

To test whether the human fusiform face area (FFA) responds not only to faces but to anything human or animate, we used fMRI to measure the response of the FFA to six new stimulus categories. The strongest responses were to stimuli containing faces: human faces (2.0% signal increase from fixation baseline) and human heads (1.7%), with weaker but still strong responses to whole humans (1.5%) and animal heads (1.3%). Responses to whole animals (1.0%) and human bodies without heads (1.0%) were significantly stronger than responses to inanimate objects (0.7%), but responses to animal bodies without heads (0.8%) were not. These results demonstrate that the FFA is selective for faces, not for animals. *NeuroReport* 10:183–187 © 1999 Lippincott Williams & Wilkins.

**Key words:** Category-specific impairments; Extrastriate cortex; Face perception; FFA; fMRI; Fusiform face area; Visual cortex

## The fusiform face area is selective for faces not animals

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### Introduction

Numerous behavioral and physiological studies have provided evidence that the brain contains special-purpose mechanisms that are selectively involved in the perception of faces. Recent evidence from neuroimaging in humans has demonstrated a region in the fusiform gyrus called the fusiform face area, or FFA [1], which responds both strongly [2,3] and selectively [1,4,5] to faces. That is, the response of the FFA to faces is at least twice as large as the response to non-face stimuli such as inanimate objects, flowers, houses, and human hands. On the other hand the FFA response has been shown to generalize across a wide variety of face stimuli, and is of similar magnitude for front-view faces, profile faces, inverted grey-scale faces [7], two-tone 'Moon-eye' faces, cat faces and cartoon faces, despite substantial differences in the low-level visual features present in these stimuli [6]. Given both the specificity and generality of the FFA response, the most parsimonious hypothesis is that this region is selectively involved in face perception.

However, it remains possible that the FFA might respond more generally to anything animate, or perhaps to anything human. The very weak response which has been reported to hands [1] and to photographs of the backs of human heads [6] suggest that stimuli containing non-face human body parts are not sufficient to drive the area strongly. However, there are several reasons to think that photographs of animals might be. First, the response to cat faces

is as strong as the response to human faces [6]. Second, a recent report found that the face area can be activated by animal stimuli even when their heads are occluded [8]. Third, deficits in identifying animals are often [9] (though not always [10,11]) associated with prosopagnosia.

Even if the FFA itself does not respond strongly to animals, there is evidence that other cortical regions may be specialized for processing animals or living things. Several imaging studies [12–14] have reported regions showing greater responses to animals than inanimate objects (though one [15] found this for only black and white, not colored stimuli), and a number of neuropsychological cases with category-specific impairments for animals but not tools [10,13,16] have been reported. Although the animal-specific impairments usually affect higher-level semantic tasks, in at least one case [10] a deficit for recognizing animals (but not faces) was reported using the object decision task, which does not require naming or understanding.

The primary aim of the present study was to test whether the FFA responds selectively to faces as previously claimed, or if instead it responds more generally to animals. Because animals have faces, which have already been shown to activate the FFA, [6] three different kinds of animal pictures were used as stimuli: photographs of whole animals, animals without their heads showing, and animals with only the head visible. A second purpose of the study was to test whether any region of the ventral occipitotemporal pathway shows a stronger response

to animals than to inanimate objects. We also measured the fMRI response to photographs of humans, either whole or with only head or body showing, both as comparison cases for the animal conditions and to test whether the FFA responds to components of human forms other than faces.

**Materials and Methods**

*Subjects:* Five healthy normal adults (four women), ages 21–39, with normal or corrected-to-normal vision, volunteered or participated for payment. All subjects gave informed written consent, and all procedures were approved by MIT and MGH human subjects committees.

*Stimuli:* All stimuli consisted of greyscale photographs or photorealistic drawings 300 × 300 pixels in size (which fit within a square of ~10° on a side). Original photographs of animals and people were digitally edited in Adobe Photoshop to create head only and body only versions (Fig. 1a). Note that stimuli were not resized after editing; the head only and body only components constitute non-normalized subsets of the corresponding whole stimulus. There were six main experimental conditions, created by crossing animals/people × whole/head only/body only. Two other conditions, front-view face photos and inanimate objects, were also included in the experiment to provide benchmarks of maximal and minimal FFA responses to visual stimuli.

