

Revisiting the Role of the Fusiform Face Area in Visual Expertise

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It has previously been reported (Gauthier *et al.*, 2000, *Nat. Neurosci.*, 3:191-197) in a functional magnetic resonance imaging (fMRI) study that objects of visual expertise (cars and birds) activate the right fusiform face area (FFA) more strongly than non-expertise stimuli, and it was argued that the right FFA is involved in expertise specific rather than face specific visual processing. This expertise effect, however, may be due to experts taking advantage of the 'faceness' of the stimuli: birds have faces and three-quarter frontal views of cars resemble faces. This expertise effect may also be caused by a biased attentional modulation: with a blocked fMRI design, experts may attend more to a block of expertise than a block of non-expertise stimuli. In this study, using both side-view car images that do not resemble faces and bird images in an event-related fMRI design that minimizes attentional modulation, an expertise effect in the right FFA is observed in both car and bird experts (although a baseline bias makes the bird expertise effect less reliable). These results are consistent with those of Gauthier *et al.*, and suggest the involvement of the right FFA in processing non-face expertise visual stimuli.

Keywords: face perception, FFA, fMRI, learning, visual expertise

Introduction

Consistent with prior patient research on prosopagnosia (e.g. Sergent and Signoret, 1992; McNeil and Warrington, 1993), in functional magnetic resonance imaging (fMRI) studies a cortical region in the fusiform gyrus called the fusiform face area (FFA) has been shown to respond much more strongly to faces than to any other class of stimulus (Sergent, *et al.*, 1992; Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997). These findings have led to the hypothesis that the FFA contains specialized mechanisms for face processing. Researchers currently disagree, however, on whether the mechanisms involved in face processing are dedicated to face processing only — the Face Specificity Hypothesis — or whether they are also involved in the processing of any class of visual stimuli that share the same basic configuration and for which the observer has gained substantial visual expertise — the Expertise Hypothesis (e.g. Kanwisher, 2000; Tarr and Gauthier, 2000; Bentin and Carmel, 2002; McKone and Kanwisher, 2005; for an excellent review of this debate, see Liu and Chaudhuri, 2003).

Behavioral studies have shown that visual expertise for a particular class of visual stimulus can generate performance similar to that observed in face perception. For example, similar to the finding that face recognition is better for right-side up than upside-down faces (the inversion effect), dog show judges exhibited worse performance in recognition of dog pictures presented and tested upside down than right-side up (Diamond and Carey, 1986). Likewise, in a series of behavioral studies

conducted by Gauthier and colleagues (Gauthier and Tarr, 1997, 2002; Gauthier *et al.*, 1998), after extensive training on a novel class of objects called 'greebles'—photorealistically-rendered 3D objects that all share a common configuration—observers showed behavioral profiles similar to those obtained with faces. Recent developments in brain imaging techniques provided researchers with tools to investigate the neural mechanisms involved in expertise stimulus processing and new ways to address the expertise debate. In an fMRI study, Gauthier *et al.* (2000) measured responses to car and bird stimuli in car and bird experts while these experts carried out an identity matching task and a location matching task. Gauthier *et al.* (2000) observed higher fMRI activation in the right FFA and the right occipital face area (OFA) of bird and car experts viewing stimuli within their domains of expertise than outside their domains of expertise. Moreover, it was found that the level of behavioral expertise significantly correlated with the strength of the fMRI expertise response only in the right FFA when participants performed the location matching task. In another fMRI study, Gauthier *et al.* (1999) reported that after extensive training with 'greebles', observers showed a higher fMRI response in the right FFA for matching upright than inverted 'greebles'. In addition, experts showed a higher fMRI response in both FFAs to passively viewed 'greebles' than novices. These results are consistent with the Expertise Hypothesis and suggest that the same neural mechanisms may be involved in the processing of both faces and non-face expertise visual stimuli.

There were, however, a number of drawbacks in the fMRI expertise studies. First, Gauthier *et al.* (1999, 2000) used stimuli that contained face parts or face-like parts in a face-like symmetrical arrangement: Gauthier *et al.* (2000) used birds, which have faces with easily identifiable eyes and mouth, and three-quarter frontal views of cars, which could be argued to resemble faces (with the symmetrical headlights of a car being eyes as depicted in various cartoon drawings); and Gauthier *et al.* (1999) used greebles which share structure similarity with faces [their key distinguishing features consist of two horizontally displaced parts arranged symmetrically above two vertically displaced parts in a facelike configuration' (Kanwisher, 2000)]. Showing an expertise effect with 'facelike' stimuli can simply reflect the ability of face mechanisms to be recruited for facelike stimuli after training; it does not provide strong support for the Expertise Hypothesis, which asks whether face mechanisms can be recruited for the processing of non-facelike stimuli after acquisition of visual expertise (Kanwisher, 2000). Second, Gauthier *et al.* (1999, 2000) used a blocked fMRI design. In this design, trials of the same type (e.g. cars) were presented in the same block which allowed participants to anticipate the kind of images that would be presented next. For

example, in Gauthier *et al.* (2000), car experts might find cars to be more interesting to look at than birds, and vice versa for bird experts. Non-face objects have been shown to activate the face areas, although the activations are much smaller than those for faces (e.g. Kanwisher, *et al.*, 1999; Haxby *et al.*, 2001). It is therefore possible that even if expertise does not modulate FFA responses, different amount of attentional modulation (Wojciulik *et al.*, 1998) would result in a higher FFA response to expertise than non-expertise objects. As such, the use of face-like stimuli and possible attentional confound challenge the validity of the expertise effects reported by Gauthier *et al.* (1999, 2000).

