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The fusiform face area subserves face perception, not generic within-category identification

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The function of the fusiform face area (FFA), a face-selective region in human extrastriate cortex, is a matter of active debate. Here we measured the correlation between FFA activity measured by functional magnetic resonance imaging (fMRI) and behavioral outcomes in perceptual tasks to determine the role of the FFA in the detection and within-category identification of faces and objects. Our data show that FFA activation is correlated on a trial-by-trial basis with both detecting the presence of faces and identifying specific faces. However, for most non-face objects (including cars seen by car experts), within-category identification performance was correlated with activation in other regions of the ventral occipitotemporal cortex, not the FFA. These results indicate that the FFA is involved in both detection and identification of faces, but that it has little involvement in within-category identification of non-face objects (including objects of expertise).

The FFA in human extrastriate cortex is activated about twice as strongly in fMRI experiments when people view faces as when they view other kinds of objects[1,2]. Previous experiments have shown that activation in the FFA is correlated with the percept of a face in binocular rivalry[3], the face/vase illusion[4,5], contrast reversal[6,7] and even face imagery[8,9]. The precise function of the FFA, however, remains unresolved[1,10–18]. Some researchers have suggested that the FFA may also be engaged in within-category identification of non-faces[11,12], and yet others have suggested that important information about faces lies outside the FFA[13]. Here we tested the main hypotheses that have been proposed for the function of the FFA: (i) detecting the presence of a face[19], (ii) identifying specific faces[20–22], (iii) within-category identification of stimuli from any object class[10,11] (*e.g.*, discriminating roses from other flowers) and (iv) within-category identification of stimuli from categories for which the subject has gained expertise[12,23].

To measure the neural correlates of detection and identification, we presented brief masked stimuli[24,25] in a rapid event-related fMRI design[26] and compared the blood oxygenation level–dependent (BOLD) signal on trials where subjects succeeded versus failed to detect and identify the stimuli (**Fig. 1a**). In each scan, subjects viewed 120 images from one category (*e.g.*, 120 faces or 120 birds) and 60 texture patterns. Half of the objects contained different images of a specific within-category target (*e.g.*, 60 Harrison Ford images or 60 pigeon images) and the rest were different objects from the same category (*e.g.*, 60 other faces or 60 birds from other species). Subjects were instructed to indicate whether the stimulus was: (i) the pre-specified within-category target, (ii) another object or (iii) not an object (*i.e.*, a texture). The three trial types occurred with equal probability in counterbalanced order. Importantly, for each of the three trial types, we used numerous pictures that appeared in various viewing conditions and backgrounds (**Fig. 1b**). Thus, subjects performed a within-category identification task rather than identifying a particular picture.

This design enabled us to compare the magnitude of the response in the FFA when subjects (i) correctly identified the target (an identification hit, **Fig. 1c**), (ii) detected the presence of the object but were unable to identify it (a detection hit) or (iii) did not detect the presence of the object at all (a detection miss). We reasoned that a higher response in detection hit trials than in detection miss trials for faces would implicate the FFA in face detection, and a higher FFA response for identification hits than for detection hits on faces would implicate it in face identification; the same logic was applied to the detection and identification of non-face objects.

RESULTS

Behavioral responses

Identification performance was approximately at threshold ($d' = 1.2 \pm 0.3$), and as expected[27,28], detection performance was better ($d' = 2.3 \pm 0.2$; $P < 10^{-5}$, *t*-test). Importantly, there were no statistically significant differences across categories in detection ($F_{1,5} < 0.5, P > 0.6$, one-way ANOVA) or identification performance ($F_{1,5} < 2$, $P > 0.1$, one-way ANOVA). Performance on face detection and identification were not different from object detection and identification (**Supplementary Table 1** online).

Involvement of the FFA in face detection and identification

For each subject, we defined a face-selective region in the mid-fusiform gyrus (the FFA) that responded more strongly to faces than to objects at a significance of $P < 10^{-4}$ (uncorrected) at the voxel level (**Fig. 2**). We then extracted the time courses of activation from this region of interest (ROI) in the event-related experiments (**Fig. 2c**). Time courses for the experimental conditions were deconvolved[26,29]

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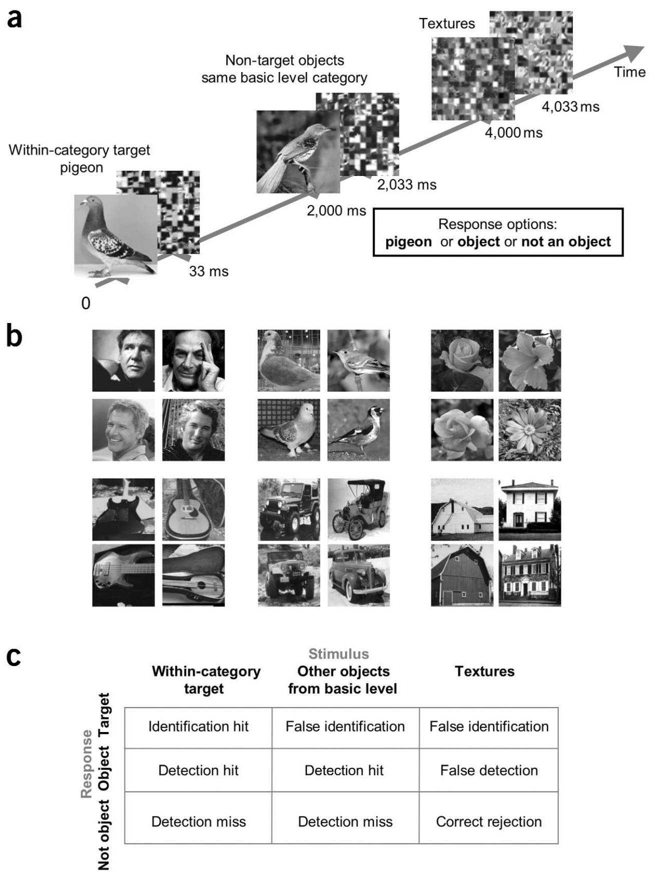


