

Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects

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Part of the ventral temporal lobe is thought to be critical for face perception, but what determines this specialization remains unknown. We present evidence that expertise recruits the fusiform gyrus 'face area'. Functional magnetic resonance imaging (fMRI) was used to measure changes associated with increasing expertise in brain areas selected for their face preference. Acquisition of expertise with novel objects (greebles) led to increased activation in the right hemisphere face areas for matching of upright greebles as compared to matching inverted greebles. The same areas were also more activated in experts than in novices during passive viewing of greebles. Expertise seems to be one factor that leads to specialization in the face area.

Evidence for specialization in the fusiform gyrus for human face perception comes from both neuroimaging and neuropsychological studies^{1–8}. We explored the possibility that this putative 'face area' may be the result of our extensive experience with faces—a hypothesis that stems from behavioral work on face recognition. Initial studies demonstrated that inversion is more detrimental to the recognition of faces than of objects¹⁰ and that upright faces are recognized more holistically than objects^{11,12}, which led to the suggestion that faces are recognized using specialized visual mechanisms. However, similar behavioral effects have since been obtained with non-face objects for expert subjects (for example, dog show judges or handwriting experts)^{13–16}. Based on such results, we reasoned that the activation in the face area may likewise depend on a subject's expertise with a given object category.

Subjects were trained with novel objects called greebles¹⁴ (Fig. 1) until they were as fast at categorizing such stimuli at the individual level as they were at categorizing them at the more general 'family' level; such a change in performance is considered to be diagnostic of expertise^{14,15,17}. Five adult subjects were scanned using fMRI (see Methods) in an initial session before any exposure to the greebles, at three different times during training and twice after having reached our criterion for Greeble expertise. To isolate expert processing, we compared tasks with upright and inverted images for faces and for greebles. In this comparison, the within-class stimuli are well matched in every perceptual aspect but expertise, which should be specific to the familiar upright orientation^{13,14,18}.

RESULTS

We localized the brain areas more involved in face than object processing by subtracting the activation when subjects passively viewed non-face common objects from that obtained when viewing faces (localizer task⁶). This led to the selection of two 8 × 8 voxel (each voxel, 1.3 × 1.7 mm; see Methods) regions of inter-

est (ROIs) located bilaterally in the middle and the anterior fusiform gyri. These ROIs are consistent with the brain regions previously associated with face processing in multiple studies^{1,2,5–9} (see coordinates in Fig. 2). In each fMRI session, subjects performed sequential-matching judgments in four conditions, with unfamiliar faces and greebles in the upright or inverted orientation. Confirming the initial preference of these ROIs for faces, more upright-specific activation was found for faces than for greebles in both middle and anterior fusiform gyri (with no effect of hemisphere) in the first two scanning sessions (Table 1 and Fig. 2). In addition, this preference for faces over greebles was stronger in the right hemisphere ($F_{1,4} = 10.24$, $p \leq 0.05$).

Our prediction was that expertise training with upright greebles would lead to an increase in activation for upright minus activation for inverted greebles in the face-specific ROIs but no comparable change for faces. The data were combined into three blocks (sessions 1 and 2, 3 and 4, 5 and 6; see Methods). An ANOVA was used to test the prediction that the activation for greebles would increase with training to the level of activation obtained for faces in the average of all sessions (contrast, faces block 1 = faces block 2 = faces block 3 = greebles block 3 > greebles block 2 > greebles block 1).

This prediction contrast was highly significant ($F_{1,4} = 88.9$, $p \leq 0.005$) but also left a significant residual, indicating that the prediction did not account for all of the variance in the omnibus interaction. We also obtained a main effect of hemisphere ($F_{1,4} = 12.97$, $p \leq 0.03$) and an interaction of hemisphere with ROI ($F_{1,4} = 8.15$, $p \leq 0.05$). In the right hemisphere, there was more activation in the middle fusiform gyrus (Scheffé test, $p = 0.05$) but not in the anterior fusiform gyrus. The interaction of the contrast with hemisphere ($F_{1,4} = 8.5$, $p \leq 0.05$) left no significant residual: the predicted pattern was present in the right but not the left hemisphere. Thus, by the end of training, the preference for faces over greebles in right hemisphere face-specific

areas was reduced and no longer statistically significant (Fig. 2). Although there was no ROI interaction (middle/anterior fusiform gyri), the expertise effect was most dramatic in the right middle fusiform gyrus, where the difference between faces and greebles was reduced sevenfold. The finding that the activation for upright minus inverted faces did not increase (and in fact decreased, although not significantly) in this area confirms that the expertise effect for greebles is not due to a general practice effect, which should be common to both categories of stimuli. When activation was compared to a fixation baseline in the right middle fusiform gyrus, there was no significant change with training for faces but significantly more activation for upright greebles in the last training block than in earlier blocks (both $t_4 > 3$, $p \leq 0.05$).