More recently, an fMRI study by Grill-Spector *et al.* (2004) reported that while FFA activation was correlated on a trial-by-trial basis with both detection and identification of specific faces, it was not correlated with detection and identification of cars in car experts. A closer examination of Grill-Spector *et al.* (2004) shows that while car experts were asked to identify specific faces (e.g. Harrison Ford among distractor faces), they were not asked to perform the equivalent task on car identification (e.g. a BMW among other sedans). Rather, they were asked to distinguish between two categories of vehicles (jeeps from cars). Because identifying jeeps from cars did not require expertise in cars (even non-car experts could perform the task quite well), the study by Grill-Spector *et al.* may have not tapped into the mechanisms specific to expertise processing in the FFA. Grill-Spector *et al.* (2004) also reported that the FFA did not respond to the car images at all in the car experts (fig. 5 of Grill-Spector *et al.*, 2004), which was different from what was found by Gauthier *et al.* (2000), and therefore argued against a car expertise effect in the FFA. However, because the overall FFA response in Grill-Spector *et al.* (2004) was quite low due to masking, response to cars in the FFA, if it existed and if it was scaled according to the face response, would have been very close to the noise level of the signal. It is therefore not surprising that a car expertise effect in terms of a higher response amplitude was not observed by Grill-Spector *et al.* (2004). Overall, the null finding by Grill-Spector *et al.* does not argue against the expertise hypothesis in the FFA.

Given the unique approach fMRI studies provides and the weaknesses of the existing fMRI studies in addressing the expertise debate, it would be important to replicate the expertise effect in Gauthier *et al.* (2000) with images that do not resemble faces and with a paradigm that reduces the influence of attention. In order to do so, in the present study, the following two manipulations were adopted: First, to reduce the resemblance of non-face expertise stimuli to a face, side view car images were used. Although front and three-quarter views of cars may resemble faces due the arrangement of the headlights, side views of cars share much less similarity with face profiles. Second, to reduce the influence of attention, an event-related fMRI design was used in which trials containing different images were pseudorandomly presented and thus preventing observers from anticipating the content of the next image. To match the original study by Gauthier *et al.* (2000), both car and bird experts and both car and bird images were included in the study. Because birds have faces and Gauthier *et al.* (2000) showed that the overall activations in the face areas were higher for birds than for cars or objects, it is likely that the perception of birds naturally recruits face areas even before an observer becomes a bird expert. This makes it difficult to objectively evaluate the role of the face areas in bird expertise.

As such, while results from car and bird experts viewing bird stimuli were included, the main focus of the present study is on whether a car expertise effect could be observed in the right FFA in the car experts.

The present study used the 'region of interest' (ROI) approach. With this approach, in an independent localizer, the right and the left FFAs were first identified as the ROIs in each observer. The amplitudes of the fMRI response in these ROIs were then measured in the event-related scan when observers viewed faces, birds, cars, and objects.

Materials and Methods

Participants

Six car experts (five right-handed and one left-handed) and six bird experts (five right-handed and one left-handed), all males, having normal or correct to normal vision, were recruited and paid for participating in the experiment. Informed consent was obtained from all subjects and the study was approved both by Massachusetts Institute of Technology Committee on the Use of Humans as Experimental Subjects and by Massachusetts General Hospital (MGH) Committee on the Use of Humans as Experimental Subjects.

The car experts were recruited from the BMW Club of Boston. The bird experts were recruited from the bird clubs in the Boston area. All participants took a car and bird behavioral discrimination test to quantify their expertise in cars or birds (Gauthier *et al.*, 2000). To increase the likelihood of finding an expertise effect in the present study, only participants whose behavioral expertise performance matched the averaged behavioral expertise level in Gauthier *et al.* (2000) or higher were included in the study. One car expert (right-handed) was excluded from the analyses because a right FFA could not be found in his fMRI scan and one bird expert (right-handed) was also excluded because he did not pass the behavioral expertise test. Results of the behavioral expertise test from the five car experts and five bird experts included in the study are shown in Table 1. Car experts were significantly better than bird experts in the car-matching test [$F(1,8) = 18.63$, $P = 0.003$], and the reverse was true for the bird-matching test [$F(1,8) = 70.40$, $P < 0.001$]. The interaction between car/bird behavioral test results and expert groups was also significant [$F(1,8) = 116.48$, $P < 0.001$].

