

# The Effect of Face Inversion on Activity in Human Neural Systems for Face and Object Perception

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## Summary

The differential effect of stimulus inversion on face and object recognition suggests that inverted faces are processed by mechanisms for the perception of other objects rather than by face perception mechanisms. We investigated the face inversion using functional magnetic resonance imaging (fMRI). The principal effect of face inversion on was an increased response in ventral extrastriate regions that respond preferentially to another class of objects (houses). In contrast, house inversion did not produce a similar change in face-selective regions. Moreover, stimulus inversion had equivalent, minimal effects for faces in in face-selective regions and for houses in house-selective regions. The results suggest that the failure of face perception systems with inverted faces leads to the recruitment of processing resources in object perception systems, but this failure is not reflected by altered activity in face perception systems.

## Introduction

Neuropsychological, developmental, and psychophysical evidence suggests that face perception is mediated by mechanisms that are different from those that mediate the perception of other objects (Farah, 1996). This dissociation between neural mechanisms for face and object perception is supported by the effects of face inversion on perception in normal subjects (Yin, 1969; Valentine, 1988; Rhodes et al., 1993; Farah et al., 1998) and in patients with selective impairments of face and object recognition (Yin, 1970; Farah et al., 1995; Moscovitch et al., 1997). These effects suggest that inverted faces do not engage face perception mechanisms but are processed instead by mechanisms for the perception of other objects.

In normal subjects, stimulus inversion is more detrimental to face recognition than to the recognition of other objects, suggesting that face recognition may be a specialized process that is more sensitive to stimulus orientation (reviewed by Valentine, 1988). In patients with a selective impairment of face recognition (prosopagnosia), the recognition of inverted faces can be relatively normal, suggesting that inverted face perception may be mediated by their intact object perception mechanisms. In fact, some prosopagnosic patients perform

worse on tasks with upright faces than on tasks with inverted faces (Farah et al., 1995), suggesting that upright faces may evoke erroneous processing by damaged face perception mechanisms and that erroneous processing interferes with processing by intact object perception mechanisms. Inverted faces, on the other hand, apparently do not evoke processing by the damaged face mechanisms, thereby allowing intact object perception mechanisms to operate without interference (but see de Gelder et al., 1998, for evidence that inversion superiority in agnostic patients may not be limited to faces). In a patient with object agnosia, face perception was normal but recognition of inverted faces was severely impaired (Moscovitch et al., 1997), suggesting that intact face perception mechanisms by themselves cannot process inverted faces effectively.

With functional brain imaging, it is now possible to investigate how intact human neural systems for face and object perception interact to accomplish inverted face perception. Functional brain imaging studies have indicated the locations of cortical areas specialized for face perception. In particular, a portion of the fusiform gyrus in the posterior temporal lobe has been identified that consistently shows greater activation during face perception tasks than during tasks that involve the perception of nonsense, control stimuli (Sergent et al., 1992; Haxby et al., 1994; Clark et al., 1996) or other objects (Kanwisher et al., 1996, 1997; Puce et al., 1996; McCarthy et al., 1997). Face-selective activity has also been reported in other areas, particularly in the superior temporal sulcus and inferior occipital gyrus (Clark et al., 1996; Kanwisher et al., 1997).

The anatomical locations of cortical areas that participate in nonface object perception have been less well characterized. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies have shown that object perception activates ventral occipitotemporal extrastriate cortex with a distribution that is highly similar to activations seen in studies of face perception (Köhler et al., 1995; Malach et al., 1995; Martin et al., 1995, 1996). Direct comparisons of cortical responses to faces relative to responses to other stimuli (Kanwisher et al., 1996, 1997; Puce et al., 1996; Ishai et al., 1997, *Neuroimage*, abstract; Aguirre et al., 1998; Epstein and Kanwisher, 1998; Chao et al., 1998, *Soc. Neurosci.*, abstract) have revealed regions that do respond significantly more to other objects than to faces. These regions are located near the face-selective fusiform region in the parahippocampal, fusiform, and inferior temporal gyri.

We decided to investigate the neural basis of the effect of inversion on face perception using fMRI. Specifically, we tested whether inverted faces, as compared to upright faces, evoke less activity in cortical regions most responsive to upright faces and more activity in cortical regions most responsive to nonface objects. To examine the response to nonface objects, we chose a single category of objects, namely houses, so that, as with faces, we examined the response only within a category (cf. Gauthier et al., 1997). Additionally, we

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Table 1. Accuracy and Reaction Times for the Delayed Match-to-Sample Tasks

Task	Accuracy (% correct)	Reaction Time (ms)
Upright faces	96.1 ± 1.4 <sup>a</sup>	668 ± 14
Inverted faces	93.3 ± 2.0	834 ± 17 <sup>b</sup>
Upright houses	94.4 ± 1.8	687 ± 18
Inverted houses	93.3 ± 1.3	689 ± 15

<sup>a</sup> Mean ± SEM.<sup>b</sup> Differs from other conditions,  $p < 0.001$ .

wished to use a category of objects for which people typically perceive the unique identity of each individual exemplar, similar to how faces are typically perceived as unique individuals. The results showed that the only selective effect of face inversion was an increase of activity in extrastriate cortical regions that respond more to houses than to faces. The effects of face inversion in face-selective regions were small and nonselective, as house inversion caused similar effects in house-selective regions. These results indicate that inverted faces do not fail to evoke activity in neural systems for face perception. Instead, they suggest that the perceptual processes reflected by that activity are insufficient to uniquely identify an inverted face, leading to the recruitment of processes that are more specific to the perception of nonface objects.

## Results

### Task Performance

Performance measures on the matching task demonstrated a selective effect of stimulus inversion on face perception. Whereas inversion of houses did not affect reaction time, inversion of faces slowed reaction time by 166 ms ( $p < 0.001$ ) (Table 1). Face and house matching with upright stimuli had equivalent reaction times, indicating that these tasks were matched for difficulty. Accuracy was high for all tasks (93%–96%).

