

Expertise for cars and birds recruits brain areas involved in face recognition

Isabel Gauthier^{1,2}, Pawel Skudlarski², John C. Gore² and Adam W. Anderson²

¹ Present Address: Department of Psychology, Vanderbilt University, Wilson Hall, Nashville, Tennessee 37240, USA

² Department of Diagnostic Radiology, Yale University Medical School, Fitkin Basement, 333 Cedar Street, New Haven, Connecticut 06510, USA

Correspondence should be addressed to I.G. (isabel.gauthier@vanderbilt.edu)

Expertise with unfamiliar objects ('greebles') recruits face-selective areas in the fusiform gyrus (FFA) and occipital lobe (OFA). Here we extend this finding to other homogeneous categories. Bird and car experts were tested with functional magnetic resonance imaging during tasks with faces, familiar objects, cars and birds. Homogeneous categories activated the FFA more than familiar objects. Moreover, the right FFA and OFA showed significant expertise effects. An independent behavioral test of expertise predicted relative activation in the right FFA for birds versus cars within each group. The results suggest that level of categorization and expertise, rather than superficial properties of objects, determine the specialization of the FFA.

Face and object recognition differ in at least two ways. First, faces are recognized at a more specific level of categorization (for example, 'Adam') than most objects (for example, 'chair' or 'car'). Second, although we are experts with faces, we have much less experience discriminating among members of other categories. Level of categorization and expertise are relevant even for unfamiliar faces and objects. A person passed on the street may be encoded at the individual level and recognized the next day, whereas a mug may be replaced by another mug without our noticing. Processing biases for different categories depend on our experience with levels of categorization and our expertise in extracting diagnostic features¹.

Viewing faces activates a small extrastriate region called the fusiform face area (FFA)²⁻¹⁰. Neuropsychological studies suggest that the brain areas responsible for face and object processing can be dissociated¹¹⁻¹⁴. According to one view, extrastriate cortex contains a map of visual features¹⁵⁻¹⁶, suggesting that the same region should not be recruited for processing different object categories when the relevant features differ.

On the other hand, prosopagnosia is often associated with deficits discriminating among nonface objects within categories. For example, a bird watcher became unable to identify birds¹⁷, whereas another patient could no longer identify car makes¹⁸. Thus, one hypothesis holds that prosopagnosia is a deficit in evoking a specific context from a stimulus belonging to a class of visually similar objects¹⁹. At least some prosopagnosic patients have difficulty with classes in which objects are both visually and semantically homogeneous^{20,21}. Evidence from brain-lesion studies is still under debate^{13,22}; however, additional data from brain imaging may help resolve these questions.

Several lines of research converge to suggest that level of categorization and expertise account for a large part of the activation difference between faces and objects. First, behavioral effects²³⁻²⁵ once thought unique to faces have been obtained with objects, often with expert subjects²⁶⁻²⁹. Second, nonface objects elicit more

activation in the FFA when matched to specific labels as compared to more categorical ones (for example, 'ketchup bottle' versus 'bottle')^{3,30}. Third, expertise with animal-like unfamiliar objects ('greebles') recruits the right FFA⁴. However, it remains unclear whether expertise with any homogeneous category is capable of recruiting the neural substrate of face recognition.

This experiment had three purposes. First, we tested whether long-term expertise with birds and cars would recruit face-selective areas. Second, the interaction between level of categorization and expertise was investigated. Third, we tested how these two factors depend on attention to stimulus identity. The FFA typically activates more for faces than objects, even during passive viewing⁷. This suggests that faces are processed automatically at the subordinate level. Here we asked whether this is also true for other expertise domains.

RESULTS

We tested 11 car experts and 8 bird experts with many years of experience recognizing car models or bird species (Table 1). The right and left FFA and right occipital face area (OFA) were defined in passive-viewing localizer scans (see Methods). The OFA is also face selective³¹ and active in greeble experts⁴. A right FFA was found in all subjects (median size, 6 voxels), a left FFA was found in 13 subjects (4 bird experts, 9 car experts; median size, 5 voxels) and a right OFA in 15 subjects (7 bird experts, 8 car experts; median size, 7 voxels).

Subjects also underwent identity and location scans. Stimulus presentation was identical in both conditions, and subjects detected immediate (1-back) repetitions in either the identity of the picture or its location while ignoring the other dimension. Blocks of 16 grayscale faces, objects, cars or birds shown sequentially were alternated with periods of fixation (Fig. 1). Pilot experiments indicated that the absence of color cues did not eliminate the advantage of experts over novices. Behavioral data in the scanner was available for 16 of the 19 subjects. Performance was better in the identity

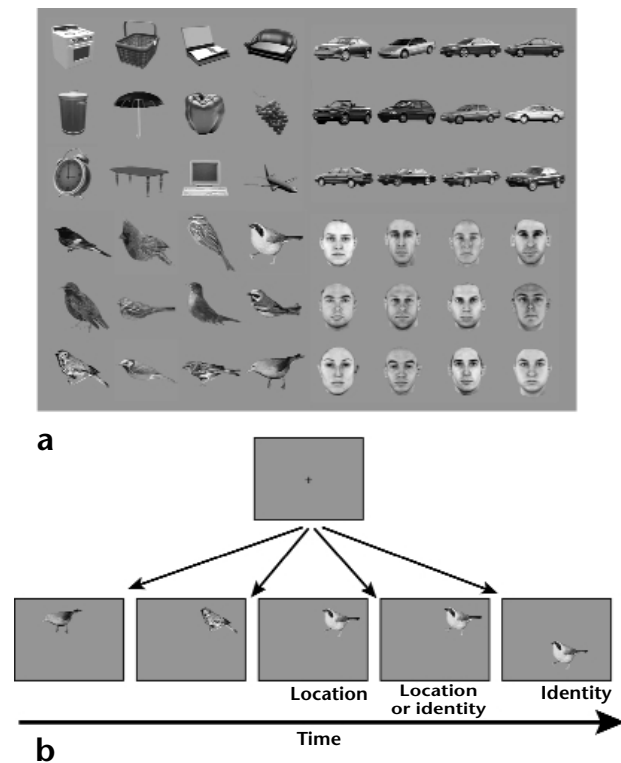


Fig. 1. Examples of stimuli and tasks for the fMRI protocol. (a) Images (256×256 pixels in size, 256 grays) from each of 4 categories (Caucasian faces without hair, passerine birds from New England, car models for the years 1995 and 1998 and various familiar objects) were used in the fMRI study. (b) Example of stimulus presentation during the fMRI runs. Subjects made 1-back repetition judgments regarding either location or identity (an identity repeat would show identical images, although sometimes in different locations—see Methods for details).