Design and Procedure

Localizer Scan

The design of the localizer scan was based on Kanwisher *et al.* (1997); see also Kourtzi and Kanwisher (2000, 2001). Grayscale photographs of front view faces, side view cars, side view birds, and canonical view objects were presented. All images were cutouts on a white background and were presented within a 300 × 300 pixel area. There were 21 × 16 s blocks within a scan, including 16 stimulus blocks and five fixation blocks, with the fixation blocks interleaved between every four stimulus blocks. Of the 16 stimulus blocks, there were four blocks of faces, four blocks of objects, two blocks of cars, two blocks of birds and four blocks of other images that were not analyzed further for the purpose of the present study. Each stimulus block contained 20 exemplars from the same stimulus category. Each exemplar was presented for 300 ms followed by a 500 ms blank interval. During the scan, to engage participants' attention on the stimuli, they were asked to press a response button whenever an immediate repetition of the same image occurred. There were two repetitions within a stimulus block and all other images presented in a given block were unique. To balance for

Table 1
Information of the participants in the present study

Experts	<i>n</i>	Age (SE)	Years of expertise	Car matching <i>d'</i> (SE)	Bird matching <i>d'</i> (SE)
Car experts	5	29.2 (3.5)	21.8 (2.5)	3.22 (0.31)	0.75 (0.13)
Bird experts	5	41.8 (5.7)	33.0 (5.2)	1.52 (0.25)	3.16 (0.26)

the presentation order of the different stimulus blocks within a scan, two versions of the localizer scan were used, with the second version consisting of the second half of the first version followed by the first half of the first version. Each version of the localizer scan was run twice on each participant. Thus a total of four localizer scans were run on each participant. Each localizer scan lasted 5 min and 36 s.

Event-related Scan

For the event-related scans, grayscale photographs of front-view faces, side-view cars, birds of different views, and canonical view objects were presented. None of the images used in the event-related scan appeared in the localizer scan. All images were cutouts on a white background and were presented within a 459×459 pixel area. There were a total of 125 event-related trials in a scan, with 25 trials for each stimulus condition and 25 fixation trials. Twenty-five different exemplars were used for each stimulus condition and thus a given exemplar was never repeated in a scan.

Each image was surrounded by a black frame centered on the image, and was presented either slightly above or below the center fixation dot. To engage the participants' attention on the display during the experiment, they were asked to judge the location of each image with respect to the fixation dot by pressing one of two response buttons. In fixation trials, the display was just an empty black frame and participants were asked to judge the location of the black frame with respect to the fixation dot. This procedure ensured that the task was identical for all five display conditions (four stimulus conditions and a fixation condition).

As in previous studies (Kourtzi and Kanwisher, 2000, 2001), the order of presentation for trials from the different display conditions were counterbalanced such that trials from each display condition were preceded and followed equally often by trials from each of the other display conditions for two trials back and two trials forward. To further balance for order effects, five different versions of the event-related scans were created by rotating the serial position of items from each display condition (e.g. in version 2, the face stimuli took the positions of the car stimuli in version 1 and the car stimuli took the positions of the bird stimuli in version 1, so on and so forth). Each participant was scanned with all five versions of the event-related scans with the order of the five versions rotated among the participants.

There was an 18 s fixation period at the beginning of the scan, followed by two filler trials (to counterbalance for the trial orders and were not included in the analysis), 125×3 s event-related single trials and a 21 s fixation period at the end of the scan. Each trial contained a 200 ms of stimulus presentation followed by a 2800 ms of blank fixation. Each scan lasted 7 min.

MRI Acquisition

fMRI data were acquired using a Siemens Allegra 3T Head-only MRI scanner at the Massachusetts General Hospital -Nuclear Magnetic Resonance Imaging (MGH-NMRI) Center in Charlestown, MA. Gradient echo pulse sequences with T_R s of 2.0 and 1.5 s were used for the localizer scans and the event-related scans, respectively. Fifteen near coronal slices parallel to the brain stem were collected with a head coil. There was 0 mm distance between the slices, and the thickness of the slices was either 4 or 5 mm, depending on the head size of the participant. The in-plane resolution was 3.125×3.125 mm. One hundred and sixty-eight functional images were collected for each localizer scan and 280 functional images were collected for each event-related scan.

Data Analysis

All data acquired were motion corrected using the fs-fast software developed at the MGH-NMRI center. Data were averaged over the four localizer scans in each participant before the right and the left FFAs were identified in the fusiform gyrus of each participant with the criterion that the difference between the face and the object activation was significant at $P < 0.0001$ on a Kolmogorov-Smirnov test (uncorrected for multiple spatial hypothesis). Using these areas as independent ROIs, in each participant, data collected in the event-related scans were extracted and averaged from all the voxels within the ROIs. In each event-related scan, the hemodynamic responses of the 25 trials for each display condition at each of the 10 corresponding time points

(total of 15 s) were then averaged. These event-related time courses were subsequently converted to percent signal change for each of the four stimulus conditions by subtracting the corresponding value for the fixation trials and then dividing by that value. The resulting time course for each stimulus condition was then averaged across the five scans for each participant and then averaged across participants (Kourtzi and Kanwisher, 2000, 2001).

