone (i.e., face processing can be considered particularly important for survival). The previous limitations show that there is little if any compelling evidence to support the expertise explanation of FFA activation. Future work in this area might benefit from use of untapped stimulus classes that have absolutely no face-like properties. Moreover, proponents of this view must explain how weak and inconsistent expertise effects might explain the robust and consistent face processing effects. Perhaps expertise effects could be strengthened by employing a stimulus class associated with a level of expertise that rivals faces, possibly through extensive training. However, such stimulus classes have long been sought out and no compelling results have been revealed; therefore, it is anticipated that the expertise explanation of FFA activity will eventually dissipate.

In response to the evidence that face processing is distributed across the ventral occipital-temporal cortex, Kanwisher and Yovel (2006) have articulated multiple arguments. It was first claimed that the FFA does not contain information that can be used to discriminate between non-face objects, based on evidence from Spiridon and Kanwisher (2002). This empirical study specifically tested whether FFA
activity could be used to identify non-face stimuli, using a correlation analysis like Haxby et al. (2001) described previously. It was found that FFA activity could discriminate between faces versus objects with very high accuracy (98 percent) and could discriminate between houses versus objects with intermediate accuracy (66 percent). Based on these results, it was argued that the FFA was not part of a homogenous distributed pattern across ventral temporal cortex, and rather that this region was selective for faces. It is notable that the FFA was most highly associated with faces; however, activity in this region was also associated with non-face objects, which is consistent with all of the findings detailed in this chapter. As stated previously, the point is not whether the FFA responds more to faces, but rather is whether or not the FFA responds only to faces. When non-face object responses are observed in the FFA, such results show that this region is not particularly selective for faces. Moreover, the argument that the FFA should show a similar magnitude of activity to all object classes is a straw man, similar to that proposed above when arguing that face and non-face expertise effects should be equivalent. This strategy of suggesting an opponent's theory would predict equivalence, when it would not, and then discounting that prediction could be interpreted as intentionally misleading. In reality, proponents of the distributed object processing view would predict exactly the pattern of results observed by Spiridon and Kanwisher. Specifically, the number of face-like features shared by faces and non-face objects should produce a relatively greater response to faces in the FFA because faces have more of these features, while features of faces and non-face objects that are processed in other regions of the ventral occipital-temporal cortex should produce activation outside of the FFA. A second argument against the distributed face processing view is that face activations outside of the FFA might not be used in perceptual performance (Cohen and Tong, 2001, made the same argument). The problem with this argument is that FFA proponents are choosing the region believed to be responsible for face perception, the FFA, and ignoring all other activations. Such selection bias -- choosing results that support a favored hypothesis and ignoring results that don't fit that hypothesis -- is poor scientific practice, and cannot be considered as a valid basis for an argument. The third argument against the distributed processing view is that FFA responses to non-face objects is due to spatial blurring of neighboring regions that process non-face objects into the FFA, which can happen with fMRI because of the limited spatial resolution of this technique. For instance, Schwarzlose, Baker, and Kanwisher (2005) reported that headless bodies activated a region adjacent to the FFA, and spatial blurring of such activity could produce a body response in the FFA even though bodies might not actually be processed in this region. This is the first sound argument, and makes the testable prediction that non-face objects processed in regions
spatially adjacent to the FFA (such as bodies) will produce the greatest magnitude of FFA response. However, the evidence contradicts this prediction. Table 2.1 shows that objects, rather than bodies, produced the greatest magnitude of activation in the FFA. This finding indicates that the FFA response to non-face objects is not simply due to spatial blurring, and such FFA responses can rather be attributed to non-face object processing within the FFA. Thus, the preceding arguments against the distributed face processing view by Kanwisher and Yovel (2006) can all be discounted. However, because the existence of the FFA is the majority view, even an ill founded challenge appears to be sufficient for the widespread belief in the FFA to continue.

Whether the FFA exists, or not, should be based on evidence. To date, the evidence only supports the distributed processing view and is inconsistent with the existence of the FFA. To reiterate, the FFA consistently responds to non-face objects, and face processing is not restricted to a spatially circumscribed area. Therefore, there is little if any empirical basis that the term face or the term area should be used to label a fusiform face area. A more accurate description of this region is that it responds maximally to faces, but also responds to non-face objects, and that face processing is shared across numerous other regions in the ventral occipital-temporal cortex and beyond. This description fits other object classes as well, indicating that faces are processed in ventral occipital-temporal cortex in the same way as all other objects. It is important to highlight that distributed object processing proponents can explain the FFA results -- the region of activity with the maximal response to faces -- but FFA proponents cannot explain the numerous face processing activations that support the distributed processing view.

It is almost certain that the present arguments will not dissuade FFA proponents, even though some of the most compelling evidence against their position comes from their own work. Still, it is useful to consider what type of findings could provide support for the existence of an FFA. First, a face processing region should be extremely selective for faces, otherwise there is a question of whether the region is processing a feature that is shared with other objects (Desimone, 1991). As mentioned previously, the FFA produces approximately twice the response to faces than non-face objects, which is far from being selective unless the definition of selective is relaxed to fit the results.

For arguments sake, assume that the FFA was completely face selective (i.e., produced no response to non-face objects). Such selectivity has been reported in single-cell responses within the medial temporal lobe (Kreiman, Koch, and Fried, 2000). For instance, an entorhinal cortex neuron responded to animals but did not respond to stimuli from 8 other categories. Thus, following the logic of naming object selective regions based on their response category, this could be labeled the entorhinal animal cell (the EAC). However, the same group
of investigators conducted an analysis of the response properties of
1425 medial temporal lobe neurons and concluded that each neuron
responded to 50 to 150 distinct object representations (Waydo,
Kraskov, Quiroga, Fried, and Koch, 2006). While these results
may seem at odds, the apparent object selectivity in the first study can
be attributed to the limited of stimulus categories employed (similar to
the results of Barton et al., 2002, that suggested apparent face
selectivity in the FFA, until Barton et al., 2004, employed a larger
number of stimulus classes and showed this region did not selectively
process faces). These results might have implied that FFA investigators
should use numerous object categories to assess whether the FFA is
selective for faces. However, Downing et al. (2006) already conducted
this experiment and face selectivity was weak, with faces producing
less than twice the magnitude of response as the next most responsive
category (Figure 2.5). Moreover, as reviewed above, all the evidence
has shown that face processing occurs in numerous brain regions. A
strategy that might prove fruitful to proponents of the majority view is to
attempt to identify a particular type of computation that is specific to the
FFA that does not occur in the other face processing regions. If this
could be convincingly shown, some form of face processing
specialization might be attributed to the FFA.

CONCLUSION

The evidence reviewed in this chapter indicates that the FFA is
not selective for faces, nor is face processing localized to the fusiform
gyrus. Thus, there is no compelling evidence supporting the majority
view that the FFA is a specialized region for processing faces. By
comparison, all of the results are compatible with the minority view that
faces and non-face objects are processed in distributed regions of the
ventral occipital-temporal cortex. The major limitation of the minority
view is the absence of a neural code that details how the individual
activations reflect the processing of specific visual features that
comprise an object. It is hoped that the present considerations will
promote research in this direction. Despite the large body of evidence
to the contrary, there is currently widespread belief that the FFA exists
(for reasons further discussed in Chapter 9), and this unfounded belief
will in all likelihood continue for the foreseeable future.
SUGGESTED READINGS

**Majority view**


**Minority view**


REFERENCES