*Experimental procedures:* Each subject was run on

two or more functional localizer scans containing epochs of faces and either objects or houses, and four scans on the critical new test materials. Each subject performed two of the test scans in a passive viewing task, and two in a ‘1-back’ task in which they were instructed to press a button whenever they saw two identical pictures in a row (1–3 repetitions occurred in each epoch). Each scan lasted 5 min and 36 s and consisted of sixteen 16-second epochs with fixation periods interleaved as shown in Fig. 1b. During each epoch, 20 different photographs of the same type were shown. Each photograph was presented for 300 ms followed by a blank interval of 500 ms. There were two epochs for each of the eight stimulus types within each scan; order was counterbalanced over two versions of each experiment (ABCD–EFGH–HGFE–DCBA for version 1 and HGFE–DCBA–ABCD–EFGH for version 2). The raw data from version 1 were reordered so that the time courses from the two versions were compatible and could be averaged together. These procedures are described in more detail in previous papers [1,17].

*Scanning procedures:* Scanning was carried out on the 3 T GE scanner (modified by ANMR to perform Echo Planar Imaging) at the MGH-NMR Center in Charlestown, MA. A custom bilateral surface coil (built by Tommy Vaughn) provided a high signal-to-noise ratio in posterior brain regions. High resolution anatomical and functional images were collected using twelve 6 mm near-coronal slices extending from the occipital pole into the posterior

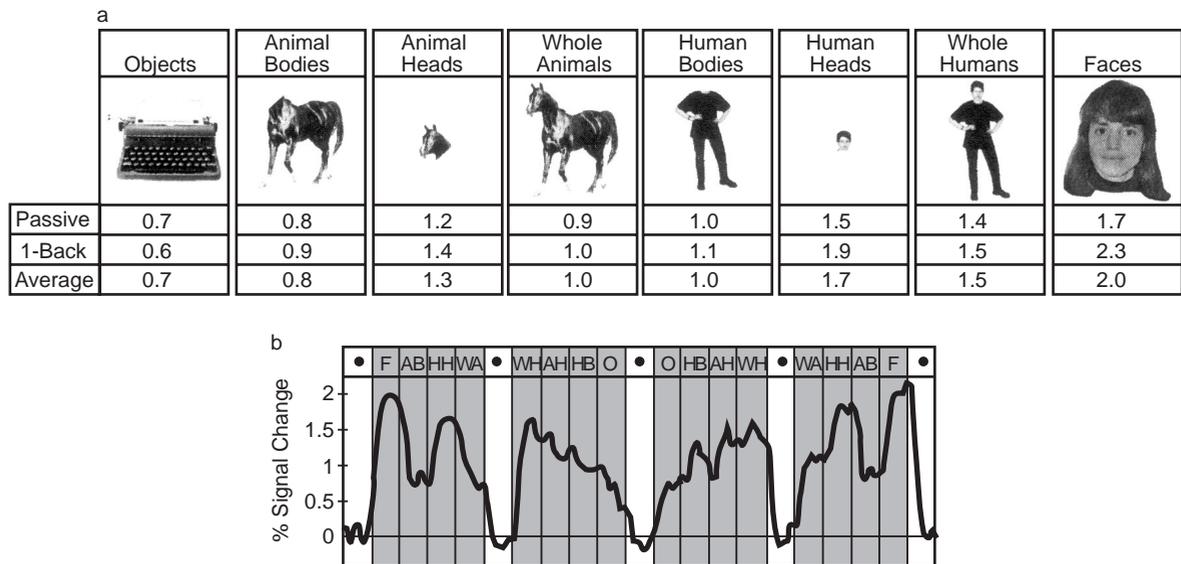


FIG. 1. (a) Examples of the eight different stimulus types and the average percentage signal increase from fixation in the FFA for each averaged over all subjects. Data from passive and 1-back runs, and the average of the two, are given separately. Percentage signal change was calculated individually for each subject using that subject's fixation activation as baseline and then averaging across subjects. (b) The time course of the percentage change in MR signal intensity in the FFA over the period of the scan. O, objects; AB, animal bodies; AH, animal heads; WA, whole animals; HB, human bodies; HH, human heads; WH, whole humans; F, faces; black dot indicates fixation epochs.

third of the temporal lobe. Standard imaging procedures were used (gradient echo pulse sequence, TR = 2 s, TE = 30 ms, flip angle = 90°, 180° offset = 25 ms, 168 images/slice). A bite bar was used to minimize head motion.