Results

A right and a left FFAs were identified in all 10 participants using the localizer scan. Overall, the right FFA was significantly bigger than the left FFA [$F(1,8) = 21.15, P = 0.002$], and the FFAs were bigger (marginally significant) in the bird than in the car experts [$F(1,8) = 3.31, P = 0.11$]. There was also a marginally significant interaction between expert group and the sizes of the FFAs [$F(1,8) = 3.94, P = 0.082$] such that the differences in size between the left and the right FFAs were bigger in the bird than in the car experts.

The amplitudes of the fMRI responses in the right and the left FFAs in the event-related scans while participants viewed faces, birds, cars and objects are reported below as percent fMRI signal changes compared to the fixation condition. The statistical tests were performed at the peaks of the fMRI responses, which occurred at 4.5 s after stimulus onset.

Response in the Right FFA

Results from the event-related scans are plotted in Figure 1. Overall, responses were higher for faces than for birds [$F(1,8) = 27.44, P = 0.001$], higher for birds than for cars [$F(1,8) = 49.18, P < 0.001$] and higher for cars than for objects [$F(1,8) = 6.73, P = 0.03$]. In addition, stimulus conditions interacted significantly with expert group [$F(3,24) = 4.23, P = 0.016$].

While the response for objects was well matched between the two expert groups ($F \ll 1$ for the differences between the two), the response for faces was slightly higher in the car than in the bird experts [although not significant; $F(1,8) = 1.81, P = 0.22$]. In fact, the difference between face and object responses was significantly smaller in the bird than in the car experts [$F(1,8) = 8.40, P = 0.02$]. This indicates that response saturation made higher activations to be more compressed in the bird than in the car experts.

Comparing Responses between Bird and Car Stimuli

The difference in response amplitude between bird and car stimuli was significant for both the car experts [$F(1,4) = 8.67, P = 0.042$] and the bird experts [$F(1,4) = 51.59, P = 0.002$]. There was also a significant interaction between car/bird stimuli and expert group [$F(1,8) = 7.07, P = 0.029$], showing a bigger difference between these two stimulus condition in the bird than in the car experts and thus indicating a strong expertise effect in these two groups of experts. Note that the expertise effect was observed despite the fact that bird response might be somewhat compressed in the bird experts.

Gauthier *et al.* (2000) reported a significant correlation between percent fMRI signal change for bird minus car and relative behavioral expertise (behavioral bird expertise d' minus behavioral car expertise d') in both the car and the bird experts. This correlation, however, was not observed in the present study: for the car experts, $r = 0.41, F < 1$, and for the bird experts (in the opposite direction as predicted by the expertise hypothesis), $r = -0.91, F(1,3) = 14.18, P = 0.033$. It is possible that with an event-related design, there was more variance in

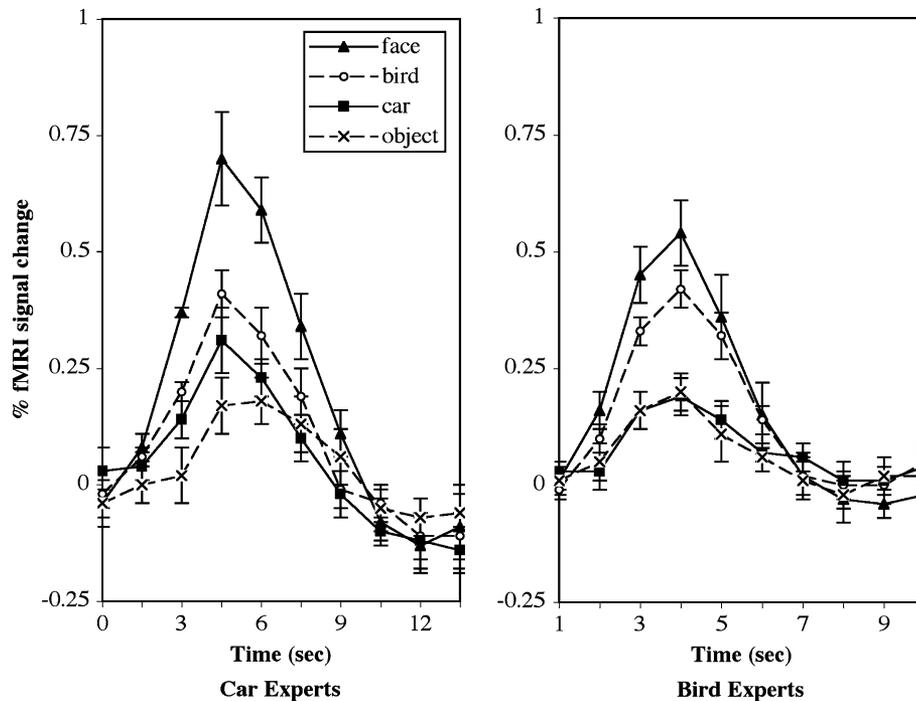


Figure 1. fMRI percent signal change compared to fixation in the right FFA. Expertise effects were found in the interaction of car/bird stimuli and expert group, the interaction of car/object stimuli and expert group, and the interaction of face/bird stimuli and expert group (although baseline differences made the last interaction — a bird expertise effect — less reliable).

the data, especially with a small sample size of five. When data from both expert groups were combined, there was indeed a marginally significant correlation between fMRI signal difference and behavioral expertise difference for bird minus car, $r = 0.62$, $F(1,8) = 5.03$, $P = 0.055$, consistent with the expertise hypothesis (for this reason, all correlations presented below were performed over all the participants). This correlation is plotted in Figure 2A.