than the location runs (identity performance \pm s.e., 89.4 ± 2.1 ; location, 86.0 ± 2.3 ; $F_{1,14} = 9.98$, $p < 0.01$) and this effect was larger for birds and objects than for cars and faces (task \times category interaction, $F_{1,14} = 5.86$, $p < 0.01$). These categories varied more in shape, making location judgments more difficult.

The percent signal changes in the three regions of interest (ROIs) were assessed using a fixation baseline. First, we describe all significant effects pooled across task, coming back to this factor later. The level of categorization effect was measured by comparing activation in novices to cars or birds versus objects. The effect of level of categorization was significant in the right FFA ($F_{1,17} = 14.36$, $p < 0.02$) and in the left FFA ($F_{1,11} = 8.76$, $p = 0.02$). This effect was marginal in the right OFA ($F_{1,13} = 3.67$, $p < 0.08$). The interaction between level and group was significant in both the right FFA ($F_{1,17} = 6.61$, $p < 0.02$) and the left FFA ($F_{1,11} = 6.47$, $p < 0.05$). *Post-hoc* tests ($p < 0.05$) indicated that the level effect was only significant for car experts viewing birds. It may be tempting to believe that birds activate the FFA because of their faces¹⁰. However, the difference between birds and cars for novices was not significant in either area ($p > 0.5$ for both), and the group effect arises from a difference in activity for common objects (larger in birders).

Inspection of Fig. 2 suggests baseline differences between categories and between groups. First, responses to birds were larger than to cars in FFAs of both hemispheres (right, $F_{1,17} = 11.13$, $p < 0.05$; left, $F_{1,11} = 5.47$, $p < 0.05$). Again, although animal faces may activate this area more than objects¹⁰, here we found no difference between cars and birds in novices. Bird experts showed more activation for any object category than car experts, although not significantly in any ROI. Given these baseline trends, it was crucial to measure the effect of expertise by comparing activation for cars and birds in the two groups. The predicted expertise effect was significant (a group \times category interaction) in the right FFA (Figs. 2 and 3; $F_{1,17} = 19.22$, $p < 0.0005$) and in the right OFA ($F_{1,13} = 4.86$, $p < 0.05$). There was no expertise effect in the left FFA ($F < 1$).

One important question is whether this expertise effect arises from the same area as face expertise. To test this, we used a set of criteria (see Methods) based on a definition of face cells in neurophysiology³². This defines a smaller FFA than any other definition to our knowledge (also eliminating the majority of OFA and left FFA ROIs, which were not analyzed further). We call this ROI the center of the FFA (median = 3 voxels), in which each voxel is highly face selective. Even in this ROI, both the level of categorization effect in novices ($F_{1,17} = 6.37$, $p < 0.02$) and the expertise effect were present ($F_{1,17} = 10.25$, $p < 0.006$; Fig. 3). These effects also held when analyzed in a subset of subjects whose FFA could be defined using described criteria^{6,10} (see supplemental material at http://neurosci.nature.com/web_specials/). To assess the magnitude of the expertise effect, we plotted the main effects and interaction separately for the center of the right FFA³³ (Fig. 4). The statistically significant expertise effect contributed a difference of about 0.4% signal change between groups, whereas the group and category main effects contributed about 0.3% and 0.1% signal change, respectively, and were not significant ($F < 1$ for both). Corresponding values in the larger right FFA ROI were 0.2, 0.1 and 0.3, respectively. The expertise effect alone accounted for 32% of the difference between faces and objects in the right FFA defined at $t = 2$ and for 36% in the center of the right FFA.

We measured the center of mass of the signal change for activated voxels for birds, cars and faces (relative to objects). This was done in a ROI of 25×25 voxels (each 1.3 mm by 1.7 mm, $y \times x$ over 3 slices in Talairach space, centered on the right and left FFA from the localizer). The only significant differences for cars or birds relative to faces were obtained in novice subjects

Table 1. Subject information and behavioral results.

	Bird experts	Car experts
Mean age \pm s.e.	34.4 \pm 2.0	31 \pm 2.5
Mean years experience \pm se	18 \pm 3.3	20.6 \pm 3.8
Behavioral data during fMRI		
(% correct identity \pm s.e.; location \pm s.e.)		
Objects	86 \pm 3; 81 \pm 4	93 \pm 3; 88 \pm 3
Faces	85 \pm 3; 82 \pm 3	92 \pm 3; 91 \pm 3
Cars	84 \pm 3; 81 \pm 3	92 \pm 2; 91 \pm 2
Birds	87 \pm 3; 81 \pm 4	92 \pm 3; 89 \pm 3
Behavioral data pre-test ($d' \pm$ s.e.)		
Birds upright	2.53 \pm 0.10	1.06 \pm 0.07
Cars upright	1.41 \pm 0.12	2.42 \pm 0.14
Birds inverted	2.23 \pm 0.20	1.01 \pm 0.09
Cars inverted	0.84 \pm 0.13	1.58 \pm 0.20