### Correlations between Response Topographies for Different Stimulus Types

Correlations between the signal increases for each stimulus type, relative to control tasks with scrambled pictures, in the voxels that showed a significant overall experimental effect ( $Z > 4$ ), were calculated to provide omnibus indices of the similarity of response topographies across the full extent of cortex that responded more to these meaningful stimuli than to nonsense control stimuli. This analysis revealed that the topography of the response to inverted stimuli was most similar to the topography of the response to upright stimuli of the same category. The correlation between the response topographies for upright and inverted houses ( $R^2 = 0.81$ ) was slightly larger than that for upright and inverted faces ( $R^2 = 0.74$ ). The topographies of responses to faces and houses were most dissimilar when faces were upright ( $R^2 = 0.22$  for the comparisons of upright faces both to upright and to inverted houses) but became more similar when faces were inverted ( $R^2 = 0.40$  and  $0.45$  for the comparisons of inverted faces to upright

and inverted houses, respectively). These results demonstrate that with inversion, the response to faces migrated to a topography that was more like that associated with house perception. The regional distribution of these changes in response due to inversion was further analyzed by identifying regions that showed consistent differential responses to faces and houses.

### Identification of Regions Showing Differential Responses to Faces and Houses

Six bilateral regions were identified that consistently demonstrated differential responses to faces and houses (Figure 1 and Table 2). Five of these regions were identified bilaterally in all six subjects. The sixth region, in the superior temporal sulcus, was identified on the right in four subjects and on the left in two subjects. In this report, we will refer to these regions as “face selective” and “house selective.” In this context, “selectivity” refers only to the difference in response to these two stimulus categories and is not meant to imply that these regions would respond selectively to faces and houses as compared to all other visual stimuli.

Two adjacent pairs of regions in ventral occipitotemporal cortex consisted of a more lateral face-selective region and a more medial house-selective region. A more posterior pair in the occipital lobe consisted of a face-selective region in the inferior occipital gyrus and inferior part of the mid occipital gyrus and a house-selective region in ventral occipital cortex that contains part of the posterior fusiform gyrus and ventral occipital gyri (O3 and O4 in Duvernoy, 1991). A second, more anterior pair in ventral temporal cortex consisted of a face-selective region in the lateral portion of the fusiform gyrus, including the occipitotemporal sulcus, and a house-selective region in the medial portion of the fusiform gyrus, including the collateral sulcus. In some subjects, the more medial house-selective fusiform region extended into the lingual gyrus. A small face-selective region was identified in some subjects in the superior temporal sulcus. An extensive house-selective region was identified in dorsolateral occipital cortex.

On average, 63.0 cm<sup>3</sup> (SD = 25.0 cm<sup>3</sup>) of imaged brain showed a significant activation during face or house perception tasks as compared to control tasks with scrambled pictures ( $Z > 4$  for omnibus test of experimental effect). Of this, 57% (36.0 cm<sup>3</sup>, SD = 15.8 cm<sup>3</sup>) showed a significant difference in the amplitude of the responses to faces and houses ( $|Z| > 1.96$ , volume  $> 0.34$  cm<sup>3</sup>,  $p < 0.05$ ), of which 92% (33.3 cm<sup>3</sup>, SD = 15.0 cm<sup>3</sup>) was in the six regions listed in Table 2.

Regions that showed significantly different responses to faces and houses outside of the six regions listed in Table 2 tended to be smaller and seen in only a few subjects. Face-selective responses that were less consistent across subjects were observed in posterior occipital cortex on both the right (N = 3, mean volume = 0.7 cm<sup>3</sup>) and left (N = 1, 1.7 cm<sup>3</sup>), in parietal cortex on both the right (N = 2, 2.3 cm<sup>3</sup>) and left (N = 2, 0.4 cm<sup>3</sup>), and in the cerebellar vermis (N = 1, 1.3 cm<sup>3</sup>). House-selective responses that were less consistent across subjects were observed in the inferior temporal gyrus, lateral to the face-selective lateral fusiform region on

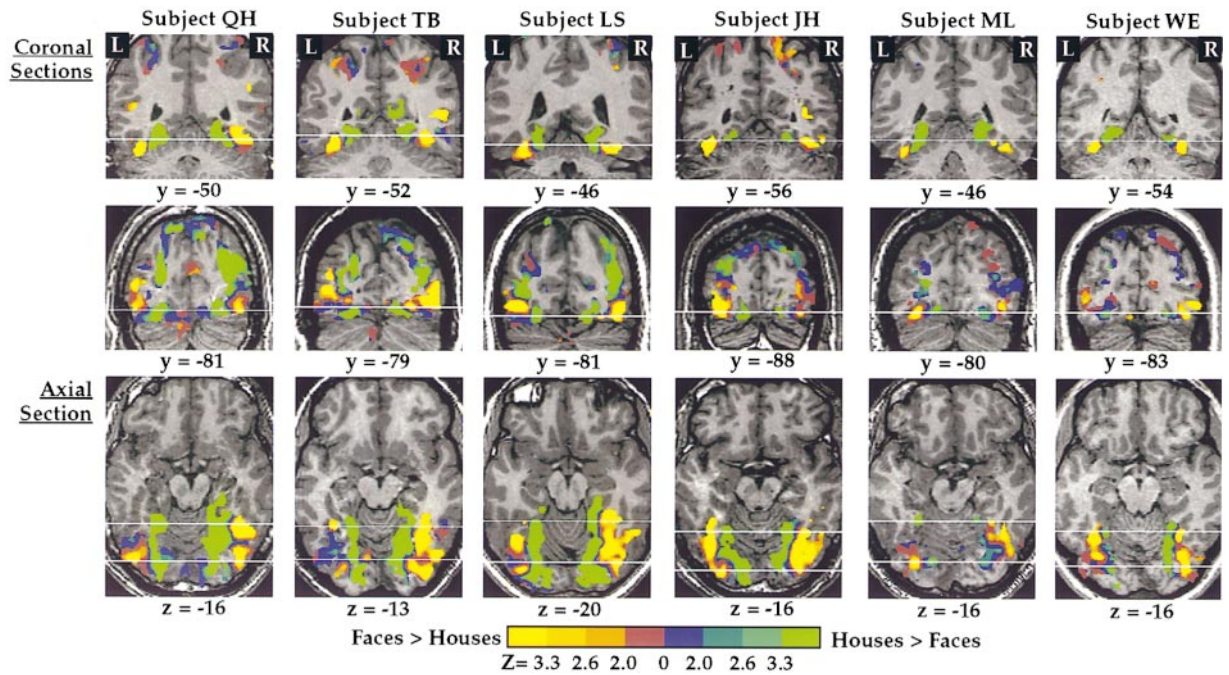


Figure 1. Contrast between Activations during Face and House Perception in All Six Subjects, Based on Analysis of Both Passive Viewing and Delayed Matching Time Series