Comparing Responses between Car and Object Stimuli

The difference in response between car and object stimuli was significant in the car experts [$F(1,4) = 23.81$, $P = 0.008$] but not in the bird experts ($F \ll 1$), and the interaction between car/object stimuli and expert group was significant [$F(1,8) = 9.34$, $P = 0.016$]. Moreover, the correlation between behavioral car expertise d' and fMRI percent signal change for cars minus objects was marginally significant [$r = 0.61$, $F(1,8) = 4.70$, $P = 0.062$], showing that as expertise in cars increased, the differences in activation between cars and objects also increased (Fig. 2B). These results were therefore consistent with a car expertise effect. Note that the expertise effect observed in the car experts was not due to the difference between car and object response being more compressed in the bird than in the car experts, because in the bird experts, responses to cars and objects were virtually identical to each other and identical to the object response in the car experts.

Comparing Responses between Other Stimulus Categories

Because higher responses were more compressed in the bird than in the car experts, the differences between bird minus object, face minus car, and face minus bird were all smaller in the bird experts than it ought to be if response saturation was well matched between the two expert groups. This made the comparison between bird and object, face and car, and face and

bird unreliable in term of assessing a car and a bird expertise effects. Nonetheless, when these comparisons were carried out, although we failed to observe a bird expertise effect in the bird and object comparison and a car expertise effect in the car and face comparison, we did observe a significant bird expertise effect in the bird and face comparison: the difference in response between bird and face stimuli was significant in the car experts [$F(1,4) = 40.83$, $P = 0.003$] but not in the bird experts [$F(1,4) = 3.58$, $P = 0.13$], and the interaction between bird/face stimuli and expert group was significant [$F(1,8) = 9.34$, $P = 0.016$], showing a smaller difference between responses to faces and birds in the bird than in the car experts. Moreover, the correlation between behavioral bird expertise d' and fMRI percent signal change for face minus bird was significant [$r = -0.74$, $F(1,8) = 9.50$, $P = 0.015$], showing that as expertise in birds increased, the differences in activation between faces and birds decreased (Fig. 2C). Although these results suggested a bird expertise effect, it should be interpreted with caution: because higher responses were more compressed in the bird than in the car experts, we were biased in finding a bird expertise effect.

Overall, results from the right FFA showed a strong expertise effect as indicated by a significant interaction between responses to car/bird stimulus and the expert group. When examined alone, a significant car expertise effect was also found. Although differences in response saturation between the two expert groups prevented the bird expertise effect from being objectively assessed, we did find evidence consistent with a bird expertise effect as well.

Response in the Left FFA

Results of the event-related scans are plotted in Figure 3. Overall, response was higher for faces than for birds [$F(1,8) = 108.67$,