		Stimulus	
Response	Within-category target	Other objects from basic level	Textures
Target	Identification hit	False identification	False identification
Object	Detection hit	Detection hit	False detection
Not object	Detection miss	Detection miss	Correct rejection

Figure 1 Experimental design. (**a**) In each scan, subjects viewed images from one object category, as well as texture patterns. Images were presented for a duration close to each subject's identification threshold. (**b**) Examples of stimuli used. For each category, within-category targets are shown on the left and non-targets on the right (see Methods). (**c**) The table shows all possible trial outcomes according to both stimulus type and response.

based on subjects' behavioral responses (**Fig. 1c**). Texture trials that were correctly rejected served as the baseline.

Our data show that the activation in both the right and left FFA was significantly higher for face detection hits than misses (right: $P < 10^{-5}$; left: $P < 10^{-4}$; *t*-test), as well as for face identification hits than face detection hits (right: $P < 0.005$; left: $P < 0.01$, *t*-test). Importantly, the higher activations for identification hits versus detection hits and also for detection hits versus detection misses were statistically significant for each of the individual subjects (**Fig. 2b**). Furthermore, in the FFA, the magnitude of the effect of success at face detection was larger than that of success at face identification (right FFA: $P < 0.001$; left FFA: $P < 0.01$, *t*-test).

Notably, the signal in the FFA was also higher when non-target faces were falsely identified than when they were simply detected (**Fig. 2d**, non-targets). A two-way ANOVA found a main effect of reported identification (right FFA: $F_{2,1} = 5.5$, $P < 0.02$; left: $F_{2,1} = 4$, $P < 0.05$), but no main effect of correctness (both hemispheres: $F < 1$, $P > 0.5$) or interaction between correctness and success at identification (both hemispheres: $F < 1$, $P > 0.4$). These data suggest that FFA activation is correlated with subjects' perception of the target, rather than the correctness of their report. Finally, when we shuffled the pairings of behavioral responses and BOLD responses across subjects, the differences among conditions no longer reached statistical significance (**Fig. 2e–g** and **Supplementary Note** online). Thus, the higher FFA BOLD signal on trials in which faces were successfully identified or detected does not simply reflect differential responses to different stimuli.

Role of other face-selective foci in detection and identification

What is the role of other face-selective foci in face perception? Data from our localizer scan revealed two additional extrastriate regions[30] that responded more strongly when subjects viewed faces than when they viewed objects (**Fig. 2a**). These include a lateral occipital region near an area involved in processing visual motion (medial temporal area hMT+) and a region in the posterior bank of the superior temporal sulcus[30] (pSTS). We extracted the time course from these additional ROIs in the face experiments to examine their role in face detection and identification (**Fig. 3**).

The lateral occipital region showed significantly higher activation on face-detection hit trials compared to face-detection miss trials (both right and left hemisphere: $P < 0.001$, *t*-test). The activation in the right (but not left) face-selective lateral occipital region was also higher on face-identification hit trials compared to face-detection hit trials ($P < 0.05$, *t*-test). A two-way ANOVA with factors region of interest (FFA versus lateral occipital) and success (identification hit/detection hit/detection miss) revealed an interaction (right: $F_{1,2} = 6.69$, $P < 0.01$; left: $F_{1,2} = 5$, $P < 0.01$).

Surprisingly, whereas the pSTS region was significantly activated by faces in the localizer experiment (**Fig. 3a**), its activation was not correlated with face detection or identification, and it did not respond above baseline even on face identification hits. A two-way ANOVA with factors region of interest (pSTS versus FFA) and performance (success versus failure at identification) revealed both a main effect of ROI ($F_{1,2} = 112$, $P < 0.001$) and a significant interaction ($F_{1,2} = 9.2$, $P < 0.001$). The lack of activation in the pSTS region to face stimuli in the event-related experiments indicates that activation in this area is not necessary for face detection or identification.

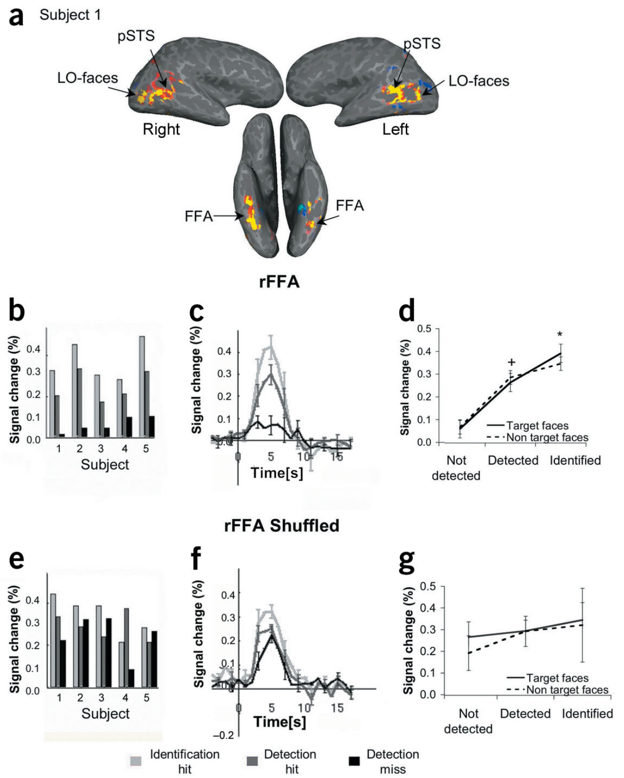
Taken together, these results indicate that in addition to the FFA, the face-selective region in lateral occipital cortex is also involved in both face detection and identification, but the face-selective region in pSTS is not necessary for either.