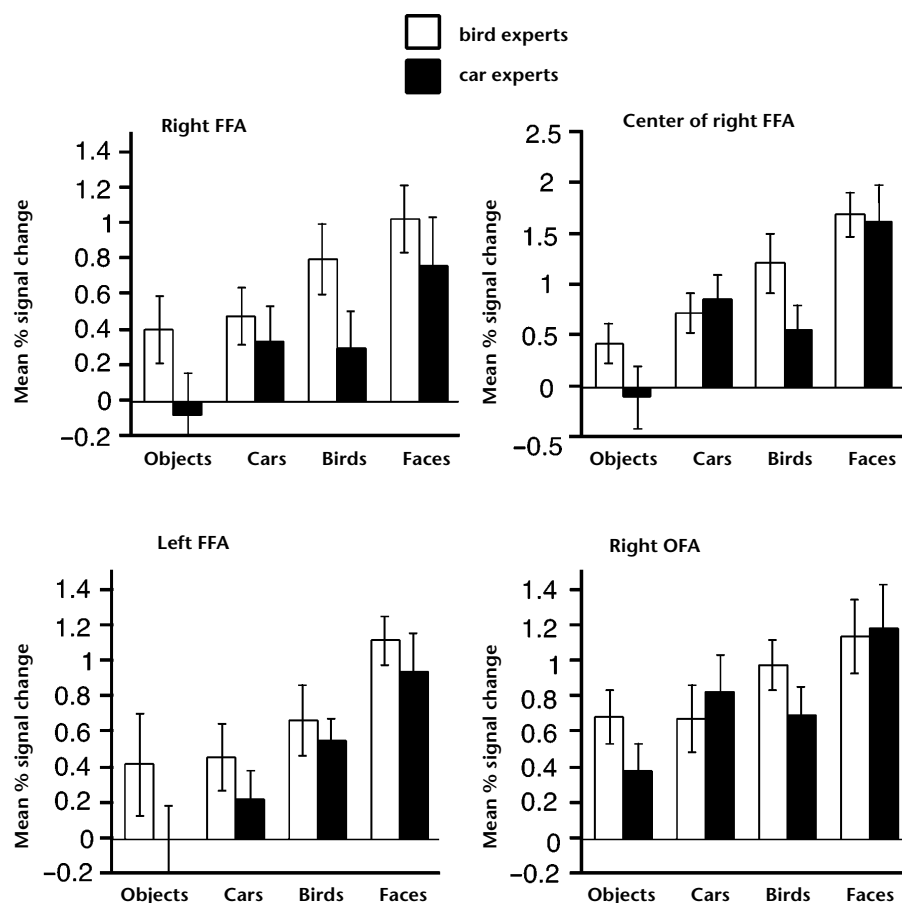


Fig. 2. Mean percent signal change for each object category in the two expert groups in three face-specific ROIs and in the center of the right FFA. The average percent signal increase from fixation for each object category in the different ROIs was averaged across subjects in each ROI for each expert group. Error bars indicate standard error of the mean. The Talairach coordinates for the center of each ROI \pm standard error were right FFA, $x = 38 \pm 2$, $y = -50 \pm 1$, $z = -7 \pm 1$; left FFA, $x = -38 \pm 2$, $y = -56 \pm 4$, $z = -6 \pm 2$; right OFA, $x = 40 \pm 2$, $y = -75 \pm 3$, $z = -3 \pm 1$.

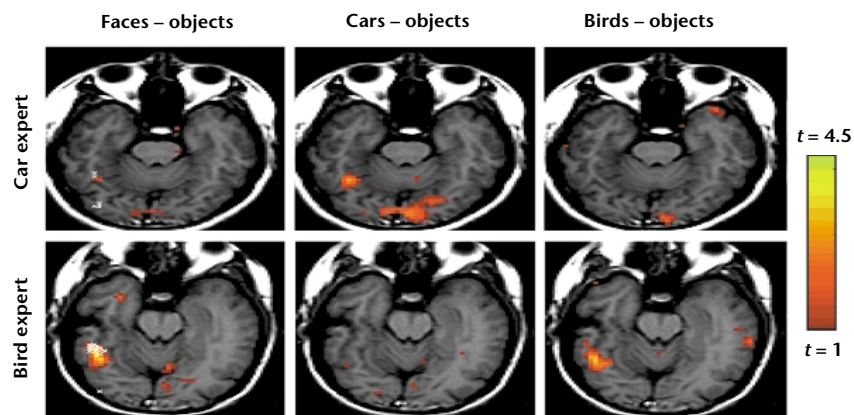
(see Table 2). Center of mass for expert categories was indistinguishable from that obtained for faces (even using a lenient statistical test). We also compared the activation distribution in the right FFA for the three categories by averaging nonspatially smoothed individual maps, centered on the most face-selective voxel in the localizer. This is shown in a 5×5 voxel (each $3.125 \times$

$3.125 \times 7 \text{ mm}^3$) window in Fig. 5. Experts (and to some extent birders viewing cars) showed a distribution of activation for birds and cars that was relatively limited to the localizer peak of the FFA. The mean percent signal change in the center voxel was compared to that in the 8 voxels surrounding it, and to the surrounding 'outside' 16 voxels. An ANOVA (3 regions \times 3 categories \times 2 groups) revealed a main effect of region ($F_{2,22} = 7.18$, $p < 0.004$) with more activity in the center than in both outer regions. Because of greater activity for faces than birds and cars only in the center, the category \times region interaction was marginal ($F_{4,44} = 2.18$, $p < 0.09$), consistent with our other analyses. Crucially, there was no significant difference among the three categories in activity for each of the two surrounding regions, suggesting that activation is as focused for objects as for faces.

As a more direct way of assessing the expertise effect, we measured the correlation between behavioral performance outside the scanner with the signal change in the three ROIs during the location and identity tasks. In the behavioral test, subjects judged whether sequentially presented pairs of birds and cars (upright or inverted) belonged to the same species or car model. The expertise effect was significant

(group \times category interaction; Table 1), bird experts being more sensitive for birds than cars and *vice versa* for car experts ($F_{1,17} = 59.40$, $p < 0.0001$). The effect of orientation and interaction of category with orientation were significant, with the inversion effect stronger for cars than for birds ($F_{1,17} = 14.27$, $p < 0.002$). Both groups were poorer with inverted than upright cars,

Fig. 3. The right FFA shows an expertise effect for birds and cars. One axial oblique slice through the FFA for one expert for each category shows the t -maps obtained when comparing the activation for faces, cars and birds with the activation elicited by objects during the location I-back runs. The voxels marked by white crosses indicate the right FFA and OFA as defined in the passive viewing runs for these two subjects. (In this car expert, the OFA was actually in the slice immediately below and is shown on the same slice as the FFA only to illustrate its in-plane location.) Note that the center of the right FFA may be slightly different depending on the task (here passive viewing versus I-back location) and that its size varies between subjects.



whereas the inversion effect for birds only approached statistical significance in birders ($p = 0.068$).