Talairach atlas (1988) coordinates for the coronal and axial sections are indicated below each image. White lines indicate the levels at which the axial and coronal sections intersect. Voxels shown in color demonstrated a significant overall experimental effect ( $Z > 4.0$ ) and a positive activation during face or house perception tasks as compared to the control tasks. The color in which each voxel is displayed reflects an independent test of the significance of the contrast between face and house perception. The locations of the more anterior coronal sections (top row) were selected to illustrate the locations of the face-selective, lateral and house-selective, medial fusiform regions. Note that face-selective superior temporal sulcus activations are also evident in subjects QH, TB, and JH. The locations of the more posterior coronal sections were selected to illustrate the locations of the face-selective inferior and mid occipital gyri and the house-selective posterior fusiform regions. House-selective superior occipital regions are also evident in all subjects in these sections.

both the right ( $N = 2, 0.5 \text{ cm}^3$ ) and left ( $N = 2, 0.5 \text{ cm}^3$ ), in the cuneus on both the right ( $N = 2, 1.5 \text{ cm}^3$ ) and left ( $N = 1, 0.6 \text{ cm}^3$ ), and in right parietal cortex ( $N = 1, 0.3 \text{ cm}^3$ ).

#### Effect of Stimulus Inversion

Mean time series for the ventral occipitotemporal regions—averaging across voxels in each region, across repetitions of stimulus blocks, and across subjects—are

Table 2. Regions Showing Differential Responses to Faces and Houses

Region	Selectivity	Hemisphere	N	Volume ( $\text{cm}^3$ )	Coordinates		
					x	y	z
<u>Ventral Occipital</u>							
Inferior and Mid Occipital Gyri	F > H	Left	6	$2.1 \pm 1.1$	$-37 \pm 5$	$-81 \pm 3$	$-8 \pm 7$
		Right	6	$2.3 \pm 2.2$	$42 \pm 5$	$-79 \pm 7$	$-7 \pm 6$
Posterior Fusiform Gyrus	H > F	Left	6	$2.5 \pm 1.8$	$-21 \pm 5$	$-82 \pm 10$	$-14 \pm 6$
		Right	6	$3.1 \pm 2.4$	$24 \pm 3$	$-83 \pm 9$	$-11 \pm 5$
<u>Ventral Temporal</u>							
Lateral Fusiform Gyrus	F > H	Left	6	$2.4 \pm 1.3$	$-39 \pm 2$	$-55 \pm 8$	$-23 \pm 6$
		Right	6	$2.9 \pm 1.4$	$39 \pm 2$	$-59 \pm 6$	$-16 \pm 3$
Medial Fusiform Gyrus	H > F	Left	6	$3.0 \pm 1.0$	$-27 \pm 2$	$-52 \pm 5$	$-14 \pm 3$
		Right	6	$4.2 \pm 2.1$	$24 \pm 3$	$-55 \pm 8$	$-12 \pm 4$
<u>Other</u>							
Superior Temporal Sulcus	F > H	Left	2	$0.3 \pm 0.4$	$-52 \pm 1$	$-61 \pm 1$	$4 \pm 0.3$
		Right	4	$0.9 \pm 0.6$	$43 \pm 4$	$-57 \pm 7$	$12 \pm 7$
Posterior Superior Occipital	H > F	Left	6	$4.9 \pm 3.3$	$-23 \pm 6$	$-87 \pm 3$	$7 \pm 9$
		Right	6	$5.2 \pm 3.4$	$31 \pm 4$	$-86 \pm 6$	$14 \pm 10$

Volumes were calculated on data before spatial normalization. Coordinates are in the space of the Talairach and Tournoux brain atlas (1988). All volumes and coordinates are mean  $\pm$  SD.



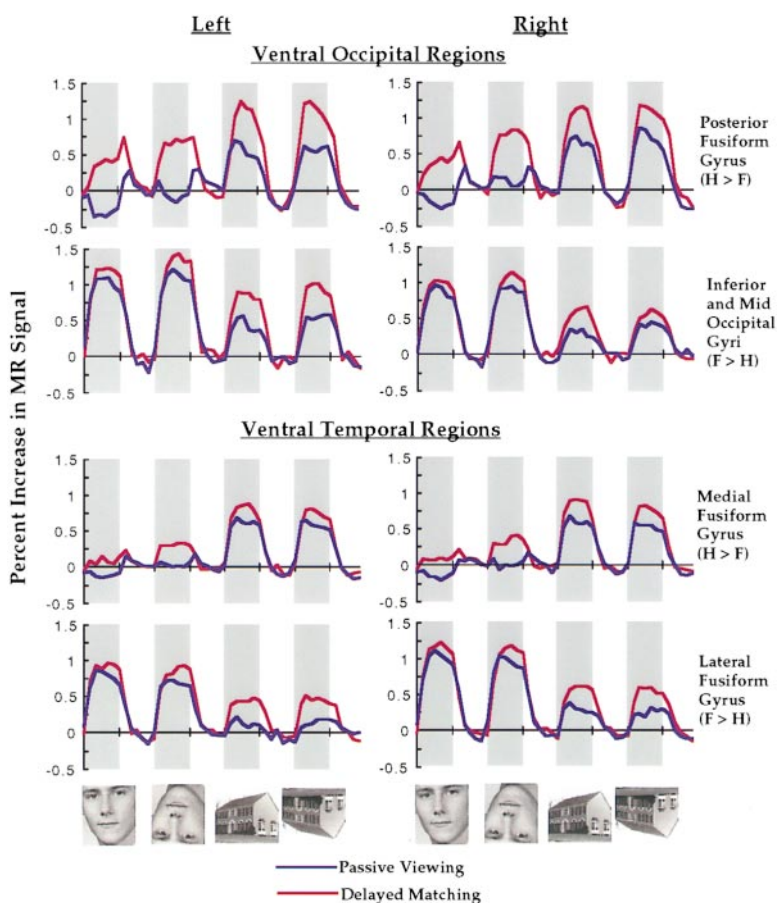


Figure 2. Mean Time Series for Two Ventral Occipital and Two Ventral Temporal Regions. Data are averaged over subjects and repetitions of task blocks. Gray bars indicate presentation of meaningful stimuli and the intervening white areas indicate the presentation of control stimuli. The order of meaningful stimuli is indicated by the pictures of upright and inverted faces and houses.

shown in Figure 2. The magnitude of signal increases for each stimulus type, relative to control tasks with scrambled pictures, are listed in Table 3A.