A two-dimensional correlation map (see Methods) was used to measure the similarity of the spatial distributions of activation, independent of their position in the image. This analysis was conducted to test whether the expertise effect with greebles reflected mostly a change in magnitude or in location.

The activation map for upright minus inverted sequential-matching was compared to the activation map for faces minus objects (viewed passively) in a 16×16 voxel ROIs (each voxel 3.125×3.125 mm). In this case, the interaction of the predicted contrast with hemisphere did not reach significance ($F_{1,4} = 5.25$, $p = 0.084$), but was in the same direction with a stronger expertise effect in the right hemisphere ROIs. Again, despite the absence of an interaction with ROI, the expertise effect seems somewhat stronger in the right middle fusiform gyrus. Planned comparisons confirmed that the only significant difference between sessions in any of the ROIs for the two tasks occurred for greebles in the right middle fusiform gyrus: the upright-specific activation for greebles in this ROI was more strongly correlated with the localizer task (faces minus objects) in Sessions 5–6 than in Sessions 1–2 ($t_4 = 2.8$, $p \leq 0.05$). Moreover, in the 5th session, the distance between the upright-specific activations for greebles and faces in this ROI was not reliably different from 0 mm. This pattern suggests an increase in the magnitude of activation in the face area

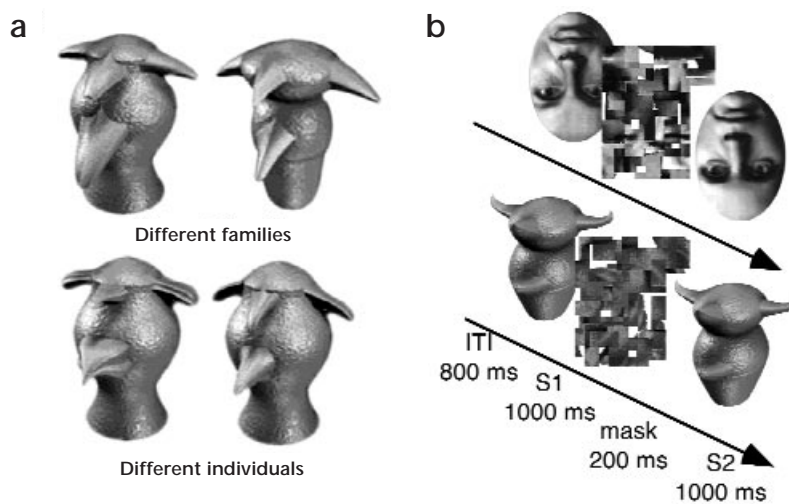


Fig. 1. Greebles and sample trials from the sequential-matching task. (a) Two greebles from different 'families', as defined by the shape of the large central part, as well as two individual greebles from the same family, differing only in the shape of the smaller parts. (b) Design of sample trials in the sequential-matching task used in the fMRI experiments. Stimuli were presented for 1 s, separated by a brief (200 ms) pattern mask to prevent matching from retinal persistence.

with expertise for greebles, rather than the displacement of activation for greebles within the 16×16 voxel ROI.

To test whether the orientation by expertise interaction obtained could be due to better performance in the sequential-matching task, we analyzed the accuracy of the five subjects in this task during the first five sessions. (Mean values are given in Fig. 3.) Subjects made no more than 13% errors in the sequential-matching task for any of the conditions or at any point in the experiment. A session by category by orientation ANOVA revealed a significant effect of session ($F_{4,16} = 3.12$, $p = 0.045$) and a statistically marginal interaction of category and orientation ($F_{1,4} = 7.04$, $p = 0.057$). Faces led to a stronger inversion effect than greebles, and subjects got faster with training in all conditions. Crucially, the session by category by orientation interaction, which could be confounded with the expertise effect obtained in the face area, was not significant ($F_{4,16} < 1$). Note that the sequential-matching task used in the scanner was not meant to be sensitive to expertise (because we wanted to avoid a