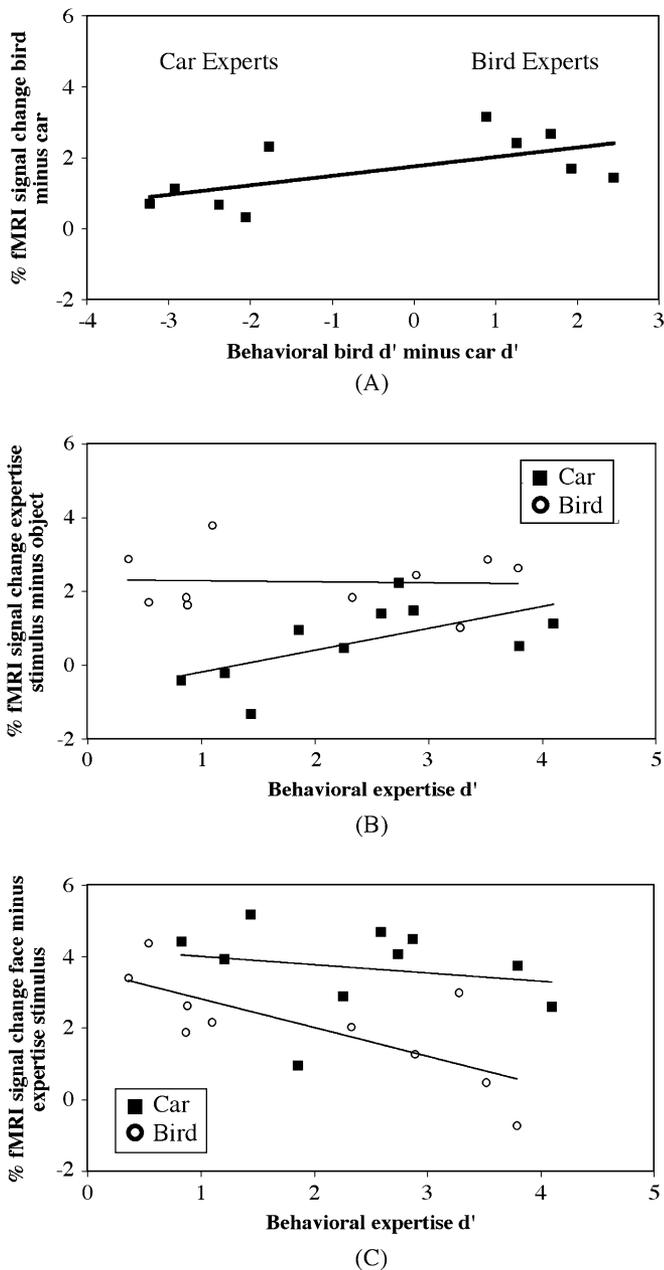


Figure 2. Correlations between fMRI signals in the right FFA and behavioral expertise. (A) The correlation between fMRI bird minus car and behavioral bird d' minus car d' ; (B) the correlation between fMRI expertise stimulus minus object and behavioral expertise d' ; and (C) the correlation between fMRI face minus expertise stimulus and behavioral expertise d' . The correlation between fMRI bird minus car and behavioral bird d' minus car d' and the correlation between fMRI car minus object and behavioral car d' were marginally significant. The correlation between fMRI face minus bird and behavioral bird d' was significant. These results are consistent with there being a car and a bird expertise effects in the right FFA.

$P < 0.001$], higher for birds than for cars [marginally significant, $F(1,8) = 4.06$, $P = 0.08$] and higher for cars than for objects [marginally significant, $F(1,8) = 3.66$, $P = 0.09$]. The overall interaction of stimulus category and expert group was not significant [$F(3,24) = 1.312$, $P = 0.29$].

Response for objects did not differ significantly between the two groups of experts ($F < 1$), and response for faces did not differ either ($F < 1$). Although the difference between face

minus object was somewhat smaller in the bird than in the car experts, it was not significant [$F(1,8) = 2.71$, $P = 0.14$].

Comparing Responses between Bird and Car Stimuli

The difference in response between bird and car stimuli was not significant in neither the car experts, $F(1,4) = 1.37$, $P = 0.31$, nor the bird experts, $F(1,4) = 3.15$, $P = 0.15$. The interaction between car/bird stimuli and expert group was far from being significant, $F < 1$. The correlation between fMRI signal difference and behavioral expertise difference for bird minus car was not significant either, $r = 0.22$, $F < 1$. These results indicated the absence of an expertise effect. The correlation results are plotted in Figure 4A.

Comparing Responses between Expertise and Object Stimuli

The difference in response between car and object stimuli was marginally significant in the car experts [$F(1,4) = 4.47$, $P = 0.10$] but not significant in the bird experts ($F < 1$). The interaction of car/object stimuli and expert group was not significant ($F < 1$). The correlation between behavioral car expertise d' and fMRI percent signal change for cars minus objects was not significant either [$r = 0.46$, $F(1,8) = 2.10$, $P = 0.19$].

The difference in response between bird and object stimuli was marginally significant in car experts [$F(1,4) = 5.85$, $P = 0.073$] and significant in bird experts [$F(1,4) = 19.334$, $P = 0.012$]. The interaction between bird/object stimuli and expert group, however, was not significant ($F < 1$). The correlation between behavioral bird expertise d' and fMRI percent signal change for bird minus objects was not significant either ($r = 0.01$, $F < 1$). The correlation results are plotted in Figure 4B.

Comparing Responses between Expertise and Face Stimuli

The difference in response between car and face stimuli was significant in both car experts [$F(1,4) = 59.72$, $P = 0.002$] and bird experts [$F(1,4) = 17.18$, $P = 0.014$]. The interaction of car/face stimuli and expert group, however, was not significant [$F(1,8) = 1.14$, $P = 0.32$]. The correlation between behavioral car expertise d' and fMRI percent signal change for face minus cars was not significant either ($r = 0.15$, $F < 1$).

The difference in response between bird and face stimuli was significant in both car experts [$F(1,4) = 75.74$, $P = 0.001$] and bird experts [$F(1,4) = 36.01$, $P = 0.004$]. The interaction of bird/face stimuli and expert group was marginally significant [$F(1,8) = 4.27$, $P = 0.073$]. The correlation between behavioral bird expertise d' and fMRI percent signal change for face minus bird, however, was not significant [$r = -0.42$, $F(1,8) = 1.70$, $P = 0.23$]. The correlation results are plotted in Figure 4B.