The greatest effect of stimulus inversion was an increased response to faces in the house-selective regions (Table 3B). The increase in response due to face inversion was significant in all house-selective regions (mean change = +0.26%,  $p < 0.0001$  in all cases) and significantly greater ( $p < 0.0001$  in all cases) than the change in response due to house inversion (mean change = +0.002%). This effect indicates that face inversion decreased the difference between the responses to houses and faces in house-selective regions by 38% on average (45% in the posterior superior occipital region, 42% in the posterior fusiform region, and 27% in the medial fusiform region). This result suggests that perceptual operations more suited to the perception of nonface objects are selectively recruited for the processing of inverted faces.

The effect of face inversion on the response in posterior and medial fusiform house-selective regions was equivalent for delayed matching and passive viewing tasks ( $p > 0.05$  in both cases). For passive viewing, the increase was from a level of activity that was less than during passive viewing of scrambled pictures to a level of activity that was equivalent. Independent data from a separate experiment, however, indicate that passive viewing of both faces and scrambled pictures evokes

an increase in activity relative to rest (experiment 1 in Haxby et al., 1997, NeuroImage, abstract). In this experiment, passive viewing of scrambled pictures, upright faces, and upright houses was contrasted to a resting control ( $N = 5$ ). Relative to rest, passive viewing of faces evoked an increase in activity in both the posterior and medial fusiform house-selective regions (1.42% and 0.36%, respectively,  $p < 0.001$ , in both cases). The activity increase seen in these regions during passive viewing of inverted relative to upright faces, therefore, represents an increase in a positive neural response to faces.

House inversion did not have the same effect on the response in face-selective regions that face inversion had on the response in house-selective regions. Overall, the response to houses in these regions increased by only 0.02%. The only significant effect of house inversion in a face-selective region was an increase in inferior and mid occipital gyri, which was much smaller than the effect of face inversion in the adjacent, posterior fusiform, house-selective region (0.08% versus 0.31%, respectively,  $p < 0.0001$ ) (Table 3B).

Contrary to our prediction, face inversion did not have a selective effect on activity in face-selective regions. Instead, the effect of face inversion in the face-selective regions and the effect of house inversion in house-selective regions showed a similar pattern of small increases in occipital regions and small decreases in temporal regions. The difference between occipital increases and

Table 3. Percent Activation Relative to Control Tasks with Scrambled Pictures (A) the Effect of Stimulus Inversion Averaged over Tasks and Hemispheres (B) and the Effect of Task Averaged over Hemispheres (C)

Region	Selectivity	Task <sup>a</sup>	(A) Percent Activation over Control								(B) Inversion Effect (Inverted - Upright)				(C) Task Effect (DM - PV)			
			Faces				Houses				Faces		Houses		Faces		Houses	
			Upright		Inverted		Upright		Inverted		Faces	Houses	Faces	Houses	Faces	Houses	Faces	Houses
			Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left
Ventral Occipital																		
Inferior and mid occipital gyri	F > H	PV	0.90	1.06	0.94	1.16	0.31	0.45	0.44	0.58	0.10 <sup>b</sup>	0.08 <sup>b</sup>	0.12 <sup>bc</sup>	0.18 <sup>c</sup>	0.35 <sup>c</sup>	0.26 <sup>c</sup>		
		DM	0.99	1.21	1.08	1.38	0.60	0.87	0.58	0.96								
Posterior fusiform gyrus	H > F	PV	-0.27	-0.18	-0.03	0.16	0.58	0.67	0.61	0.75	0.31 <sup>ce</sup>	0.06	0.69 <sup>cd</sup>	0.74 <sup>ce</sup>	0.47 <sup>c</sup>	0.49 <sup>c</sup>		
		DM	0.47	0.48	0.74	0.86	1.11	1.09	1.17	1.17								
Ventral Temporal																		
Lateral fusiform gyrus	F > H	PV	1.05	0.81	1.00	0.73	0.32	0.13	0.29	0.17	-0.05 <sup>b</sup>	0.00	0.12 <sup>bc</sup>	0.16 <sup>cd</sup>	0.32 <sup>c</sup>	0.31 <sup>c</sup>		
		DM	1.16	0.94	1.14	0.91	0.62	0.48	0.59	0.50								
Medial fusiform gyrus	H > F	PV	-0.09	-0.15	0.06	0.03	0.65	0.62	0.61	0.56	0.21 <sup>ce</sup>	-0.06 <sup>b</sup>	0.24 <sup>c</sup>	0.32 <sup>cd</sup>	0.20 <sup>c</sup>	0.18 <sup>c</sup>		
		DM	0.12	0.12	0.34	0.38	0.82	0.86	0.76	0.77								
Other																		
Superior temporal sulcus	F > H	PV	0.48	0.41	0.34	0.32	0.02	-0.02	-0.05	-0.01	-0.11 <sup>c</sup>	-0.04	-0.01	-0.05	-0.03	-0.04		
		DM	0.52	0.29	0.32	0.18	0.00	-0.06	-0.01	-0.13								
Posterior superior occipital cortex	H > F	PV	0.08	0.03	0.32	0.23	0.69	0.60	0.70	0.67	0.26 <sup>ce</sup>	0.01	0.50 <sup>c</sup>	0.59 <sup>cd</sup>	0.50 <sup>c</sup>	0.45 <sup>c</sup>		
		DM	0.58	0.53	0.89	0.83	1.20	1.11	1.17	1.09								

<sup>a</sup> Passive viewing (PV) or delayed matching (DM).

Significantly different from zero, <sup>b</sup> p < 0.05, <sup>c</sup> p < 0.001.

Significantly different effect for faces and houses, <sup>d</sup> p < 0.05, <sup>e</sup> p < 0.001.