A group analysis was performed on the fMRI data during all 1-back tasks with cars and birds (see Methods). This less precise analysis allowed us to seek other regions showing an expertise effect regardless of the category, beyond the ones we could define functionally. This showed an area in right ventral temporal cortex that was more activated in experts than novices (Fig. 6). In addition to this stream of activation, going from the right OFA toward the right FFA, a bilateral region in the parahippocampal gyrus was also more active in experts. This area overlaps with the parahippocampal place area (PPA)³⁴, functionally defined as the region responding more to scenes than objects. (It also responds more to objects than faces.) Further work will be required to identify the role of this area in perceptual expertise. The only region more activated in novices than experts was a small bilateral area of the lateral occipital gyrus, superior to the OFA. This area has been found to activate more for letter strings than faces³⁵, and its selective activation for novices could reflect a switch from a featural to a more configural strategy.

In each ROI, we correlated the percent signal change for birds minus cars with relative expertise, the difference in sensitivity (d') for upright birds minus upright cars. As the 2 groups combined would produce a bimodal distribution, the correlation coefficients were calculated for each group separately using our largest homogeneous sample (the 12 subjects scanned with axial slices.) For both groups, relative expertise was positively correlated with relative percent signal change for birds versus cars in the right FFA and only for the location task (car experts, $r = 0.75$; bird experts, $r = 0.82$; $p < 0.05$ for both; Fig. 7).

We also considered task effects beyond that found in the correlation analyses. The only ROI showing a significant influence of task was the right FFA, where this factor interacted with level of categorization ($F_{1,17} = 6.58$, $p < 0.02$): the subordinate-level advantage was larger when novices attended to the identity than to the location of the stimuli. In prior studies^{6,10}, the effect of task in the FFA was

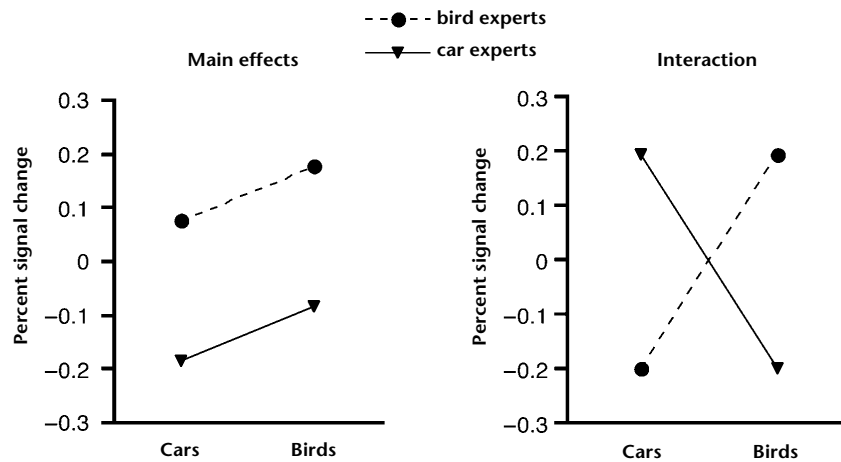


Fig. 4. Main effects with grand mean and interaction partialled out and interaction effect with the grand mean and main effects partialled out, in the center of the right FFA. Each observed condition mean can be reconstructed by adding the value for the main effects and the interaction effect to the grand mean (in this case, 0.845).

small (1-back identity versus passive viewing; but see ref. 36). We also found no effect of task on the advantage of faces over objects in the right FFA ($p > 0.28$), nor on the expertise effect. Expertise may influence how objects are automatically processed, an idea that we come back to in our discussion.

DISCUSSION

Previous studies suggest that level of categorization and expertise contribute to the specialization of the FFA. The present results show how their contributions add up to account for a considerable part of the difference typically found between objects and faces.

In our experiment, experts would know more names for the birds or cars than novices would. However, naming is not likely to account for the effects in the FFA because unfamiliar faces activated this area the most, whereas common objects that are easily named elicited the least activation. In addition, expertise effects for novel objects can be obtained in the FFA for unfamiliar exemplars of a trained category⁴.

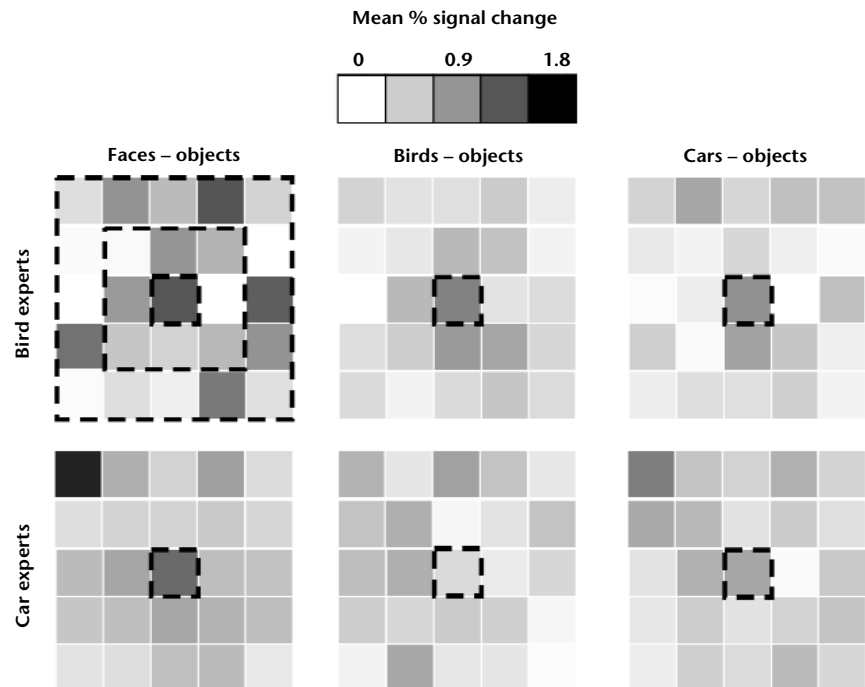
Why would faces recruit the FFA more than expert recognition of objects? There are many possibilities. First, the FFA may be dedicated to face recognition (innately or through experience), although it may mediate the processing of other objects to some extent. At the least, our study demonstrates that an innate bias is unnecessary for objects to recruit this area with expertise. Second, we cannot claim to have equated objects with faces on level of categorization and expertise²². The faces may constitute a more visually homogeneous set than our bird or car images. Faces are recognized as individual exemplars, whereas even experts mainly recognize cars and birds at the model/species level. Although our subjects had years of experience with cars or birds, they still had been practicing face recognition for many more years. Thus, face recognition being in a sense 'more subordinate' and relying on 'greater expertise' may be what make it seem 'special', leaving little contribution for a component of object category *per se*. Additionally, categorization level and expertise may