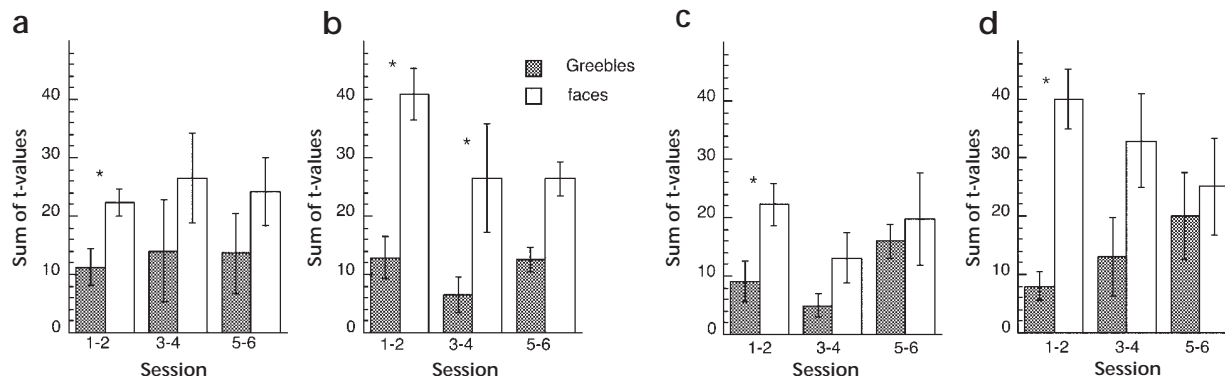


Fig. 2. Training effect for faces and greebles in four face-specific ROIs. The t -values were summed in each ROI in the upright minus inverted sequential matching comparison. Average Talairach coordinates of the center of the ROI for the five subjects, with standard error: (a) left anterior fusiform gyrus, $x = -43 \pm 3$, $y = -17 \pm 4$, $z = -29 \pm 3$; (b) right anterior fusiform gyrus, $x = 41 \pm 5$, $y = -16 \pm 4$, $z = -30 \pm 2$; (c) left middle fusiform gyrus, $x = -40 \pm 3$, $y = -46 \pm 4$, $z = -12 \pm 1$; (d) right middle fusiform gyrus, $x = 41 \pm 2$, $y = -51 \pm 4$, $z = -12 \pm 1$. * $p \leq 0.01$, paired t -tests for faces versus greebles.

Table 1. Mean Talairach coordinates for our middle fusiform gyri ROIs and other activations in the middle fusiform gyri in a few selected studies.

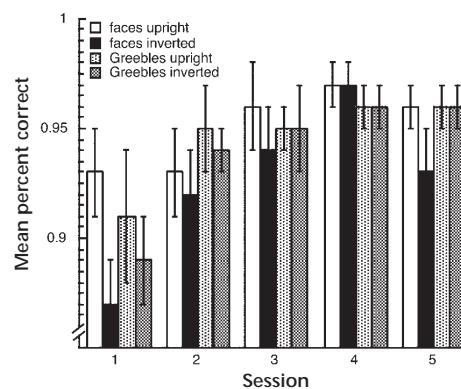
Study	Comparisons	Right/ left	Anterior/ posterior	Superior/ inferior
Present study	Passive viewing faces – objects	41 –40	–55 –46	–10 –12
Kanwisher <i>et al.</i> (1997)	Passive viewing faces – objects	40 –35	–55 –63	–10 –10
Dolan <i>et al.</i> (1997)	Passive viewing (learning-dependent effect specific to faces but not objects) with two-tone images	44	–38	–28
Malach <i>et al.</i> (1995)	Object detection (versus textures)	42	–73	–18
Stern <i>et al.</i> (1996)	Picture encoding (novel – repeated)	35	–38	–15
Wagner <i>et al.</i> (1998)	Words (semantic – nonsemantic task)	–37	–58	–9
	Words, semantic task, subsequently remembered – forgotten	–43	–55	–9
Corbetta <i>et al.</i> (1991)	Selective – divided attention for shape	–45	–51	–12