Role of the FFA in within-category identification of non-faces

To test whether the FFA response is correlated with detection or identification of non-face objects, we analyzed the FFA activation in the same five subjects in experiments in which they attempted to detect and identify non-face objects (**Fig. 4**). In contrast to the results for faces, identification hits for flowers, houses and guitars were not associated with increased FFA activation compared to detection hit trials (both hemispheres, $P > 0.1$, *t*-test). Furthermore, FFA activation was not correlated with a stronger signal for detection hits versus detection misses for non-faces (both hemispheres, $P > 0.1$, *t*-test, except birds). We also did not find negative correlations between the FFA response and detection (or identification) of non-faces (**Fig. 4**). These findings argue against the involvement of the FFA in within-category identification or detection of these non-face objects.

Further supporting the category-specificity of the detection and identification effects, ten different two-way ANOVAs revealed significant interactions between stimulus (faces versus every other category) and performance (identification hit/detection hit /detection miss for each hemisphere (right FFA: all $F_{1,2} > 4$, all $P < 0.02$; left FFA: all $F_{1,2} > 6.5$, all $P < 0.001$ for all categories except birds). These analyses indicate that the increase in FFA activation for identified and/or detected stimuli compared to stimuli that were not detected was greater for faces than for all other stimulus categories tested.

Figure 2 Right FFA hemodynamic response in face experiments. (**a**) Face-selective regions in one representative subject. Face-selective regions (yellow) were defined as regions that respond more strongly to faces than houses, cars and novel objects ($P < 10^{-4}$) at the voxel level. Blue voxels indicate voxels that passed the opposite contrast. Face-selective ROIs: (i) fusiform face area (FFA; Talairach coordinates (*x, y, z*) for the center of the FFA: right, 39 ± 3, –40 ±7, –16 ± 5; left, –37 ± 4, –42 ± 7, –16 ± 5), (ii) face-selective region in the lateral occipital cortex (LO-faces; right, 45 ± 5, –70 ± 3, 2 ± 9; left, –48 ± 3, –76 ± 6, 6 ± 3) and (iii) posterior STS (pSTS; right, 56 ± 3, –53 ± 4, 8 ± 7). (**b**–**d**) Right FFA (rFFA) activation when hemodynamic signal was deconvolved according to each subject's behavioral responses. (**e**–**g**) Shuffling control. (**b**,**e**) Individual subject data: the amplitude of hemodynamic responses in the rFFA for target face trials. (**c**,**f**) Group average data: deconvolved event-related time courses from the rFFA averaged across five subjects. Percentage signal change was calculated relative to a baseline from trials in which textures were correctly rejected. Error bars denote standard error of the mean (s.e.m.) across subjects at each time point. (**d**,**g**) FFA signal as a function of success at face detection and identification for target and non-target faces. Responses are averaged across five subjects. Asterisks indicate identification hits that were significantly higher than detection hits ($P < 0.001$, *t*-test). Crosses indicate detection hits that were significantly higher than detection misses ($P < 0.001$, *t*-test). Error bars indicate s.e.m.



The BOLD signal from the FFA was positively correlated with successful identification and detection of birds (identification hit > detection hit, right: $P < 0.001$; left $P < 0.001$; detection hit > detection miss, right: $P < 0.001$; left $P < 0.2$, *t*-test). Future research will be necessary to examine whether this finding reflects a response to bird faces or a role for the FFA in the perception of some non-face stimuli.

The FFA response was also weakly dependent on perceptual performance for car stimuli in three non-expert subjects (**Fig. 4**). Across the five non-expert subjects, a higher activation was found for car identification hits compared to detection hits only in the right FFA ($P < 0.03$, *t*-test). However, the FFA response to car detection hits was not significantly higher than for detection misses in either hemisphere (both *P*s > 0.1, *t*-test).

Can expertise explain the profile of activation in the FFA?

Does the correlation between FFA activation and successful identification of cars or birds reflect our subjects' expertise at identifying these categories compared to the other object categories[12]? To test this hypothesis, we conducted a *post-hoc* test of behavioral expertise for birds and cars[12]. According to this test, none of our subjects was expert with cars or birds (mean *d*′ scores (± s.d.) were 1.3 ± 0.5 for cars and 0.9 ± 0.4 for birds). Thus, expertise with non-face stimuli cannot explain the weak correlation we observed between FFA activation and success in car or bird identification.