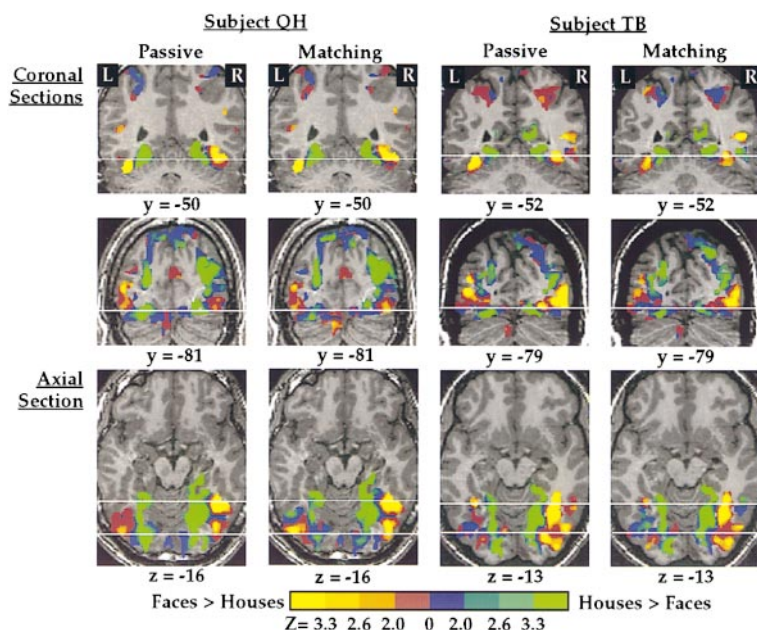


Figure 3. Contrast between Activations during Face and House Perception in Two Subjects, Showing Results for the Passive Viewing and Delayed Matching Tasks Separately. Scans have been spatially normalized into the coordinate space of the Talairach and Tournoux brain atlas (1988). Talairach atlas coordinates for the coronal and axial sections are indicated below each image. White lines indicate the levels at which the axial and coronal sections intersect. Voxels shown in color demonstrated an overall experimental effect ( $Z > 4.0$ ) and a positive activation during face or house perception tasks as compared to the control tasks. The color in which each voxel is displayed reflects an independent test of the significance of the contrast between face and house perception. Note that the data sets for the passive and matching tasks are independent, yet they demonstrate precise agreement on the locations of borders between face- and house-selective regions.

temporal decreases was significant for face inversion in the inferior occipital and lateral fusiform face-selective regions ( $p < 0.001$ ) and for house inversion in the posterior and medial fusiform house-selective regions ( $p < 0.002$ ). The similarity of the effects of face and house inversion in these regions suggests that the face inversion effects in face-selective regions are not related to the selective effect of stimulus inversion on face perception.

#### Response Selectivity in Regions of Interest

Surprisingly, house-selective regions consistently responded more selectively to houses than face-selective regions responded to faces. In ventral occipital cortex, the mean response to upright faces in the house-selective posterior fusiform region was only 0.12%, whereas the mean response to upright houses in the adjacent face-selective inferior and mid occipital gyri was 0.56%. In ventral temporal cortex, the mean response to upright faces in the house-selective medial fusiform region was 0%, whereas the mean response to upright houses in the adjacent face-selective lateral fusiform region was 0.38%. These differences between regions in the size of responses to nonpreferred stimulus categories were highly significant ( $p < 0.0001$  in all cases).

#### Differences between the Delayed Matching and Passive Viewing Tasks

The differences between responses to faces and houses were highly similar for the passive viewing and delayed matching tasks. Figure 3 illustrates that these two tasks produced nearly identical maps of face- and house-selective regions. Analysis of the time series (Figure 2 and Table 3C) also demonstrated the similarity in the direction of selectivity but also showed that the delayed matching task evoked a larger response than did passive viewing in all regions except the superior temporal sulcus. Surprisingly, matching increased the response

to the nonpreferred stimulus more than the response to the preferred stimulus in most regions. For upright stimuli, this difference was significant in the posterior fusiform house-selective region and in the inferior occipital and lateral fusiform face-selective regions. For inverted stimuli, this difference was significant in all house-selective regions and in the face-selective lateral fusiform region.

#### Hemispheric Differences

Although we found that face-selective and house-selective regions were consistently bilateral, some hemispheric differences in the strength of activation or the selectivity of response were found. The regions on the right tended to have larger volumes than those on the left (Table 2), although this difference was not significant ( $p = 0.06$ ). In face-selective regions, the amplitudes of activations in the inferior and mid occipital gyri were greater on the left than on the right (mean difference = 0.24%,  $p < 0.001$ ), whereas the amplitudes of activations in the lateral fusiform gyrus and superior temporal sulcus were greater on the right than on the left (mean differences = 0.19% and 0.13%, respectively,  $p < 0.001$  for both). The selectivity of response (faces versus houses) demonstrated a small but significant difference between the right and left hemispheres in only the lateral fusiform gyrus (mean difference between face and house activations = 0.64% versus 0.58% for the right and left hemispheres, respectively,  $p = 0.03$ ). In house-selective regions, only the posterior superior occipital region showed an asymmetry of activation (right  $>$  left, mean difference = 0.07%,  $p < 0.01$ ), and no regions showed a hemispheric difference in selectivity.

#### Discussion

The results of this study demonstrated that the behavioral effect of face inversion is associated with a selective increase in activity in the parts of the ventral object

vision pathway that are more responsive to nonface objects. House inversion did not cause a similar increase in activity in regions more responsive to faces.

The only selective effect of face inversion was the increased response in house-selective regions. Face inversion did not selectively diminish the response to faces in face-selective regions. Such an effect was expected based on the behavioral and neuropsychological evidence that inverted faces do not effectively engage face perception mechanisms. Face inversion was associated with small increases in the activation of the face-selective regions in the inferior and mid occipital gyri and with small decreases in the activation of face-selective regions in the lateral fusiform gyrus and superior temporal sulcus. However, similar occipital increases and temporal decreases were seen with house inversion in house-selective regions. These changes, therefore, do not appear to be related to the failure of face perception mechanisms.

The results indicate that neural systems for the perception of nonface objects are recruited to facilitate the perception of inverted faces, but inverted faces do not fail to engage the face perception system. The diminished ability to perceive discriminating attributes in inverted faces indicates that the representations embodied by activity in face-selective regions during inverted face perception are less distinctive than are the representations embodied by activity in these same regions during upright face perception. Yet the small face inversion-related alterations of response in face-selective regions were equivalent to small house inversion-related alterations of response in house-selective regions, even though house inversion had no effect on house perception. Thus, the activity in these regions does not appear to reflect the quality of the representations embodied by that activity. This finding is consistent with another recent fMRI study of the effect of face inversion (Kanwisher et al., 1998). They concluded that inverted face stimuli fail to engage the face-selective fusiform area only when subjects cannot see a face in the inverted stimuli, as was the case with inverted two-tone Mooney faces but not with inverted grayscale faces.

Activation of face-selective areas by inverted faces may reflect direct engagement of these areas, but that activation is insufficient to form a distinct representation of the individual shown. Consequently, the brain recruited additional processing resources elsewhere in the ventral visual pathway, namely in house-selective regions, to augment the distinctiveness of the representation of an inverted face. These resources may be related to features of object shape that are not as typical of faces. Alternatively, the recruitment of these additional resources may reflect a different processing strategy, such as a change from a more holistic representation of a face to a representation based more on a decomposition of the face into its individual parts (Farah et al., 1998).