potential confound from performance effects alone and because expertise is thought to recruit the fusiform gyrus face area automatically during face processing and therefore should also do so for greebles). The behavioral results confirm that the sequential-matching task was sufficiently easy to be performed quite well even by novices. Therefore, a simple difference in task performance cannot account for our fMRI results. Moreover, we have multiple sources of evidence that our subjects' expertise with greebles increased dramatically during the experiment, as we monitored performance during training, and subjects were also tested in a series of behavioral tasks measuring their configural processing of unfamiliar greebles (I.G. & M.J.T., unpublished data). First, their mean response time for recognizing individual greebles during the training decreased from 1150 ms to 450 ms by the end of the training. Second, they demonstrated a decrease in the basic-level advantage, an effect that is diagnostic of real-world expertise¹⁷. Specifically, novices recognized greebles at the family level significantly faster (a difference of 200 ms) than at the individual level, whereas, by the end of the training, expert subjects were as fast at both levels (450 ms for both levels of categorization). Third, as in previous studies, expertise led subjects to process greebles in a more configural fashion^{14,15}. For instance, experts were more sensitive than novices to changes in the configuration of the Greeble parts. This suggests that the expertise by orientation interaction obtained in the face-selective region of the middle fusiform gyrus with greebles is most likely due to a qualitative change in subjects' processing of greebles, in particular, configural processing of the type typically obtained with faces^{11–13}.

As another test of a greeble expertise effect, six greeble experts (the same subjects as in the previous section plus the first author) were compared with six novices in a passive-viewing task using greebles, faces and common objects. Experts, but not novices, engaged the face-selective region of the middle fusiform gyri for greebles as well as for faces (Fig. 4). An analysis on the sum of *t*-values in the middle fusiform gyri ROI yielded a significant group by category interaction ($F_{1,10} = 5.31$, $p \leq 0.05$), with no effect or interaction for hemisphere. However, using this dependent variable, novices showed more activation than experts in the middle fusiform gyri when passively viewing faces (novices, 78.4 ± 12 s.e.; experts, 29 ± 9) but there was no difference for greebles (novices, 12.1 ± 5 ; experts, 12.7 ± 4). The difference for faces in greeble novices cannot be attributed to practice because we used both

groups' pre-training passive-viewing data for faces. This difference can therefore only reflect a spurious effect of subject selection (for instance, the novice subjects may just happen to have larger face areas on average). However, a different dependent measure (the maximum *t*-value in the ROI), which did not show this bias for faces, also revealed the predicted interaction ($F_{1,10} = 5.31$, $p \leq 0.05$). There was comparable activation for faces between the groups (novices, 2.6 ± 0.22 ; experts, 2.2 ± 0.28) but more activation for greebles in experts (novices, 0.96 ± 0.18 ; experts,

1.61 ± 0.14). There was no expertise effect in the anterior fusiform gyri but a significant interaction of group by category ($F_{1,10} = 10.6$, $p \leq 0.01$) was obtained in the lateral occipital gyrus, which was more activated by greebles in experts than novices, with the following maximum *t*-values for faces (novices, 2.0 ± 0.19 ; experts, 1.5 ± 0.19) and greebles (novices, 1.5 ± 0.22 ; experts, 1.9 ± 0.14). The Talairach coordinates¹⁹ for the center of our average lateral occipital gyrus activation were $x = 48$, $y = -72$, $z = -6$ on the right and $x = -43$, $y = -78$, $z = -4$ on the left. These coordinates correspond to BA19 and are similar to the lateral occipital complex described in several studies^{20–22}. The lateral occipital gyrus area is unlikely to have a role similar to that of fusiform areas in expertise, because it shows inverted-specific activation for both faces and greebles during sequential matching. This area has been activated in studies comparing objects or faces to stimuli lacking an obvious shape interpretation (for example, scrambled features or textures)^{21,22}. A variety of visual cues (motion, texture or luminance) can also activate this region as long as they define an object²⁰. The typical interpretation of such results is that lateral occipital complex is involved in the bottom-up analysis of shape. Our orientation and expertise effects extend this interpretation, suggesting that this area may also be implicated in top-down processing. Note that this area may also be involved in mental rotation tasks²³, possibly explaining its activation with inverted stimuli in our sequential-matching tasks.

**Fig. 3.** Mean percent correct during the sequential matching tasks with faces and greebles, upright and inverted.

DISCUSSION

Our results have important implications for interpreting the role of the fusiform 'face area' in visual object recognition. First, our experiments indicate that an inversion effect can be obtained for faces in face-specific areas, and that a similar inversion effect can be produced for novel objects after expertise training. A previous study²⁴ found little evidence for an inversion effect in the right middle fusiform gyrus 'face area' for grayscale faces but a larger effect with two-tone faces. The authors suggested that the 'face area' may be involved simply in the detection, but not in the identification of faces (because detection is very difficult for inverted two-tone faces, but note that recognition is therefore directly compromised). In contrast, our results suggest that the face selective region of the fusiform is implicated in recognition at the individual level because training at this level led to an expertise effect. This account converges with behavioral work associating the inversion effect with expertise for recognition at the individual level^{26,27}. It is also more consistent with the syndrome of prosopagnosia, in which face recognition deficits follow lesions in the ventral temporal lobe; prosopagnosic patients typically have no difficulty detecting faces but cannot recognize them at the individual level^{26,27}.