It is possible, however, that expertise effects would be clearer if we tested subjects with greater behavioral expertise. To address this possibility, we scanned five car experts (see Methods) in the car and face conditions of the same experiments described above. These data revealed three things. First, no correlation was found between the response of the rFFA and success in car identification or detection in car experts (**Fig. 5a**; car identification hits > detection hits: $P > 0.1$, *t*-test; car detection hits > detection misses; $P > 0.1$, *t*-test). Importantly, when the full data set was pooled over car novices and car experts (ten subjects), we no longer obtained a significantly higher response in the rFFA for car identification hits than detection hits (car identification hits > detection hits: $P > 0.1$, *t*-test; car detection hits > detection misses: $P > 0.1$, *t*-test). Second, there was no correlation across subjects between the degree of behavioral expertise for cars, and the response on car identification hit trials compared to car detection hit trials (**Fig. 5b**). Third, we replicated in the car experts our finding that the rFFA is involved in face detection and face identification (**Fig. 5a**; face identification hits > detection hits, $P < 0.05$, *t*-test; detection hits > detection misses, $P < 0.05$, *t*-test). A two-way ANOVA of category (face versus car) crossed by performance (success versus failure at identification and detection) revealed a main effect of category ($F_{1,3} > 22$, $P < 0.0001$) and an interaction between cars and faces ($F_{1,2} > 3.2$,

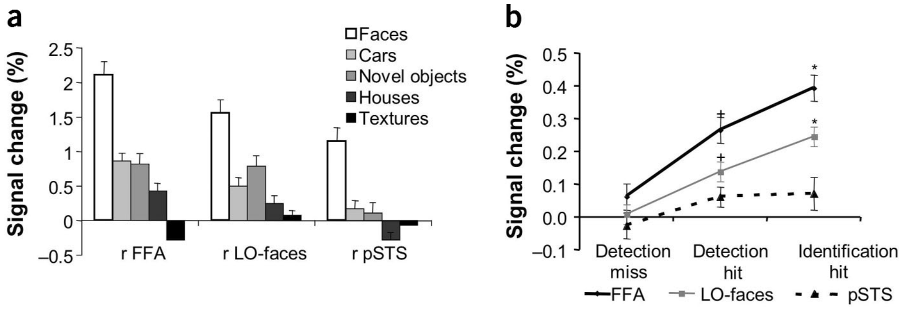


Figure 3 Involvement of face-selective regions of interest in face detection and face identification. (**a**) Average amplitude of activation (five subjects) in the localizer scan in three face-selective ROIs in the right hemisphere. (**b**) Average amplitude of the deconvolved hemodynamic response in the event-related experiments for face-selective ROIs (five subjects). Crosses indicate detection hits greater than detection misses ($P < 10^{-3}$, *t*-test). Asterisks indicate identification hits greater than detection hits ($P < 10^{-2}$, *t*-test). Error bars indicate s.e.m.

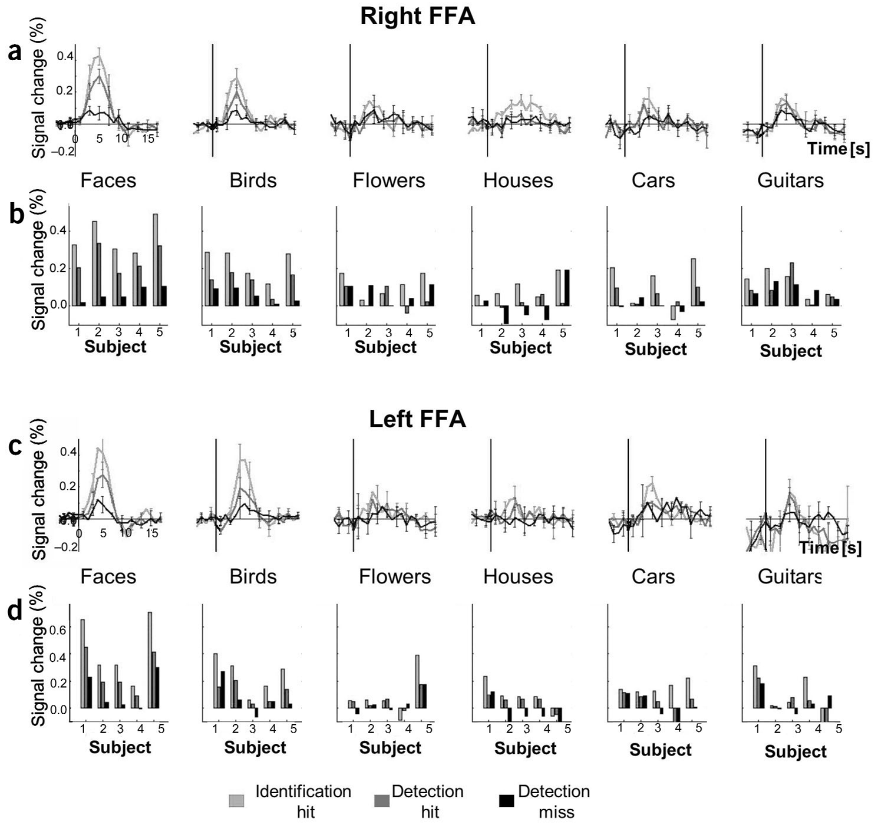


Figure 4 Hemodynamic response from the FFA for six categories as a function of detection and identification performance. (**a**,**c**) Group data: deconvolved hemodynamic response averaged across five subjects. Percentage signal change was calculated relative to a baseline from trials in which scrambled pictures were correctly rejected. Error bars denote s.e.m. at each time point. (**b**,**d**) Individual subject data: the amplitude of individual subjects' hemodynamic responses for target trials.

$P < 0.05$). These findings argue against a role of the rFFA in within-category identification of objects of expertise.

Involvement of other cortical areas

In addition to the ROI analyses described above, for each subject and category we searched for any voxels in occipitotemporal cortex that were activated more strongly for identification hits than detection hits (with $P < 10^{-2}$ at the voxel level, no spatial smoothing). This analysis allows a search for regions that may be involved in within-category identification, without restricting the analysis to predefined regions of interest.