A second possibility is that face-selective regions can only process inverted faces effectively using input that has been preprocessed by object-selective regions. This processing path for inverted faces was suggested based on the severe impairment of inverted face perception observed in a patient with object agnosia and intact

face recognition (Moscovitch et al., 1997). The response to inverted faces in house-selective regions, however, was substantially less than the response to inverted faces in face-selective regions. Because it is unlikely that this strong activation of face-selective regions was driven by the weaker activation of house-selective regions, the engagement of face-selective regions by inverted faces is probably not due solely to input via this indirect path. Moreover, scalp EEG recordings have shown that inverted faces are as effective as upright faces at evoking an early face-specific event-related potential (N170) (Bentin et al., 1996), suggesting an early direct engagement of face-specific processing resources.

Kanwisher et al. (1998) also found that face inversion led to only a small decrease in activity in the lateral fusiform face-selective area. That study, however, did not include experimental conditions to test the specificity of this finding to face inversion or to examine how inversion alters the response to faces in regions that respond more to other objects. Our results give a more comprehensive account of how inversion alters the topography of response to faces in the ventral object vision pathway. By examining several face-selective regions, we showed that face inversion also increases the response in an earlier occipital region and decreases the response in another temporal region, the superior temporal sulcus. By examining the effects of house inversion in house-selective regions, we were able to show that the face inversion effects in face-selective regions are not specific and, therefore, not related to the failure of face perception mechanisms. Most importantly, by examining how the topography of response changed in more of the ventral object vision pathway, including face-selective and house-selective regions, we showed that the effect that is specific to face inversion is the increased response outside of the face-selective areas.

Our data suggest that the face-selective and other object-selective parts of the ventral visual pathway are not single regions but are multiple, bilateral regions that act in concert to accomplish face and object recognition. The principal parts of these distributed neural systems are in ventral occipital and temporal cortex. The ventral occipital regions appear to correspond to the area Malach et al. (1995) have named LO (lateral occipital). Our results clearly indicate that area LO is not homogeneous, but, rather, has a lateral sector in the inferior and mid occipital gyri that responds preferentially to faces and a ventral sector in the posterior fusiform and ventral occipital gyri that responds preferentially to other objects.

Anterior to LO, the face perception system branches into two regions: a region in the lateral fusiform gyrus, which often abuts the ventral part of face-selective LO, and a region in the posterior superior temporal sulcus, which often lies in close proximity to the dorsal part of face-selective LO. The face-selective lateral fusiform region corresponds almost exactly to face-responsive regions we have identified in previous studies (Haxby et al., 1994; Clark et al., 1996; Courtney et al., 1997) and to the face-specific regions identified by others (Kanwisher et al., 1996, 1997; Puce et al., 1996; McCarthy



et al., 1997). The distances between the Talairach coordinates of our lateral fusiform region and those for previous reports range from 6 to 15 mm. The face-selective region in the superior temporal sulcus was also noted by Kanwisher et al. (1997) and has been associated with the perception of facial movement by Puce et al. (1998).

Previous studies have suggested that the inferior occipital face-selective region may be primarily involved in perceiving the generic facial configuration and some attributes, such as age and gender, that allow categorization of faces but do not specify identity (Bruce and Young, 1986; Sergent et al., 1992). The face-selective temporal lateral fusiform region may be more critical for perceiving the individual identity of each face (Sergent et al., 1992; Haxby et al., 1994), whereas the superior temporal sulcal region may be more critical for perceiving eye movement and other, socially relevant changes in facial configuration (Puce et al., 1998). Hasselmo et al. (1989) proposed a similar distinction between face-selective neurons in the monkey inferior temporal gyrus and superior temporal sulcus.

The distributed set of regions that respond more to houses than to faces has not been described before. The medial fusiform house-selective region appears to correspond to a bilateral region in ventral medial temporal cortex that Kanwisher et al. (1996, 1997) also found responds more to other objects than to faces. Aguirre et al. (1998) have identified a region that responds more to buildings than to faces and other objects. The location of this region coincides almost exactly with the medial fusiform house-selective region, but it is much smaller in spatial extent. They have suggested that this region is specific for perceiving objects that are used as landmarks for navigation. In other studies, however, we have found that parts of the medial fusiform region also respond more to chairs and tools than to faces (Ishai et al., 1997, *Neuroimage*, abstract; Chao et al., 1998, *Soc. Neurosci.*, abstract), neither of which is a good candidate for a landmark. If there is a region specialized for perceiving objects that facilitate navigation, therefore, it is probably a small sector of the larger region we have identified. The medial fusiform house-selective region may overlap with the parahippocampal place area (PPA) (Epstein and Kanwisher, 1998), which responds more to scenes and architectural spaces than to other objects (including houses) and faces, but unlike Aguirre et al.'s building area, the PPA has a more anterior and medial location than our medial fusiform house-selective region.

The different functional roles played by the occipital and temporal house-selective regions are unknown. One might predict a hierarchical progression similar to that of the face-selective system, with occipital cortex playing a greater role in the perception of the generic object configuration and ventral temporal cortex playing a greater role in the perception of features that distinguish a particular object from others of the same category.

Because we used only a single category of nonface objects, the ventral extrastriate systems that respond more to other objects than to faces undoubtedly extend beyond the regions we have identified (cf. Puce et al., 1996; Ishai et al., 1997, *Neuroimage*, abstract; Aguirre et al., 1998; Epstein and Kanwisher, 1998; Chao et al., 1998, *Soc. Neurosci.*, abstract). These other studies suggest that the topography of response may differ for

different nonface objects such as houses, words, rooms, landscapes, chairs, tools, and animals. Because we did not identify the regions that respond to all of these other categories, we cannot determine if face inversion also increases the response to faces in other parts of the ventral object vision pathway.