Table 2. Center of mass coordinates in the middle temporal lobe for category-selective areas, given in Talairach coordinates.

	Left hemisphere			Right hemisphere		
	x	y	z	x	y	z
Bird experts						
Faces	-31.3	-49.8	-7.6	40.8	-48.2	-8.5
Cars	-29.3*	-47.3*	-7.8	39.9	-47.5	-9.0
Birds	-30.8	-49.6	-7.9	40.3	-48.1	-8.3
Car experts						
Faces	-29.0	-48.7	-9.1	38.6	-48.1	-9.1
Cars	-28.9	-49.2	-8.1	38.3	-47.2	-8.5
Birds	-30.5*	-49.8	-7.0	41.2*	-47.8	-8.9

*Value significantly different from the coordinate for faces in the same expert group according to a least significant difference test; $p < 0.05$.

Fig. 5. Spatial distribution of percent signal change for faces, birds and cars (relative to an objects baseline) in a 5×5 voxel window in the right FFA, centered on the most strongly activated voxel in the localizer. Dashed lines indicate the three regions within which activation was averaged for analyses. Note that the highest activation during experimental runs for faces may not be identical to the highest peak in the localizer (consider car experts in the faces – objects condition).



be only two of several factors that determine the specialization of this area. (Other factors may include symmetry, properties of associated semantic knowledge, number of exemplars, value to the perceiver³⁷.)

The effect obtained in the right OFA suggests that expertise may be responsible for specialization of a large part of the face recognition system (at least in the right hemisphere). In the left FFA, we found an effect of level of categorization, with no detectable contribution of expertise. Whereas subordinate-level processing may recruit both hemispheres, here visual expert recognition of homogeneous categories seems to be mainly a right hemisphere process.

Our most striking result may be a very strong correlation between a behavioral test of object expertise and the relative activation in the right FFA for birds and cars. It is remarkable that the expertise of a subject was so accurately predicted from the activation in a small part (six voxels) of the brain, especially as the behavioral and fMRI experiments shared neither a common task nor stimulus set. In addition, this analysis suggests that activation of the right FFA was more directly correlated with expert performance than the right OFA.

There seems to be an important interaction between automaticity of processing at the subordinate level and expertise. It is argued that the preference of the FFA for faces does not depend on the task^{6,10} (but see ref. 35), a claim also supported by our results. However, we found an interaction between level of categorization and task for novices, indicating that, for most people, simply seeing an object among similar exemplars may not prompt complete subordinate-level processing. Automatic subordinate-level processing for experts could also explain a surprising finding: the correlation between behavior and activation in the right FFA was significant only when subjects attended to the location of the objects. During the identity task, subjects had to perform subordinate-level recognition with both categories, regardless of expertise. Novices may

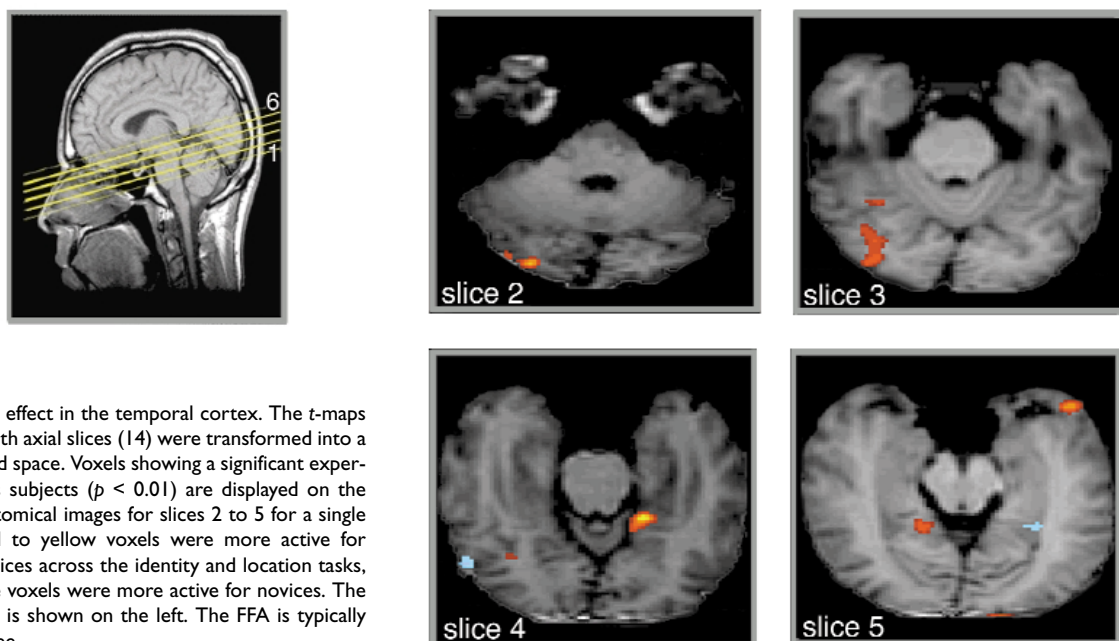


Fig. 6. Expertise effect in the temporal cortex. The t-maps for all subjects with axial slices (14) were transformed into a common standard space. Voxels showing a significant expertise effect across subjects ($p < 0.01$) are displayed on the transformed anatomical images for slices 2 to 5 for a single subject. The red to yellow voxels were more active for experts than novices across the identity and location tasks, whereas the blue voxels were more active for novices. The right hemisphere is shown on the left. The FFA is typically found in slice three.