In all subjects and for each of the six object categories, we found regions in the lateral occipital cortex and ventral occipitotemporal cortex that were correlated with successful identification (**Fig. 6**). Early visual areas did not show a differential response for identification hits, detection hits or detection misses (**Supplementary Fig. 1** online and **Supplementary Note** online). We then compared the location of regions correlated with within-category identification of faces and objects to the location of the FFA in individual subjects (**Fig. 6**, black contour). For all five subjects, we found extensive overlap between the FFA (as defined from the independent localizer scan) and regions that were correlated with successful face identification (**Table 1**). More than half (52%) of the voxels that were correlated with face identification were located within the FFA. The percentage of voxels that were correlated with non-face identification that overlapped the FFA was significantly lower (**Table 1**). Furthermore, the percentage of FFA voxels that were correlated with face identification was significantly higher than the percentage of FFA voxels that were correlated with non-face identification, for each of the non-face categories in both hemispheres (all $P < 0.01$, t-test). These data further show that most of the FFA is involved in face identification, not object identification.

Although there was extensive overlap between the FFA and regions correlated with face identification, we did find voxels outside the FFA that were correlated with successful face identification. Most of these were within other face-selective regions, or in regions that responded strongly to both faces and objects (such as the lateral occipital complex; LOC).

ROI analyses in ventral occipitotemporal cortex

We supplemented these voxel-wise analyses with an analysis of the response in several ventral occipitotemporal ROIs adjacent to the

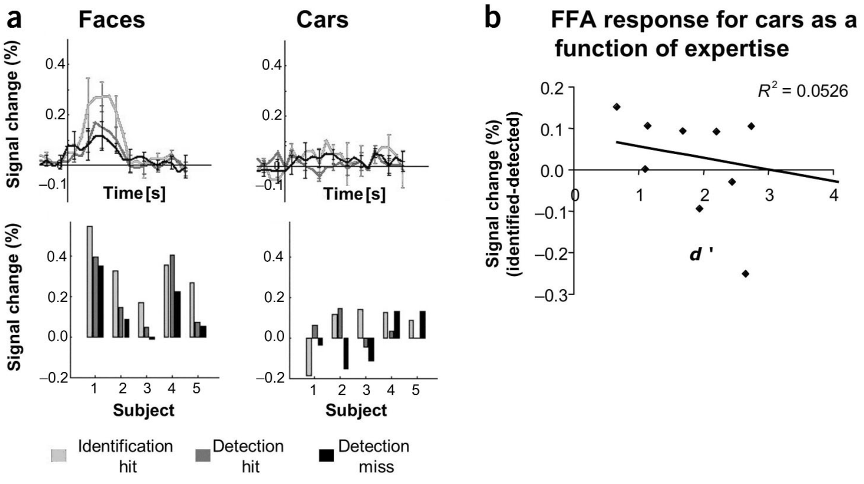


Figure 5 Car experts' data from the rFFA as a function of face and car detection and identification performance. (**a**) Left, face experiment (top, group data; bottom, individual subject data). Right, car experiment (top, group data; bottom, individual subject data). (**b**) FFA response for cars as a function of expertise. Correlation between the increase of fMRI signal in the FFA from detection hits to identification hits (reflecting the additional processing for identification) and expertise level (d') at discriminating cars.

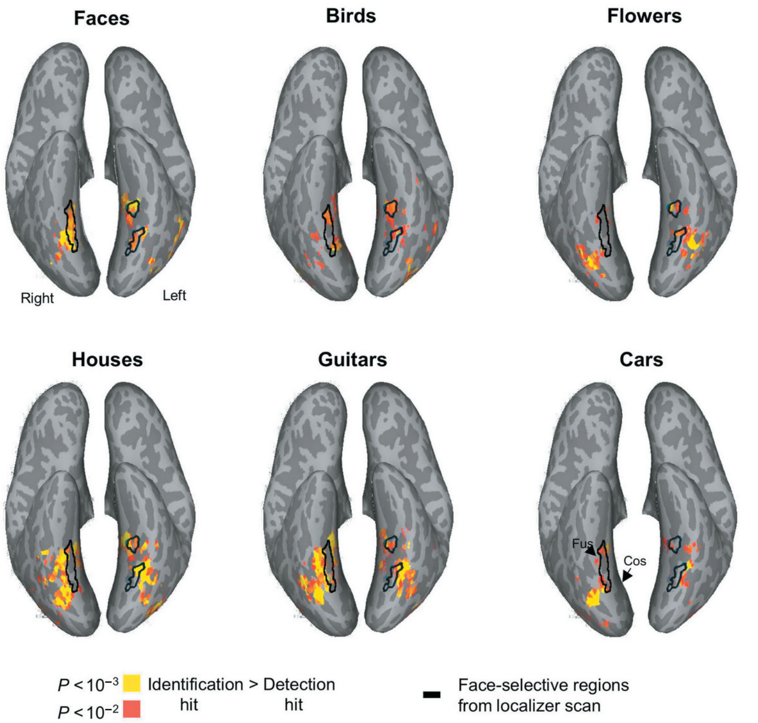


Figure 6 Location of cortical regions that were correlated with object identification and their relation to the FFA. Data are shown on the inflated brain of Subject 1 in a lateral-ventral view, (*i.e.*, brain was rotated 30° inwards to reveal both ventral and lateral surfaces). Colored patches indicate regions that were activated more strongly on identification hits than detection hits (with $P < 0.01$ at the voxel level). Colors denotes statistical significance at the voxel level (uncorrected). Black contours denote boundary of the FFA as defined by the independent localizer scan (faces > objects with $P < 0.0001$ at the voxel level). Sulci are shown in dark gray, gyri in light gray. Abbreviations: Cos, collateral sulcus; Fus, fusiform gyrus.