Second, the results from two independent tasks reveal that activation in face-specific areas can increase with expertise for novel objects. In a recent review article²⁸, it was suggested that such a finding would negate any role for a face-specific area as evidence for a 'special' face processing system. Specifically, we found that when upright grebbles were compared to inverted grebbles, an effect was obtained in the right hemisphere 'face areas', which was larger in the right middle fusiform gyrus. Using passive viewing of grebbles versus objects, the effect was stronger in the middle fusiform gyri than anterior fusiform gyri ROIs with no difference between hemispheres. Left hemisphere middle and anterior fusiform gyri 'face areas' have been reported^{1,2,5-9}, but they have been less thoroughly studied than the right middle fusiform gyrus area. (The left areas typically show effects of a smaller magnitude than the right areas, and the anterior fusiform gyrus is not imaged in fMRI studies using a surface coil.)

Our data converge most strongly to show an expertise effect in the right middle fusiform gyrus. Comparison of mean Talairach coordinates for our middle fusiform gyri 'face area' with activations found in a few selected studies (Table 1) shows that our middle fusiform gyri activation is most similar to previously described 'face areas'⁶, as well as an area activated by selective attention to shape in a PET study. The fusiform gyrus has been associated with encoding of pictures²⁹ and words (left hemisphere only)³⁰. In particular, the latter study showed activation in the left middle fusiform gyrus for a semantic minus a non-semantic task with words. We should note that it is very unlikely that our expertise effect is due to experts naming the grebbles more than novices because they were scanned with unfamiliar grebbles in each session, and the grebbles used during a single session were all from the same family, making family names non-diagnostic. There is evidence for simple learning effects in the fusiform gyrus^{31,32} in a region that falls about halfway between our middle fusiform gyri and anterior fusiform gyri ROIs (no coordinates available for ref. 32). In one study³¹, a two-tone image of a face

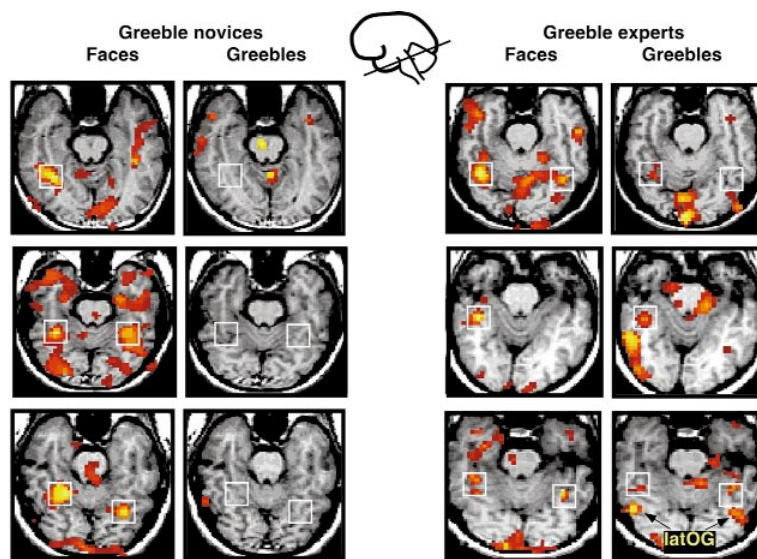


Fig. 4. Activation maps for three novices and three experts in the passive-viewing tasks with faces and grebbles. A baseline of passive viewing of objects is used in both conditions, and only the voxels showing more activation for faces or grebbles than objects are shown. Images are thresholded at an arbitrary value of $t = 0.75$. Note that we do not attribute any statistical meaning to individual subjects' t -values. The statistical significance of the effects is determined by their representation in the group sample. White squares, middle fusiform gyri ROI; arrows, lateral occipital gyrus foci for one expert (bottom right).

was only perceived as a face after presentation of a grayscale version of the same stimuli, leading to increased activation in the fusiform gyrus. In the other study³², a similar area was activated as a result of a previous study episode, when subjects made object decisions about structurally coherent (but not structurally incoherent) objects. Note that these learning effects are obtained following a single brief presentation of an image and are specific to particular exemplars of a category (that is, increased activation occurring only for the actual pictures seen but not for similar ones that are unfamiliar). In contrast, the expertise effect that we describe requires hours of intensive training and is not specific to particular exemplars because the grebbles presented during the fMRI sessions were unfamiliar and different from those used during the training procedure. The expertise effect may therefore be the signature of a different mechanism, sufficiently long-term and general to produce category preferences in the visual cortex.