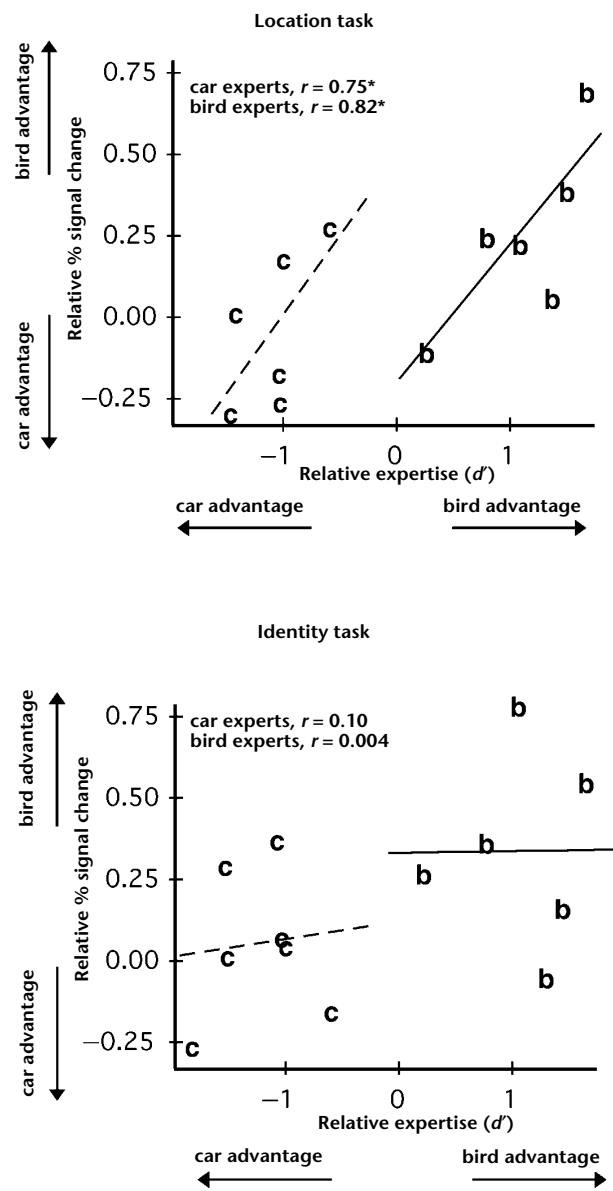


Fig. 7. Relationship between a behavioral measure of expertise and activation in the right FFA. Relative expertise is the sensitivity (d') for bird minus car matching. The dashed and full lines respectively indicate the best linear fits for car and bird experts. Significant correlation coefficients are marked with an asterisk ($p < 0.05$).

then use a featural strategy, whereas experts may use a more configural strategy^{26–28}. Perhaps only configural processing is a good predictor of behavioral expertise. In contrast, during the location task novices may not access the subordinate level, whereas experts did so automatically.

Birds and cars differ in many aspects. (Birds are small animals with moveable parts, covered with feathers that have specific markings; cars are large man-made objects made of metal and typically uniform in texture.) Combined with a previous study showing an expertise effect in the FFA with ‘greebles’⁴, our results suggest very few constraints on the structure of the objects for which expertise can recruit this small area. This is important for any theory of visual representation in the ven-

tral pathway, because it suggests that responses of neurons in extrastriate cortex may not be organized according to the visual features that they detect^{15,16}; rather, their functional organization may depend on the different processes important for object recognition. For instance, some areas may be more suited for featural processing, whereas other areas may support configural and holistic processing, hallmarks of subordinate-level expertise. Our results suggest that expert subordinate-level recognition for any category may be mediated in the same regions, either by virtue of activating common cells or through selectively activating different populations that are intermingled. Other techniques, such as single-cell recording, will be necessary to distinguish between these two alternatives.

METHODS

Subjects. Subjects, all male, included 11 car experts and 8 bird experts. Informed consent was obtained from each subject, and the study was approved by the Human Investigation Committee at the School of Medicine, Yale University. Eight subjects were left handed. Handedness did not correlate with any effect reported here.

Stimuli. One hundred and seventy six images each of passerine birds and cars were obtained from public sources on the world-wide web. Images were converted to 8-bit grayscale 256×256 -pixel format, and objects were isolated and placed on a 50% gray background. Objects were selected to be familiar to our expert population. For each category, 112 images were used in the behavioral test, whereas the remaining 64 objects from each category were used for experimental scans. Faces without hair ($n = 64$, scanned in a 3-D laser scanner, courtesy of Niko Troje and Heinrich Bülhoff, Max Planck Institute, Tübingen, Germany) and 64 images of non-living familiar objects were prepared in the same way as the cars and birds and also used in experimental scans. Localizer scans used 90 grayscale photographs of faces and 90 pictures of familiar objects.