Our results differ from those of others (Kanwisher et al., 1996, 1997; Puce et al., 1996; McCarthy et al., 1997) insofar as we find more consistent face-selective activation in multiple regions, the regions demonstrating face selectivity are more consistently bilateral, and the lateral fusiform face-selective regions have larger volumes. These differences are probably due primarily to differences in the sensitivity of methods. We based our identification of face-selective regions on larger data sets (1224 scans per subject) and used a lower statistical threshold for inclusion of voxels in the face-selective region, relying more on a spatial extent threshold to achieve an acceptably conservative level of significance. Our use of a single category of nonface objects, rather than a heterogeneous group, may also affect estimates of the size and consistency of face-selective regions. Nonetheless, in a separate experiment in which we compared the response to faces to the responses to two different categories of objects (houses and chairs) (Ishai et al., 1997, *Neuroimage*, abstract), the volumes of face-selective regions (1.7 and 1.4 cm<sup>3</sup> in the left and right lateral fusiform regions, respectively) were still much larger than those reported by others. Moreover, the responses to houses and chairs in these more stringently defined face-selective regions (42% and 59% of the mean response to faces, respectively) were equivalent to the responses to houses in the less stringently defined face-selective regions in the current study (39% of the mean response to faces). These findings suggest that the substantial response to houses in face-selective regions was not due to the inclusion of voxels that actually do not respond maximally to faces.

The face and object systems both appear to participate significantly in the perception of the nonpreferred category of objects. Surprisingly, for stimuli in their normal, upright orientation, the face system's participation in house perception is greater than the object system's participation in face perception. This result is problematic for the hypothesis that face-selective regions, especially the lateral fusiform region, constitute a "module specialized for face perception" (Kanwisher et al., 1997; McCarthy et al., 1997). If anything, the special status of face perception does not appear to be associated with a region or set of regions that are dedicated solely to face processing because these regions respond significantly to houses. Instead, face processing is special in that its representation is not as widely distributed as are the representations of other objects.

While our results indicate regions that participate in distributed neural systems for face and object recognition, it is not clear which of these regions are critical or sufficient for these functions. The more restricted representation of face processing, as compared to the representation of object processing, may explain how a lesion in ventral temporal cortex could result in a selective impairment of face recognition. If a lesion eliminated face-selective regions but did not involve some regions



that respond to other objects but only minimally to faces, those intact regions might be able to support object recognition. It is not clear whether a lesion that produces prosopagnosia must also include the face-selective regions in inferior occipital and superior temporal cortex. However, the more distributed representation of other objects would make it unlikely that a restricted lesion in ventral occipitotemporal cortex would impair object recognition and leave face recognition intact. Such cases are extremely rare, according to Farah's review of the literature on visual agnosia (Farah, 1991). In the cases that do exist, it is possible that some preserved input to the superior temporal sulcus from the face-selective inferior occipital region could support face recognition. Although the superior temporal sulcus appears to be more involved in the perception of facial movement and expression than in the perception of identity (Hasselmo et al., 1989; Puce et al., 1998), this distinction is not absolute in the monkey nor is it likely to be absolute in the human brain.

The effect of attention, as reflected in differences between responses during the passive viewing and delayed matching tasks, provides further evidence that face-selective regions participate significantly in the perception of other objects. As compared to passive viewing, the delayed matching task requires the subject to form a representation of each stimulus that is sufficiently distinct to discriminate between it and a highly similar stimulus from the same category. This demand increases the responses to both the preferred and non-preferred stimulus categories in both the face- and house-selective regions. Surprisingly, the increase in activity in both the ventral occipital and ventral temporal face-selective regions is greater for the nonpreferred category, namely houses. This result suggests that processing resources in the face perception system can augment the distinctiveness of a representation of a house, although the neuropsychological literature on selective object agnosias indicates that the participation of the face system in the perception of nonface objects is not sufficient to recognize or discriminate these stimuli (Moscovitch et al., 1997). Our results suggest only that such participation exists and apparently can facilitate perceptual performance when it acts in concert with intact object perception systems.

These considerations suggest that the representation of an object or face in ventral temporal cortex includes both the neural responses in regions that respond maximally to that stimulus and the neural responses in regions that respond more to other stimuli. Only by studying the topography of responses to meaningful stimuli across all regions in ventral extrastriate cortex can we understand how objects are represented and how representations change with stimulus transformations such as inversion.

#### Experimental Procedures

##### MR Scanning

Gradient echo, echo-planar imaging was used with a GE Signa 1.5 Tesla magnet to obtain volumes of 18 5 mm thick coronal images every 3 s (TE = 40 ms, FA = 90, FOV = 20 cm, 64 × 64 matrix) while six healthy, young, right-handed subjects performed delayed match-to-sample and passive viewing tasks. Twelve time series

were obtained, each consisting of 108 volume scans. Subjects gave written, informed consent.

During the same session as fMRI scanning, a high-resolution structural MRI scan was obtained using a fast SPGR sequence (5 mm thick slices, TR = 13.9 ms, TE = 5.3 ms, FA = 20, FOV = 20 cm, 256 × 256 matrix) that was coplanar with the functional EPI scans. In a separate session, a full-brain, high-resolution structural MRI scan was obtained, also using fast SPGR imaging (128 1.5 mm thick sagittal slices, TR = 13.9, TE = 5.3, FA = 20, FOV = 24 cm, 256 × 256 matrix).

##### Face and House Perception Tasks

Stimuli were faces, inverted faces, houses, inverted houses, and scrambled control pictures. For the delayed matching task, a single sample stimulus was presented for 1.1 s. After a 0.5 s interstimulus interval, two choice stimuli were presented for 1.9 s side by side. For the perception of meaningful stimuli, the subject indicated which choice stimulus matched the sample by pressing a button with the right or left thumb. For the control task with scrambled pictures, both choice stimuli matched the sample stimulus and the subject always responded by pressing both buttons. For the passive viewing task, stimuli were presented one at a time in the center of the screen at a rate of two stimuli per second with no interstimulus intervals. Subjects were instructed to "look at each picture and concentrate on what it looks like."

Stimuli were presented on a rear projection screen placed at the foot of the scanner bed and viewed by the subject through mirrors. Stimulus presentation and response recording were controlled by a Macintosh PowerPC computer and a Sony 800U projector using SuperLab task presentation software (Cedrus, Phoenix, AZ; Haxby et al., 1993).

Six time series consisted of only delayed match-to-sample tasks, and six time series consisted of only passive viewing tasks. All time series contained eight 18 s blocks with meaningful stimuli (two blocks for each type); 18 s blocks with control stimuli were presented at the beginning and end of each time series and between blocks with meaningful stimuli. The order of blocks was counterbalanced across time series.