Expertise is not the only factor that is thought to contribute to the specialization of the middle fusiform gyri for face processing. Faces are recognized most often at a very specific (or subordinate) level (for example, Bob versus Jim), whereas objects are typically recognized in a less specific manner, another important difference between face and object recognition. Even when objects are selected from a single category³³ or when subjects are required to discriminate between visually similar objects⁶, more activation is found for faces than objects in this area. Although this suggests that categorization level is not the only factor that determines specialization of the middle fusiform gyri, it does not preclude some role for this factor. In two studies^{34,35}, we found evidence that recognizing non-face familiar objects at a more specific level (for example, pelican rather than bird) leads to activation in the face-selective part of the middle fusiform gyri. When we compared the activation for passive viewing of faces minus objects to that of specific non-face object recognition, the acti-

vation for faces was comparable in magnitude and fell within that for specific-object recognition, but was also much more focused³⁵. It is therefore possible that level of categorization accounts for a coarse specialization in the middle fusiform gyri and that expertise with subordinate-level recognition tasks builds on this, leading to further specialization and to more focused activation. The interaction between these two factors needs to be investigated further.

Finally, an important question is what in the process of the acquisition of expertise leads to the recruitment of the putative 'face area'. We believe that the best hypothesis can be found in the behavioral literature on face and configural processing. In the last 10 years, multiple studies^{13–16,18,25} have provided evidence that configural processing is what makes face recognition different from object recognition, and that those effects are due to our expertise with faces. Our own results suggest that subjects shifted from feature-based to more configural processing as they became greeble experts (I.G. & M.J.T., unpublished data; refs. 14, 15). The range of stimuli (both more and less face-like than greebles) and the type of expertise that can recruit putatively face-specific areas should be investigated in future studies. It may be found to be very general, as suggested by the behavioral literature on expertise, or it may be more restricted. The strongest interpretation suggested by our results together with previous work^{13–16,18,25} is that the face-selective area in the middle fusiform gyrus may be most appropriately described as a general substrate for subordinate-level discrimination that can be fine-tuned by experience with any object category.

METHODS

Subjects. Five subjects (three females, two males) participated in the training procedure and were scanned in repeated fMRI sessions. These subjects were also scanned as experts in the passive-viewing tasks. Seven additional subjects (three females, four males) were scanned only in the passive-viewing tasks, six as novices and the first author as an expert. Informed consent was obtained from all subjects, and the study was approved by the Human Investigations Committee at the School of Medicine, Yale University.

Expertise training. Subjects were trained to categorize 30 8-bit grayscale greebles at the 'family' and 'individual' levels until they were as fast in making both types of judgments (approximately 7 hours over at least 4 days). The training included several tasks^{14,15}, but performance was assessed in name-verification trials, during which subjects judged whether a label (family or individual) shown for 1000 ms matched a greeble presented 200 ms later.

Stimuli and fMRI tasks. In each fMRI session, subjects performed sequential matching with faces and greebles in upright or inverted orientations (Fig. 1). There were eight sequential-matching runs per session, four with greebles and four with faces, in alternation. (Session 2 for one subject was lost due to equipment malfunction.) Five stimulus sets, each including eight grayscale faces and eight greebles of the same family (not used during training) were used in sequential-matching tasks (order of sets counterbalanced across subjects). The faces (obtained from Niko Troje and Heinrich Bülthoff, Max Planck Institute, Tübingen, Germany), scanned in a three-dimensional-laser scanner, were all cropped in the same oval shape. Session six did not include a sequential-matching task with faces. Each run included 3 repetitions of an ACBC cycle where A and B were sequential-matching epochs of 24 s showing upright or inverted stimuli (order counterbalanced in different runs) and C was 12 s of fixation of a cross. Each epoch included eight trials and showed pairs of stimuli all upright or inverted. Pictures were repeated 12 times per session, but all pairs of stimuli were unique. Subjects performed same/different identity judgments by pressing one of two buttons. Face versus object passive viewing was used as a localizer task and was performed at least twice for each subject (most often the first and fifth sessions, but some subjects were scanned

in this task up to four times, to assess within-subject replicability, which was very good). Runs were similar to those used for sequential matching, except that A and B epochs consisted of a stream of faces or familiar objects (90 objects in each category; stimulus onset asynchrony, 267 ms). Expert and novice subjects performed a passive-viewing task with greebles and objects, using 50 greebles (distractor greebles used in the training and greebles used in sequential matching) and 50 of the same familiar objects were shown in an ACBC design (where C is fixation).