FFA. These ROIs include the inferotemporal gyrus (ITG), the medial fusiform gyrus (mFUS), and the parahippocampal place area (PPA)[31] (**Fig. 7** and Methods).

The ITG, mFUS and PPA ROIs showed different patterns of response than did the FFA (**Fig. 7**). The ITG ROI was correlated with success at flower, bird and house identification ($P < 0.01$, t-test), but not with face identification. The mFUS ROI was correlated with guitar and bird identification ($P < 0.01$, t-test), but not face identification, and the PPA ROI was virtually silent when subjects were engaged in object detection and identification. There was some activation in the PPA when subjects detected and identified houses, but differences between conditions (identification hit, detection hit and detection miss) did not reach statistical significance. Importantly, we either found regions in ventral occipitotemporal cortex that were positively correlated with identification of some non-face categories (*e.g.*, ITG or mFUS) or were silent during object identification (*e.g.*, PPA), but we did not find regions that were negatively correlated with success at face detection (which would suggest that they carry information relevant to face detection or identification).

DISCUSSION

Our experiments distinguished between the neural correlates of detection and identification by using a task with three response alternatives. We found a significantly stronger response in the FFA on trials in which subjects detected a face than when they did not, and an even stronger response when they identified the target face than when they merely detected it. Thus, our data show that the FFA response is correlated with, and hence probably involved in, both the detection and identification of faces.

Three of our findings provide evidence against an alternate hypothesis—that the FFA is engaged in within-category identification of exemplars of any stimulus class[10]. First, no correlation was found between the FFA response and behavioral identification of exemplars of many other non-face categories (guitars, flowers and houses). Second, other nearby cortical regions did show significant correlations with identification of these other object categories. Third, the BOLD signal in the FFA was correlated not only with identification of individual faces, but also with simple face detection. Thus, the present data are consistent with the idea that the FFA is primarily engaged in the perceptual processing of faces[32] and not with the idea that the FFA is engaged in within-category discrimination of exemplars of any object class[10].

We also tested the hypothesis that the FFA is engaged in the discrimination of any object sharing the same basic configuration for which the subject has gained substantial expertise[11,12]. We found no trial-by-trial correlation between rFFA response and success at car identification in car experts. Furthermore, we found no correlation across subjects between the subject's degree of expertise and the magnitude of the rFFA response on car identification hits (relative to detection hits). These findings do not support the hypothesis that the rFFA is involved in within-category discrimination of objects of expertise (see also ref. 33).

In another alternate account of the function of the FFA, it has been suggested[13] that categorical information about faces and objects in the ventral visual pathway is carried not only by the strong response to preferred stimuli, but also by the weak response to nonpreferred stimuli (see also ref. 34). In our experiments, this would have resulted

Table 1 Overlap analysis of regions involved in within-category identification and the FFA

Percentage of the volume of regions that were correlated with within-category identification that overlapped the FFA

	Faces	Birds	Flowers	Houses	Cars	Guitars
Right hemisphere						
	52 ± 9	18 ± 4	5 ± 5	8 ± 4	17 ± 6	11 ± 5
Left hemisphere						
	49 ± 7	20 ± 4	11 ± 7	20 ± 11	20 ± 7	9 ± 3

Percentage of the volume of FFA that overlapped with regions that were correlated with object identification

	Faces	Birds	Flowers	Houses	Cars	Guitars
Right hemisphere						
	93 ± 6	35 ± 18	3 ± 3	20 ± 11	30 ± 9	28 ± 13
Left hemisphere						
	92 ± 4	56 ± 19	21 ± 12	30 ± 12	44 ± 18	30 ± 7