**Data analysis:** Each subject's FFA was identified from the functional localizer scans as the set of all contiguous voxels in the mid-fusiform gyrus that showed significantly greater activation to greyscale front-view faces compared to houses or to common objects in a Kolmogorov-Smirnov test using a criterion of  $p < 0.0001$  (uncorrected). For the analysis of the main experiment, image data for passive viewing and 1-back scans were separately averaged for each subject, and a time course of the magnetic resonance (MR) signal intensity was extracted from each subject's FFA (averaging over all voxels identified in the localizer scan for that subject). The average percentage signal change in the independently-localized FFA was calculated for each subject, stimulus condition and task, using the average signal intensity during fixation epochs for the same subject, experiment, and task as a baseline. Because the fMRI response typically lags 4–6 s after the neural response, our data analysis procedure treated the first image in each epoch as belonging to the condition of the preceding epoch, and omitted the next two images (during the transition between epochs) from the analysis.

We first analysed the percent signal change for the six main conditions in a three-factor (human/animal  $\times$  whole/body/head  $\times$  passive/1-back) ANOVA across subjects. Then for each pairwise comparison of interest, we ran a two-factor (stimulus condition  $\times$  passive/1-back) ANOVA across subjects. Because data were analyzed within independently defined regions of interest, no correction for multiple voxel-wise comparisons was necessary.

## Results

**FFA response:** The FFA was successfully localized in all five subjects to regions in the mid-fusiform gyri consistent with the loci reported in earlier studies [1]. The percentage signal change (PSC) from fixation for each condition in each subject's individually localized FFA was calculated. The average PSC values across subjects are given for each condition  $\times$  task combination in Fig. 1a and for the entire time course (averaged overtasks) in Fig. 1b.

The three-factor ANOVA of task (passive/1-back)  $\times$  species (human/animal)  $\times$  body part (whole/body/head) revealed a significant main effect of higher responses to humans than animals ( $F(1,4) = 11.8$ ,  $p < 0.005$ ) but no main effect of task ( $F < 1$ ).

No interactions reached significance (all  $F < 2.5$ , all  $p > 0.15$ ). Two-factor ANOVAs compared pairs of conditions crossed with task; the results of these analyses are summarized in Table 1. For these analyses, none of the interactions of condition  $\times$  task reached significance.

**Other activated areas:** For each subject, we also computed Kolmogorov-Smirnov statistics on each of the voxels scanned to test whether the response in that region was greater during viewing of (whole) animals than during viewing of objects. A parallel comparison of the response to faces versus objects in the same scans was also carried out. For these analyses, the passive and 1-back data were first averaged together to maximize signal to noise. Almost all voxels showing a significantly greater response to animals than objects also showed a significantly greater response to faces than objects; the very few voxels showing the animal effect but not the face effect showed no anatomical consistency across subjects. Thus we found no evidence of any cortical regions specialized for processing animals, in the sense of producing a much higher response to animals than to inanimate objects and faces.

**Behavioral data:** Behavioral data (from the 1-back task) from two subjects were lost due to a computer error. For the remaining three subjects, the average percentage correct detection and total number of false alarms (in parentheses) over the four epochs of each type for each condition were: faces 76% (4), whole humans 90% (4), human heads 90% (1), human bodies 81% (2), whole animals 92% (0), animal heads 100% (0), animal bodies 81% (1), objects 100% (2). While these data may suggest that

**Table 1.** Results of separate two-way ANOVAs across subjects comparing pairs of stimulus conditions  $\times$  task (passive vs 1-back). The difference in the average percent signal between the two conditions, and the significance of that difference, are given in the columns at the right. \* $p < 0.05$ ; \*\* $p < 0.02$  and \*\*\* $p < 0.01$ .