ROI selection. When the results for all localizer tasks were averaged together for each subject, two 'face-specific' activations in each hemisphere (middle fusiform gyri and anterior fusiform gyri) could be identified. These ROIs varied in location between subjects but were always posterior (middle fusiform gyri) and anterior (anterior fusiform gyri) to the cerebral aqueduct. Eight-by-eight voxel ROIs were centered on the activation peak in the middle fusiform gyri and anterior fusiform gyri, in each individual localizer task (passive viewing for faces minus objects), as well as in the upright minus inverted sequential-matching activation maps for faces in each session. These ROIs were defined in standardized space, in which each voxel is about 1.3 mm (*y*) by 1.7 mm (*x*). For the analysis on sequential matching, the face sequential-matching ROIs were used except for session six, in which the face sequential matching task was not performed. The face area was not expected to move between sessions (and there was no evidence that it did), but a reference present in each session eliminated any error due to registration between sessions. For passive viewing comparisons, the ROIs from the localizer were used. Talairach coordinates for middle fusiform gyri and anterior fusiform gyri ROIs were measured for one localizer session for each subject (Fig. 2). For passive viewing, an additional ROI (lateral occipital gyrus) was defined individually in the greebles-minus-objects comparison, because it showed salient activation in most experts viewing greebles.

fMRI imaging parameters and analyses. Imaging was performed on a 1.5 T GE Signa MRI scanner equipped with resonant gradients (Advanced NMR, Wilmington, Massachusetts) using echo planar imaging (gradient echo single shot sequence, 144 images per slice, FOV = 40 × 20 cm, matrix = 128 × 64, NEX = 1, TR = 1500 ms, TE = 60 ms, flip angle = 60°). Six contiguous seven-mm-thick axial-oblique slices aligned along the longitudinal extent of the fusiform gyrus covered most of the temporal lobe. Motion was corrected using the SPM 96 software (Wellcome Department of Cognitive Neurology, London, UK). Maps of *t*-values were created for each comparison and corrected for a linear drift in the signal. The *t*-maps were superimposed on T1-weighted anatomical images of the corresponding slice. Anatomical landmarks were defined in T1-weighted axial-oblique and midline sagittal images, and the brains were transformed in 12 subvolumes to register the results for each subject in a common coordinate system. To assess the changes in the magnitude of activation in the sequential-matching task, *t*-values over a low threshold (*t* = 0.1) were summed in an 8 × 8 voxel box centered on each ROI. Because session two was missing for one subject, and session six did not include a sequential matching task with faces, sessions were combined within three session-blocks (1–2, 3–4, 5–6).

In addition, the Pearson product moment coefficient of correlation of two activation maps was calculated as a function of the shift in two dimensions of one map relative to the other, within ROIs (approximately 16 × 16 pixels, each pixel 3.125 × 3.125 mm) centered on the localizer activation peaks. This was done for upright-specific sequential-matching activations for each category (greebles and faces) with the localizer (faces minus objects). The correlation coefficients with all localizers obtained were averaged in each session and for each subject (therefore, the different number of localizers for each subject did not matter). The maximum correlation was used as a measure of similarity in shape between an upright minus inverted activation and the face area from the localizer. The location of the maximum coefficient in the correlation map was used to measure the displacement of the activation focus in one task relative to another.