Overall, results from the left FFA did not show a strong expertise effect in neither cars nor birds.

Three-way Interactions of Stimulus, Expert Group and ROI

For all 10 participants, although the three-way interaction of car/bird stimuli, the left and the right FFAs, and the expert groups was not significant [$F(1,8) = 1.37$, $P = 0.28$], it was consistent with there being a stronger expertise effect in the right than in the left FFA. The same pattern of result was also observed in the three-way interaction of car/object stimuli,

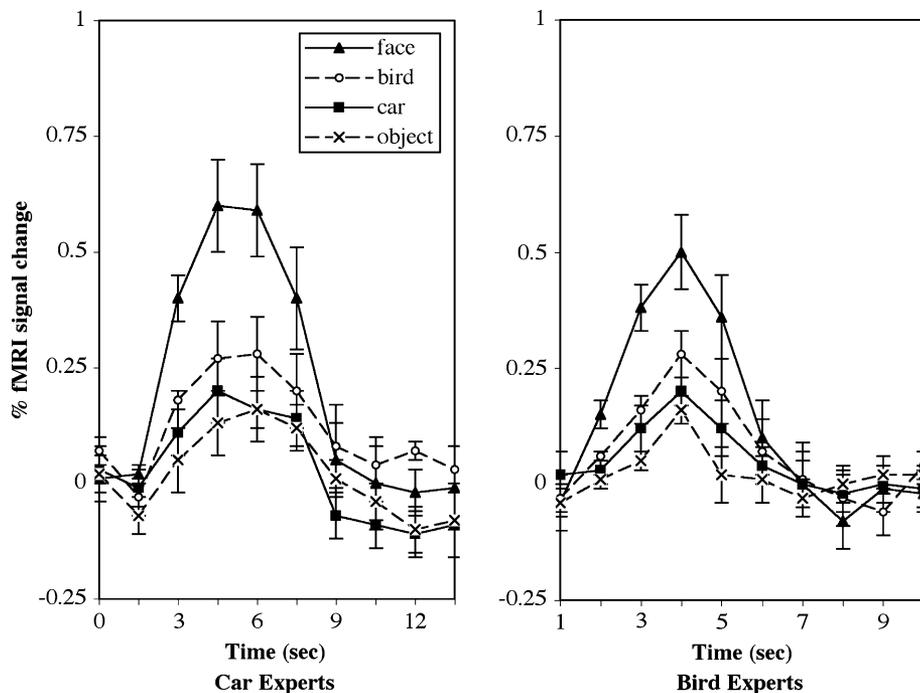


Figure 3. fMRI percent signal change compared to fixation in the left FFA. No strong expertise effect was found here.

the left and right FFAs, and the expert groups [$F(1,8) = 1.87$, $P = 0.21$].

Responses in Other Fusiform Areas

In the localizer scans, following the procedures used to identify the right and the left FFAs, the criteria that the difference between car (or bird) and object activation was significant at $P < 0.0001$ on a Kolmogorov-Smirnov test was used to identify possible fusiform 'car' and 'bird' areas in the experts. A right fusiform 'car' area was found in four car experts and two bird experts, and a left fusiform 'car' area was found in two car experts and one bird expert. Likewise, a right fusiform 'bird' area was found in three car experts and four bird experts, and a left fusiform 'bird' area was found in two car experts and four bird experts. Overall, the 'car' areas were bigger than the 'bird' areas in the car experts [marginally significant, $F(1,8) = 4.18$, $P = 0.075$] and the reverse was true in the 'bird' experts (although not significant, $F < 1$), and the interaction between the sizes of the car and bird areas and expert groups was marginally significant [$F(1,8) = 3.17$, $P = 0.11$]. This result indicated that more brain areas were activated during expertise than non-expertise visual processing. Regarding the amount of overlaps between the 'car' areas and the FFAs and between the 'bird' areas and the FFAs, there were big between subject differences and no clear pattern could be extracted at this point.

Discussion

Gauthier *et al.* (2000) reported in their fMRI study that objects of visual expertise (cars and birds) activated the right FFA more strongly than non-expertise stimuli. They also found a correlation between the level of behavioral expertise and the strength of fMRI signal to the expertise stimuli in the right FFA in a location matching test. In the present study, using an event-related fMRI design that minimized the influence of attention and side-view car images that did not resemble faces, an fMRI

expertise effect was found in the right FFA for car experts performing a location judgement test. In addition, a marginally significant correlation ($p < 0.07$) was found between behavioral car expertise and fMRI signal to car stimuli in the right FFA. Although birds have faces (and thus bird perception may naturally recruit face areas) and differences in fMRI response saturation between the two expert groups prevented the bird expertise effect from being assessed objectively, evidence consistent with a bird expertise effect was found as well. Overall, these results are consistent with those of Gauthier *et al.* and suggest that the same neural mechanisms may be involved in the processing of both faces and non-face expertise visual stimuli.