##### Analysis of Performance Data

For each subject, percent correct and median reaction time on the matching tasks for each stimulus type in each time series were calculated. Accuracy and reaction time were analyzed with repeated measures ANOVAs with three within-subjects factors (stimulus category, stimulus inversion, and time series). Planned comparisons were performed that compared inverted faces to upright faces, inverted houses to upright houses, and upright faces to upright houses.

##### Multiple Regression Analysis of fMRI Time Series

Data for each subject were analyzed separately using multiple regression (Friston et al., 1995; Haxby et al., 1999). Movement between scans was corrected by aligning all EPI scans to a mean EPI scan using AIR software (Woods et al., 1993). Images were smoothed within the coronal plane using a Gaussian filter with a FWHM of 1.2 voxels (3.75 mm). Changes in neural activity were modeled as square wave step functions coincident with the end of one stimulus block and the beginning of another. These changes were decomposed into orthogonal contrasts: (1) the difference between perception and control tasks, (2) the difference between faces and houses, (3) the difference between upright and inverted stimuli, and (4) the difference between face inversion and house inversion effects. The orthogonal, square wave contrasts were convolved with a Gaussian model of the hemodynamic response using experimentally derived estimates of lag (4.8 s) and dispersion (SD = 1.8 s). These convolved contrasts were the regressors of interest in the multiple regression analysis. Additional regressors of no interest were included in the analysis to partial out variance due to differences in mean intensity between time series and linear changes in intensity within time series. Separate analyses were performed on all 12 time series combined and for the 6 matching and 6 passive viewing time series separately.

### Correlations between Response Topographies for Different Stimuli

As an index of the similarity of the topographies of responses to the different types of stimuli, correlations were calculated for each subject between the sizes of activation for each stimulus type (increase in signal relative to the control tasks with scrambled pictures) in all voxels that showed a significant overall experimental effect ( $Z > 4.0$  for an omnibus test of the combined effect of the four regressors of interest in the analysis of all 12 time series; Rencher, 1995) and an overall increase in activity for meaningful stimuli (a positive regression weight for the contrast between meaningful and control stimuli). The mean squared correlation across subjects was calculated to obtain a single index for the similarity of response topographies for each pair of stimulus types.

### Identification of Regions Showing Experimental Effects

Regions were identified that consistently demonstrated significantly different responses for faces and houses, and the time series for these regions, averaged across voxels, were analyzed for a more sensitive analysis of the effect of stimulus inversion. Voxels were selected that demonstrated a significant overall experimental effect (see above) and a difference between responses to faces and houses ( $|Z| > 1.96$ ,  $p < 0.05$ , two-tailed, uncorrected for multiple comparisons), combining upright and inverted orientations, in the combined analysis of matching and passive time series. Correction for multiple comparisons was achieved by an analysis of the spatial extent of clusters of voxels showing differential responses to faces and houses. Only clusters of seven or more contiguous voxels with  $|Z| > 1.96$  were considered significant. Within the search space defined by the significant overall experimental effect (mean volume =  $63.0 \text{ cm}^3$ ,  $SD = 25.0 \text{ cm}^3$ ), a cluster of this size had a significance of  $p < 0.05$  in all subjects.

The contrast between all faces and all houses was used rather than the contrast between upright faces and upright houses so that any difference between upright and inverted conditions could not be attributed to a selection bias; voxels selected on the basis of the comparison between upright stimuli would show a reduced effect for inverted stimuli because of regression to the mean. Moreover, the analysis of correlations between response topographies (see Results) indicated that the response to inverted stimuli most closely resembled the response to upright stimuli of the same category, indicating that the contrast between all faces and all houses would not obscure differences between upright faces and upright houses.

The anatomical locations of clusters of voxels showing significant differences between responses to faces and houses were determined by superimposing their locations on coplanar high-resolution structural MRI scans. Six bilateral regions in occipital and temporal cortex were found that consistently showed differential responses across subjects. Voxels in significant clusters that were in each of these anatomical regions were identified and used to determine the stereotaxic coordinates of each region and to calculate mean time series, averaging across all voxels in a region, for further statistical analysis (see below). Identification of these regions sometimes involved grouping neighboring but noncontiguous significant clusters together or dividing a large cluster of contiguous voxels into different anatomical regions. Clusters of voxels that showed differential responses outside of these six regions were also noted, and their anatomical locations and volumes tabulated.

Locations of each region in the standard stereotaxic coordinates of the Talairach and Tournoux atlas (1988) were obtained. To correct partially for distortions in the EPI data, EPI data were registered to the coplanar structural MRI using a two-dimensional, rigid body alignment algorithm with AIR software (Woods et al., 1993). The coplanar structural MRI scans were registered to the high-resolution structural MRI scan, also using AIR software, and the registered statistical maps from the fMRI EPI data were similarly registered using the same resampling matrix. The high-resolution structural MRI was then resampled into the standard stereotaxic brain coordinates of the Talairach and Tournoux atlas (1988), and the registered fMRI statistical maps were shadowed into the same coordinate space using SPM96b software.

### Multiple Regression Analysis of Regional Data

For each subject and each region, a mean time series, averaging across voxels in the region and across repetitions of blocks with

the same tasks, was calculated. Separate mean control blocks were calculated for the control blocks following each type of meaningful stimulus. The average task blocks were then rearranged to a standard order: (1) upright faces, (2) control following upright faces, (3) inverted faces, (4) control following inverted faces, (5) upright houses, (6) control following upright houses, (7) inverted houses, and (8) control following inverted houses. Thus, these mean time series consisted of 48 time points (6 time points for each stimulus type and 6 time points for control blocks following each stimulus type). Each time point in these mean time series represents the average of 12 scans.

Multiple regression with orthogonal contrasts was used to analyze these data to test the significance of differences across all subjects. These analyses were similar to those performed on the individual time series data but had increased sensitivity due to averaging data across voxels and analyzing results for all subjects combined. Moreover, analysis of multiple regions made it possible to test the significance of differences between effects in different regions. For analyses of bilateral regions, contrasts tested differences between (1) all meaningful stimuli and control stimuli, (2) all faces and all houses, (3) upright and inverted faces, (4) upright and inverted houses, (5) tasks (matching and passive viewing), (6) hemispheres, (7–10) interactions between task and stimulus comparisons, and (11–14) interactions between hemisphere and stimulus comparisons. Additional regressors of no interest were included in the analysis to factor out mean intensity differences between regions and between subjects. For analysis of selected pairs of bilateral regions, the same analysis was performed with additional contrasts testing regional differences and the interactions between region, on the one hand, and stimulus comparisons, the effect of task, and hemispheric differences, on the other.

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