Behavioral task. Each subject performed 10 blocks of 56 sequential matching trials, alternating between blocks showing birds or cars. There were four conditions (upright and inverted cars and birds). Each trial showed two images from the same category and orientation. Upright and inverted trials were randomly intermixed. On each trial, a fixation cross appeared for 500 ms, followed by stimulus 1 for 1000 ms and a pattern mask for 500 ms before stimulus 2 appeared and remained on the screen until a response was made. Subjects judged whether the two images showed birds from the same species or whether cars were from the same model but different years (mostly 1995 versus 1998). No difference was found in mean sensitivity between categories for novices. However, responses to cars were slower than responses to birds for all subjects (RTs for hits with cars, 1138 ms; birds, 1046 ms; $p < 0.05$, suggesting that the cars were more difficult).

fMRI task. Experimental scans consisted of three runs of a one-back location task alternated with three runs of a one-back identity task. The only difference between identity and location runs was instructions to detect immediate repetitions in either location or identity (Fig. 1). Each run lasted 5 min, 36 s and consisted of 16 epochs (16 s each) with 5 fixation periods (16 s each) interleaved at regular intervals. During each epoch, 16 objects appeared, each shown for 725 ms followed by a 275 ms blank. Objects (each $12^\circ \times 12^\circ$) appeared in one of 8 locations within an overall area subtending $18^\circ \times 18^\circ$ of visual angle. The order of the four categories was counterbalanced across runs.

ROI selection. Regions of interests were functionally defined using two localizer scans, which included 16 epochs (16 s each) of passive viewing of faces or common objects centered on the screen (25 pictures per epoch). Each run began with 16 s of fixation, and an 8-s fixation period was included after every 2 passive viewing epochs. The right and left FFA and right OFA were defined as contiguous voxels activated at an arbitrary threshold of $t = 2$ in the middle fusiform gyri (c-d, F-G, 9–10 in Talairach space), and the same threshold was applied in the right ventral occipital lobe (c-d, H-I,

9-10) for the right OFA. The raw data were noisier than when using a higher field scanner and a surface coil^{6,10} so the same level of significance for ROI definitions could not be applied. However, the magnitude and spatial extent of the effect for a given functional area should be similar regardless of statistical power, and we used a criterion leading to ROIs comparable in size to those in published studies^{6,10}. Our FFAs show at least twice as much percent signal change for faces as for objects (each compared to fixation.) To eliminate the influence of less face-selective voxels, we defined the 'center of the right FFA' using criteria more stringent than in any published study. The only voxels selected were found within the cluster of contiguous voxels selected using the less stringent criterion, showed twofold greater percentage signal change for faces as objects (compared with fixation) and, in each subject, did not have less than half the percentage signal change for faces of the voxel showing the maximum signal change for faces.

fMRI imaging parameters and analyses. Most (16) subjects were scanned at the Yale School of Medicine on a 1.5 T GE Signa scanner equipped with resonant gradients (Advanced NMR, Wilmington, Massachusetts) using echo-planar imaging (gradient echo single shot sequence, 168 images per slice, FOV = 40 × 20 cm, matrix = 128 × 64, NEX = 1, TR = 2000 ms, TE = 60 ms, flip angle = 60 ms). Six contiguous 7-mm-thick axial-oblique slices aligned along the longitudinal extent of the fusiform gyrus covered most of the temporal lobe. Some subjects (two car experts and one bird expert) were scanned using coronal-oblique slices. Three more subjects (two car experts and 1 bird expert, I. G. *et al.*, *Soc. Neurosci. Abstr.* 25, 212.9, 1999) were scanned using coronal slices on the 3 T GE scanner at the MGH-NMR Center in Charlestown, Massachusetts. In this case, a custom bilateral surface coil was used to collect 168 images per slice in 12 near-coronal slices, 6 mm-thick. The imaging parameters were TR = 2000 ms, TE = 70 ms, flip angle = 90°, 180 degrees and offset = 25 ms.

Before statistical analysis, images from the 1.5 T scanner were motion corrected for three translation directions and the three possible rotations using SPM-96 software (Wellcome Department of Cognitive Neurology, London, UK). On the 3 T scanner, a bite bar was used to minimize head motion. Maps of *t*-values and percent signal change, both corrected for a linear drift in the signal³⁸, were created. Maps were spatially smoothed using a Gaussian filter with a full-width half-maximum value of two voxels, except for analyses in the center of the right FFA, where regions of interests were very small and no smoothing was performed.

In group composite maps, the percent signal change relative to fixation baseline for both birds and cars was multiplied with contrast weights for each subject (1 and -1 for bird experts and -1 and 1 for car experts). Under the null hypothesis of no expertise effect, the expected value for this contrast was equal to zero. We used a randomization test to assess the statistical significance of percent signal changes. A population distribution for each voxel was generated by calculating randomized mean values (1000 times) of the contrast in which randomly chosen subsets of half the subjects got reversed weights. The observed contrast, calculated without sign reversal, was assigned a *p* value or proportion of times that the observed contrast was more extreme than the randomized contrast). To show the anatomy clearly, the *p* values were overlaid on the normalized anatomical images for a single subject (threshold at *p* < 0.01; Fig. 6).

Note: Additional analysis can be found on the Nature Neuroscience web site (http://neurosci.nature.com/web_specials/).

ACKNOWLEDGEMENTS

We thank Nancy Kanwisher and René Marois for discussions and Jill Moylan, Terry Hickey and Hedy Sarofin for technical assistance. This work was supported by NINDS grant NS33332 to J.C.G. and NIMH grant 56037 to N. Kanwisher. I.G. was supported by NSERC.

RECEIVED 11 AUGUST; ACCEPTED 7 DECEMBER 1999

1. Archambault, A., O'Donnell, C. & Schyns, P. G. Blind to object changes: When learning the same object at different levels of categorization modifies its perception. *Psychol. Sci.* 10, 249–255 (1999).
2. Allison, T. *et al.* Face recognition in human extrastriate cortex. *J. Neurophysiol.* 71, 821–825 (1994).