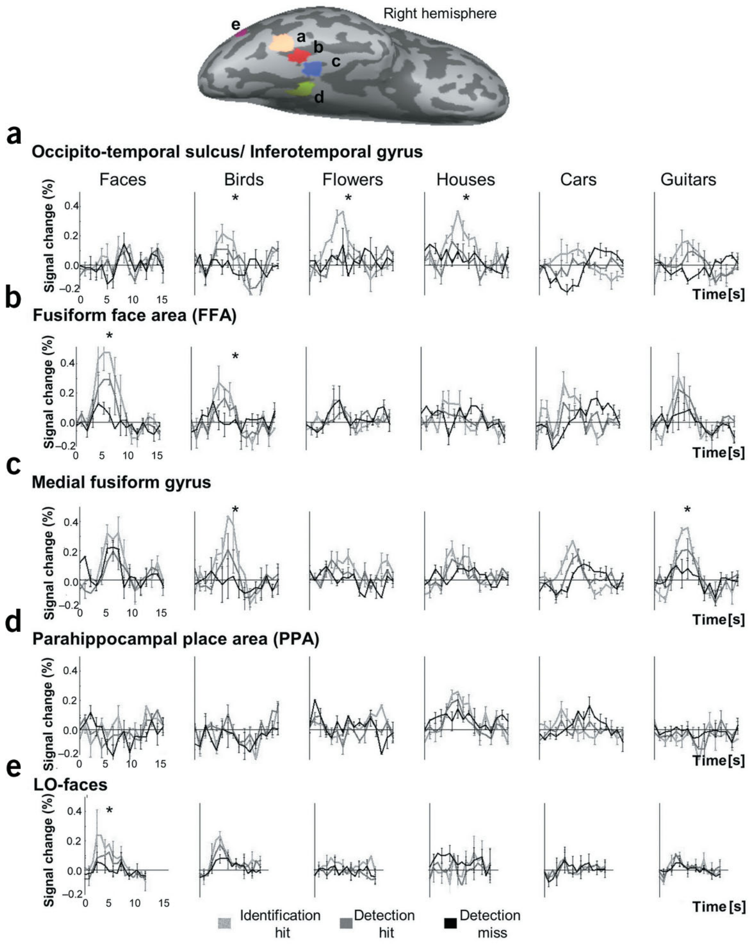


Figure 7 Deconvolved hemodynamic responses from ventral occipital cortex as a function of detection and identification performance. ROIs of average volume of 50 mm^3 were defined on a subject-by-subject basis. ROIs were rendered on the inflated brain and then projected to the high-resolution volume from which the time courses were extracted. Top, ROIs from which curves **a**–**e** were taken. (**a**–**e**) Group data averaged across the same five subjects whose data is presented in **Figures 2**–**4**. Error bars indicate s.e.m. at each time point. Asterisks indicate significantly higher signal for identification hits than detection hits ($P <$ 0.01). (**a**) Data for an ROI centered on the occipitotemporal sulcus/inferior temporal gyrus located lateral to the rFFA. In all subjects, this ROI was correlated with success at house identification Talairach coordinates (*x, y, z*) 41 ± 3, –52 ± 3, –18 ± 3. (**b**) Data for rFFA (Talairach coordinates: 39 ± 3, –40 ± 7, –16 ± 5). (**c**) Medial fusiform gyrus, medial to the FFA and lateral to the PPA (Talairach coordinates: 26 ± 1, –40 ± 3, –17 ± 3). In all subjects, this region was correlated with guitar identification. (**d**) PPA was independently defined in the localizer scans as an anterior region within the parahippocampal gyrus that responded more strongly to houses than to faces ($P <$ 0.0001) at the voxel level (Talairach coordinates: 21 ± 4, –38 ± 3, –10 ± 3). (**e**) A region in lateral occipital area that responded more strongly to faces than to objects (Talairach coordinates: 45 ± 5, –70 ± 3, 2 ± 9).

in one of two outcomes: (i) activation patterns for non-faces in the FFA that are not maximal, but positively (and significantly) correlated with subjects' perceptual perfomance or (ii) activations patterns that are negatively correlated with subjects perceptual performance (*e.g.*, the activation would become more negative on detection hits than misses). We found activations in the FFA consistent with the first prediction for birds, but not for other non-face categories. Whether this is because birds contain faces or because the FFA responds also to animals is an open question for a future study. Contrary to the second prediction, we did not observe lower FFA responses for detection hits than for detection misses (or lower responses for identification hits than for detection hits, **Fig. 4**). These findings suggest that the low rFFA response to stimuli from nonpreferred categories does not form part of the neural code used by subjects in detecting the presence of those categories (consistent with other recent results[35,36]).

The converse question is whether face categorization or identification is based exclusively on neural responses within the FFA, or whether other regions in the ventral visual pathway are also involved. Consistent with the latter hypothesis, we did find voxels outside the FFA that responded more strongly on identification and detection hits than misses for face stimuli (**Fig. 6**). Most of these voxels were either face-selective or responsive to both faces and objects. However, we did not find evidence that regions that are not strongly responsive to faces form part of object representations used for face detection or identification. For example, the PPA, which produces a consistently lower response to faces than to any other stimulus type we have tested[31,37], did not show either a positive or negative correlation with face detection or identification (**Fig. 7**). Thus, we find no evidence that weak responses to faces outside face-selective regions form part of the representation of the face.

Our data from the FFA are consistent with several other recent findings, and extend them in interesting ways. First, the correlation observed here between FFA responses and performance on face detection and identification parallels findings that the face-selective M170 response measured by magnetoencephalography (MEG) is correlated with both detection and identification of faces[38]. Second, the current data provide a possible explanation for the otherwise paradoxical report of a developmental prosopagnosic subject with an apparently normal FFA[21,39]. Face detection is preserved in prosopagnosia[40], and the present data show that face detection alone is sufficient to activate the FFA, even when the detected faces are not identified. Third, our data show that the FFA response was higher for both face identification hits and false face identifications than for face detection hit trials. This suggests that the fMRI signal in the FFA is correlated with subjects' perceptual experience rather than with the stimulus. This result parallels findings from neurophysiology[41–44] as well as neuroimaging of early visual cortex during a pattern detection task[45].

Finally, we found similar patterns of response in the FFA and in lateral occipital face-selective regions, consistent with recent evidence that lateral occipital face-selective regions may be necessary for face recognition[21]. In striking contrast, the face-selective region in the pSTS showed no response above baseline even on trials in which faces were correctly identified, indicating that strong activation of this region is not necessary for either face detection or identification. This conclusion is consistent with previous work[46–49] implicating the pSTS face region in the perceptual analysis of dynamic aspects of face stimuli, such as gaze direction and emotional expression. The fact that the face-selective region in the pSTS shows a very different profile from the FFA suggests that trial-by-trial correlations between the BOLD response and behavioral outcomes can reveal new functional dissociations not evident from a simple comparison of the mean response across conditions. The success of this method suggests that future studies using other fine-grained behavioral tasks will lead to a precise characterization of the function of many different regions within the ventral visual pathway.

In sum, our data do not support the view that the FFA is involved in within-category identification of any stimulus class, or of objects of expertise. Instead, our findings indicate that this region is engaged in the detection and identification of faces.