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1. Allison, T. *et al.* Face recognition in human extrastriate cortex. *J. Neurophysiol.* **71**, 821–825 (1994).
2. 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).
3. Damasio, A. R., Damasio, H. & Van Hoesen, G. W. Prosopagnosia: anatomical basis and behavioral mechanisms. *Neurology* **32**, 331–341 (1982).
4. Damasio, A. R., Tranel, D. & Damasio, H. Face agnosia and the neural substrates of memory. *Annu. Rev. Neurosci.* **13**, 89–109 (1990).
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**, 6336–6353 (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. Puce, A., Allison, T., Spencer, S. S., Spencer, D. D. & McCarthy, G. Comparisons of cortical activation evoked by faces by intracranial field potentials and functional MRI: two case studies. *Hum. Brain Mapp.* **5**, 298–305 (1997).
8. Puce, A., Allison, T., Gore, J. C., & McCarthy, G. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *Neurophysiology* **74**, 1192–1199 (1995).
9. Sergent, J., Otha, S. & MacDonald, B. Functional neuroanatomy of face and object processing. *Brain* **115**, 15–36 (1992).
10. Yin, R. K. Looking at upside-down faces. *J. Exp. Psychol.* **81**, 141–145 (1969).
11. Tanaka, J. W. & Farah, M. J. Parts and wholes in face recognition. *Q. J. Exp. Psychol.* **A46**, 225–245 (1993).
12. Tanaka, J. W. & Sengco, J. A. Features and their configuration in face recognition. *Mem. Cognit.* **25**, 583–592 (1997).
13. Diamond, R. & Carey, S. Why faces are and are not special: an effect of expertise. *J. Exp. Psychol. Gen.* **115**, 107–117 (1986).
14. Gauthier, I. & Tarr, M. J. Becoming a “greeble” expert: exploring the face recognition mechanisms. *Vision Res.* **37**, 1673–1682 (1997).
15. 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).
16. Bruyer, R. & Crispeels, G. Expertise in person recognition. *Bull. Psychonomic Soc.* **30**, 501–504 (1992).
17. Tanaka, J. W. & Taylor, M. Object categories and expertise: is the basic level in the eye of the beholder? *Cog. Psychol.* **23**, 457–482 (1991).
18. Rhodes, G. & Tremewan, T. Understanding face recognition: caricature effects, inversion, and the homogeneity problem. *Visual Cognit.* **1**, 275–311 (1994).
19. Talairach, J. & Tournoux, P. *Co-Planar Stereotaxic Atlas of the Human Brain. 3-Dimensional Proportional System: An Approach to Cerebral Imaging* (Thieme, Stuttgart, 1988).
20. Grill-Spector, K., Kushnir, T., Edelman, S., Itzhackz, Y. & Malach, R. Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron* **21**, 191–202 (1998).
21. Kanwisher, N., Woods, R. P., Iacoboni, M. & Mazziot, J. C. A locus in human extrastriate cortex for visual shape analysis. *J. Cognit. Neurosci.* **9**, 133–142 (1997).
22. Malach, R. *et al.* Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc. Natl. Acad. Sci. USA* **18**, 8135–8139 (1995).
23. Cohen, M. S. *et al.* Changes in cortical activity during mental rotation: A mapping study using functional MRI. *Brain* **8**, 89–100 (1996).
24. Kanwisher, N., Tong, F. & Nakayama, K. The effects of face inversion on the human fusiform face area. *Cognition* **B68**, 1–11 (1998).
25. Rhodes, G., Tan, S., Brake, S. & Taylor, K. Expertise and configural coding in face recognition. *Br. J. Psychol.* **80**, 313–331 (1989).
26. Tranel, D., Damasio, A. R. & Damasio, H. Intact recognition of facial expression, gender and age in patients with impaired recognition of face identity. *Neurology* **38**, 690–696 (1988).
27. Schweich, M. & Bruyer, R. Heterogeneity in the cognitive manifestations of prosopagnosia: The study of a group of single cases. *Cognit. Neuropsychol.* **10**, 529–547 (1993).
28. Tovée, M. J. Is face processing special? *Neuron* **21**, 1239–1242 (1998).
29. Stern, C.E. *et al.* The hippocampal formation participates in novel picture encoding: evidence from functional magnetic resonance imaging. *Proc. Natl. Acad. Sci. USA* **93**, 8660–8665 (1996).
30. Wagner, A. D. *et al.* Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science* **281**, 1188–1191 (1998).
31. Dolan, R. J. How the brain learns to see objects and faces in an impoverished context. *Nature* **389**, 596–599 (1997).
32. Schacter, D.L. *et al.* Brain regions associated with retrieval of structurally coherent visual information. *Nature* **376**, 587–590 (1995).
33. McCarthy, Puce, A., Gore, J. C. & Allison, T. Face-specific processing in the fusiform gyrus. *J. Cognit. Neurosci.* **9**, 605–610 (1997).
34. 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).
35. 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).