3. Gauthier, I., Tarr, M. J., Moylan, J., Anderson, A. W. & Gore, J. C. The functionally defined 'face area' is engaged by subordinate-level recognition. *Cognit. Neuropsychol.* (in press).
4. Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P. & Gore, J. C. Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nat. Neurosci.* 2, 568–573 (1999).
5. Haxby, J. V. *et al.* The functional organization of human extrastriate cortex: A PET-RCBF study of selective attention to faces and locations. *J. Neurosci.* 14, 6336–6355 (1994).
6. Kanwisher, N., McDermott, J. & Chun, M. M. The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311 (1997).
7. McCarthy, G., Puce, A., Gore, J. C. & Allison, T. Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* 9, 605–610 (1997).
8. Puce, A., Allison, T., Asgari, M., Gore, J. C. & McCarthy, G. Face-sensitive regions in extrastriate cortex studied by functional MRI. *Neurophysiology* 74, 1192–1199 (1996).
9. Sergent, J., Otha, S. & MacDonald, B. Functional neuroanatomy of face and object processing. *Brain*, 115, 15–36 (1992).
10. Kanwisher, N., Stanley, D. & Harris, A. The fusiform face area is selective for faces not animals. *Neuroreport* 10, 183–187 (1999).
11. Sergent, J. & Signoret, J. L. Varieties of functional deficits in prosopagnosia. *Cereb. Cortex* 2, 375–388 (1992).
12. McNeil, J. E. & Warrington, E. K. Prosopagnosia: A face-specific disorder. *Q. J. Exp. Psychol.* A 46, 1–10 (1993).
13. Moscovitch, M., Winocur, G. & Behrmann, M. What is special in face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *J. Cogn. Neurosci.* 9, 555–604 (1997).
14. Assal, G., Favre, C. & Anderes, J. P. Non-reconnaissance d'animaux familiers chez un paysan. *Rev. Neurol.* 140, 580–584 (1984).
15. Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L. & Haxby, J. Distributed representation of objects in the human ventral visual pathway. *Proc. Natl. Acad. Sci. USA* 96, 9379–9384 (1999).
16. Tanaka, K. Inferotemporal cortex and object vision. *Annu. Rev. Neurosci.* 19, 109–139 (1996).
17. Bornstein, B. in *Problems of Dynamic Neurology* (ed. Halpern, L.) 283–318 (Hadassah Medical Organization, Jerusalem, 1963).
18. Lhermitte, J., Chain, F., Escourole, R., Ducarne, B. & Pillon, B. Étude anatomoclinique d'un cas de prosopagnosie. *Rev. Neurol. (Paris)* 126, 329–346 (1972).
19. Damasio, A. R. & Damasio, H. & Van Hoesen, G. W. Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology* 32, 331–341 (1982).
20. Dixon, M. J., Bub, D. N. & Arguin, M. Semantic and visual determinants of face recognition in a prosopagnosic patient. *J. Cogn. Neurosci.* 10, 362–376 (1998).
21. Riddoch, J. M. & Humphreys, G. W. Visual processing in optic aphasia: A case of semantic access agnosia. *Cognit. Neuropsychol.* 4, 131–186 (1987).
22. Gauthier, I., Behrmann, M. & Tarr, M. J. Can face recognition really be dissociated from object recognition? *J. Cogn. Neurosci.* 11, 349–370 (1999).
23. Yin, R. K. Looking at upside-down faces. *J. Exp. Psychol.* 81, 141–145 (1969).
24. Tanaka, J. W. & Farah, M. J. Parts and wholes in face recognition. *Q. J. Exp. Psychol.* A 46, 225–245 (1993).
25. Farah, M. J., Wilson, K. D., Drain, H. M. & Tanaka, J. W. The inverted face inversion effect in prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms. *Neuropsychologia* 33, 661–674 (1995).
26. Diamond, R. & Carey, S. Why faces are and are not special: An effect of expertise. *J. Exp. Psychol. Gen.* 115, 107–117 (1986).
27. Gauthier, I. & Tarr, M. J. Becoming a 'Greeble' expert: Exploring the face recognition mechanisms. *Vision Res.* 37, 1673–1682 (1997).
28. Gauthier, I., Williams, P., Tarr, M. J. & Tanaka, J. W. Training 'Greeble' experts: A framework for studying expert object recognition processes. *Vision Res.* 38, 2401–2428 (1998).
29. deGelder, B., Bachoud-Lévi, A.-C. & Degos, J.-D. Inversion superiority in visual agnosia may be common to a variety of orientation-polarised objects besides faces. *Vision Res.* 38, 2855–2861 (1998).
30. Gauthier, I., Anderson, A. W., Tarr, M. J., Skudlarski, P. & Gore, J. C. Levels of categorization in visual object recognition studied with functional MRI. *Curr. Biol.* 7, 645–651 (1997).
31. Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B., Marinkovic, K. & Rosen, B. R. Location of human face-selective cortex with respect to retinotopic areas. *Hum. Brain Mapp.* 7, 29–37 (1999).
32. Rolls, E. T. & Baylis, G. C. Size and contrast have only small effects on the response to faces of neurons in the cortex of the superior temporal sulcus of the monkey. *Exp. Brain Res.* 65, 38–48 (1986).
33. Rosnow, R. L. & Rosenthal, R. "Some things you learn aren't so": Cohen's paradox, Asch's Paradigm, and the interpretation of interaction. *Psychol. Sci.* 6, 3–9 (1995).
34. Epstein, R., Harris, A., Stanley, D. & Kanwisher, N. The parahippocampal place area: Recognition, navigation, or encoding? *Neuron* 23, 115–125 (1999).
35. Puce, A., Allison, T., Asgari, M., Gore, J. C. & McCarthy, G. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *J. Neurosci.* 16, 5205–5215 (1996).
36. Wojculik, E., Kanwisher, N. & Driver, J. Modulation of activity in the fusiform face area by covert attention: an fMRI study. *J. Neurophysiol.* 79, 1574–1578 (1998).
37. Tranel, D., Logan, C. G., Frank, R. J. & Damasio, A. R. Explaining category-related effects in the retrieval of conceptual and lexical knowledge for concrete entities: operationalization and analysis of factors. *Neuropsychologia* 35, 1329–1339 (1997).
38. Skudlarski, P., Constable, R. T. & Gore, J. C. ROC analysis of statistical methods used in functional MRI: Individual subjects. *Neuroimage* 9, 311–329 (1999).