Comparison	PSC Difference	Significance
Human heads vs whole animals	0.7	***
Human heads vs animal heads	0.4	***
Human heads vs animal bodies	0.9	**
Faces vs whole animals	1	*
Faces vs animal heads	0.7	*
Faces vs animal bodies	1.2	*
Whole animals vs objects	0.3	*
Animal heads vs objects	0.6	***
Animal bodies vs objects	0.1	$p > 0.15$
Whole humans vs objects	0.8	***
Human heads vs objects	1	***
Human bodies vs objects	0.3	*
Whole humans vs whole animals	0.5	***
Human bodies vs animal bodies	0.2	$p > 0.25$
Human heads vs human bodies	0.7	***

the matching task was more difficult for some stimulus categories than others, note that the pattern of fMRI response across conditions was very similar in the passive condition where no task was necessary.

## Discussion

The present data clearly indicate that the FFA does not respond as strongly to any aspect of animals as it does to human faces or human heads: the FFA showed higher responses for human faces than for animal heads, whole animals, and animal bodies; the same was true when human heads were compared to each of the animal conditions (see Table 1). Thus, the FFA responds much more strongly to human faces or heads (even when they are very small), than to any aspect of animals. Because previous work has shown a very low FFA response to the backs of human heads with no face visible [6], it must be the presence of a face that produced the large response to human heads.

Does the FFA nonetheless reveal a greater response to animals than to inanimate objects? Animal heads and whole animals do indeed produce a fairly strong response, replicating and extending the earlier finding [6] of strong responses to cat faces. These results are also consistent with the finding that patient CK who has severe object agnosia but normal face recognition is fairly good at matching animal faces, as might be expected given that animal faces share many features with human faces. [18] But because whole animals and animal heads contain faces, the activation we found for these stimuli does not present evidence against the claim that the FFA responds selectively to faces. More relevant was the response to animal bodies, which was not significantly greater than the response to objects. This shows that it is the presence of a face, not the animal itself, that drives the FFA response. Note that this result differs from Chao *et al.*'s report [8] of greater responses to animals with faces occluded than to inanimate objects. It is not clear which of the methodological differences between the two studies accounts for the differing results obtained.

Finally, the data show that the FFA does not just respond to anything human, as the response to human bodies was about half the magnitude of the response to human faces. Although the response to human bodies was significantly greater than the response to objects, these effects were small, and might be attributable to top-down completion or mental imagery of the parts of the figure not shown.

No evidence was found for any other cortical regions which responded consistently more strongly to animals than to objects. Any region in a given

subject that responded more to animals than objects also responded more strongly to faces than objects. Thus our data provide no evidence for a cortical region specialized for the perception of animals. Note, however, that our use of a surface coil restricts our view to relatively posterior brain regions, and it remains possible that cortical regions specialized for animals may exist in regions anterior to our field of view. Also note that our tasks were designed to tap basic recognition processes, not higher level conceptual processes. Thus our data do not argue against the existence of domain-specific mechanisms for the semantic processing of animals [10].

In order to more fully test whether any cortical regions exist that are specialized for perceiving animals, the present experiments should be repeated with a head coil for better coverage of the entire brain. If such experiments continue to find no cortical regions that respond selectively to animals, that would suggest some constraints on the modular structure of human visual recognition. To the extent that some visual categories do not have specialized neural structures dedicated to their recognition, such a result would strengthen the argument that faces are special [19]. However, such arguments would be subject to the caveat that even well-designed imaging experiments can for a variety of technical reasons fail to detect a specialized cortical module that in fact exists.

## Conclusion

The present study found that although the FFA responded slightly more strongly to animals than to inanimate objects, this was no longer true when the animals faces were not visible. While the FFA did respond more strongly to human bodies (with heads not visible) than to objects, it responded much more strongly to faces or heads. Thus the response of the FFA is primarily driven by the presence of a face (whether human or animal), not by the presence of an animal or human *per se*. Further, no evidence was found for any other cortical regions specialized for perceiving animals.

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