METHODS

A total of 12 volunteers (8 male, 4 female) ages 22–50 who gave written informed consent participated in these experiments; 5 male subjects were car experts. The study was approved by the MIT Committee On the Use of Humans as Experiments Subjects (COUHES) and the Partners Human Research Committee. Three of the subjects (2 female and 1 male) participated in both Experiment 1 and the early visual areas control experiment (**Supplementary Note** online). Non-expert subjects participated in 2–3 scanning sessions for a total of 5–6 scanning hours per subject and an additional one-hour session in which we acquired high-resolution anatomical images. five subjects were scanned on a 3T Allegra head-only Siemens scanner, five subjects were scanned on a 3T Trio Siemens scanner at the MGH scanning facility, Charlestown, Massachusetts, and two car experts were scanned on a GE 3T scanner at the Lucas Imaging Center at Stanford University. Functional scans used a gradient echo T2* EPI sequence (10 slices; resolution 3.125 × 3.125 × 4 mm, TR = 1 s; TE = 43 ms, flip angle = 60°, for the scans performed on the Trio scanner, scanning parameters were identical except that TE = 30ms and flip angle = 90°). Slices were oriented perpendicular to the calcarine sulcus. Scanned regions covered the mid occipital lobe, posterior parietal lobe and posterior-to-mid temporal lobe. In each session, we acquired high-resolution (0.78125 × 0.78125 × 4 mm) T2-weighted anatomical images that were used to align the slices to the high-resolution whole brain volume anatomical scan. For all subjects, we acquired a high-resolution (1 × 1 × 1 mm) three-dimensional T1-weighted whole brain anatomical that was used to reconstruct the structure of the brain and create 3D surface-based cortical representations.

Visual stimulation. Visual stimuli were generated on a G3 Powerbook (Macintosh) using the Psychophysics Toolbox (www.psychtoolbox.org) and Matlab (www.mathworks.com). Stimuli were back-projected via an LCD projector on a translucent screen located on the rear of the scanner. Subjects viewed the stimuli using a front surface mirror mounted on the head coil. Stimuli subtended a visual angle of 8°. Behavioral responses were collected during the scan via a button box.

Scans to localize face-selective regions. Each scanning session included two block-design scans, each lasting 288 s, that were used to define face-selective regions. In these localizer scans, subjects passively viewed pictures of faces (that were not shown subsequently in the event-related experiments), novel objects, cars, houses and texture patterns. Images appeared at a rate of 1Hz in blocks of 16 s. Each block type was repeated four times in a scan using different images.

Rapid event-related experiments. Subjects viewed a rapid succession of event-related trials. In each 2-s trial, a black and white photograph appeared for a duration of 33 ms or 50 ms (depending on individual subject's identification threshold[28]) and was immediately followed by a random texture pattern that served as a mask. Subjects saw objects from one object category in each scan. Each 392-s scan contained 60 trials of the target subordinate category (*e.g.*, Harrison Ford), 60 trials of other items from the same basic level category (*e.g.*, other male faces) and 60 trials that contained textures. Importantly, images were not repeated in a run, so subjects had to identify a particular member of a category and not a target image. Furthermore, objects from each category and subordinate class were depicted in various viewing conditions and backgrounds to reduce the probability that subjects would use a small set of low-level features to perform these tasks. Subjects had to indicate via the button box for each trial whether the picture was (i) the within-category target; (ii) an object or (iii) not an object. Targets included Harrison Ford (vs. male faces), pigeon (vs. birds), rose (vs. flowers), jeep (vs. cars), electric guitar (vs. guitars) and barn (vs. houses). Non-target faces included both famous and unfamiliar individuals.

Behavioral data analysis. Behavioral data is summarized in **Supplementary Table 1,** online. Across subjects and categories, there were on average 93 ± 12 (mean ± s.d.) identification hit trials, 120 ± 25 detection hits and 81 ± 15 detection misses, 22 ± 5 false identifications trials, 189 ± 25 correctly detected non-targets and 81 ± 12 detection misses for non-targets.

Behavioral assessment of expertise. Methods and stimuli were identical to those used in a previous study[12]. We measured d' scores for both novices and car experts. For car experts, the average d' score was 2.47 ± 0.23 for car discrimination (expertise required a d' score ≥ 2)[12]. For novice subjects, by contrast, the average d' 1.3 ± 0.5. Car experts' exposure thresholds for identification of cars were shorter than those of novices: car experts were shown images for 33 ms, except for Subject 2, who was shown images for 17 ms. Stimulus exposure duration for novices was either 33 ms or 50 ms. Car experts' behavioral performance in the scanner was similar to novices' (cars: identification hit trials 31 ± 6% of target trials; detection hits: 40 ± 7%; detection misses: 28 ± 6%; d' identification: 0.85 ± 0.1; d' detection: 1.7 ± 0.2; faces: identification hits 30 ± 11%; detection hits: 43 ± 9%; detection misses: 28 ± 6%; d' identification: 0.85 ± 0.1, d' detection: 1.8 ± 0.3). Non-expert performance is given in **Supplementary Table 1** online.

fMRI data analysis. Analysis was done on a voxel-by-voxel basis without any spatial smoothing. All data from a scan were motion-corrected to the first run using the AFNI (afni.nimh.nih.gov) software. A linear trend was removed from each voxel. For rapid event-related experiments, we deconvolved the data using FS-FAST software (surfer.nmr.mgh.harvard.edu) to extract the hemodynamic response in each voxel for each condition and category. The deconvolution was done separately for each subject based on his/her behavioral responses. All other analyses were performed in Brainalyzer, written by K.G.-S. in Matlab (Mathworks). For visualization purposes on the inflated brain (**Fig. 6**), we spatially smoothed the data with a Hanning filter of radius 4 mm and then calculated the statistical maps, which were then projected on the inflated brain.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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