One may argue that because both a car and a bird expertise effect was found in the present study, the fact that birds have faces need not worry us in investigating the expertise hypothesis. Recall that earlier it was argued that showing an expertise effect in the FFA with face-like stimuli or stimuli containing faces is not strong support for the expertise hypothesis: it may simply reflect the fact that because the face mechanisms are already involved in representing these stimuli, they are just recruited further for expertise processing because the face mechanisms have this capability (Kanwisher, 2000). Finding a bird expertise effect with a car expertise effect, however, does not rule out the possibility that part of the bird expertise effect could still be due to the fact that birds have faces or the possibility that a bird expertise effect is acquired differently than a car expertise effect because birds have faces. Further research is needed to examine these possibilities. The best stimuli to study the expertise hypothesis are still the ones that do not resemble faces and do not contain face parts.

Rhodes *et al.* (2004) recently measured fMRI activity in the FFAs while novices and experts viewed Lepidoptera (butterflies and moths) and argued that their results supported the Face-Specific Hypothesis. A close examination of their data, however, suggests otherwise: Under the passive viewing condition,

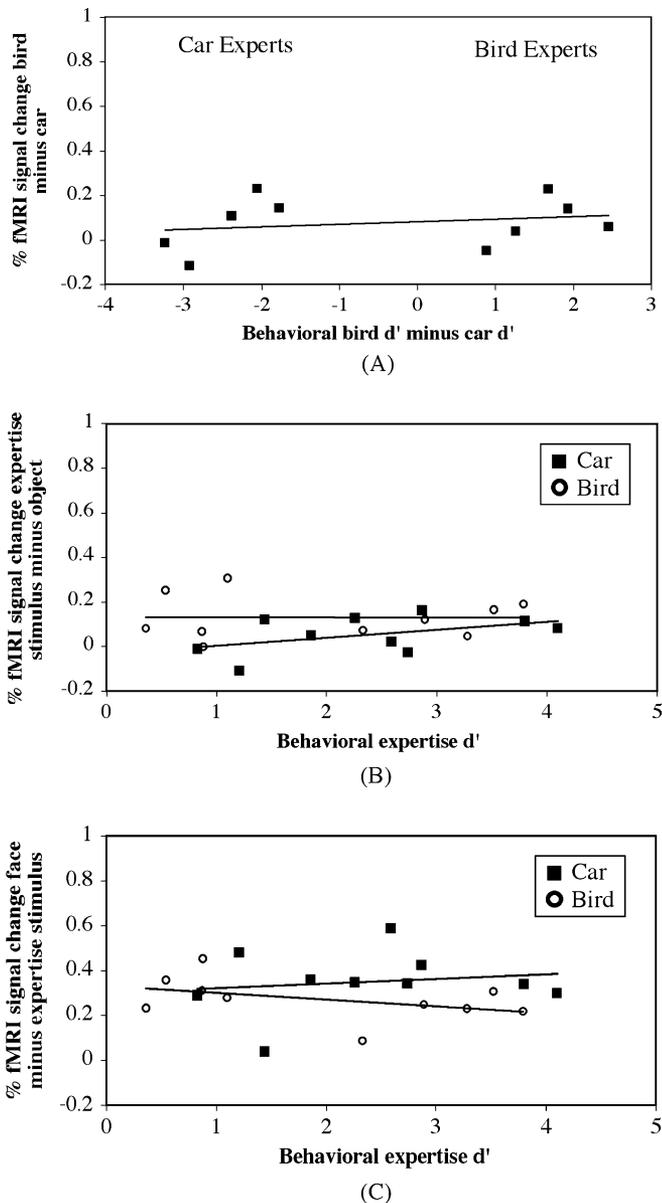


Figure 4. Correlations between fMRI signals in the left FFA and behavioral expertise. (A) The correlation between fMRI bird minus car and behavioral bird d' minus car d' ; (B) the correlation between fMRI expertise stimulus minus object and behavioral expertise d' ; and (C) the correlation between fMRI face minus expertise stimulus and behavioral expertise d' . None of the correlations reached significance, indicating the absence of an expertise effect in the left FFA.

there was a significantly larger fMRI activation for viewing Lepidoptera in the right FFA for experts than for novices; moreover, the interaction of experts versus novices and Lepidoptera versus objects was significant, thus indicating a higher activation for Lepidoptera than for objects in the experts than in the novices (see fig. 1 on p. 193 as well as the results on p. 196 of Rhodes *et al.*, 2004). The results of Rhodes *et al.* are therefore consistent with the Expertise Hypothesis, not the Face Specific Hypothesis.

Responses in Other Fusiform Areas

The present study also identified, in the fusiform areas of both groups of experts, brain areas that responded more to cars than to objects ('car' areas) and brain areas that responded more to

birds than to objects ('bird' areas). Overall, more brain areas were activated during expertise than non-expertise visual processing, due to either greater automatic processing of the expertise stimuli or greater attention to the expertise stimuli during the blocked fMRI data acquisition, or a combination of these two factors.

With regard to the amount of overlap between the expertise areas and the FFAs, due to big between-subject variances, no clear pattern could be extracted at this point. The expertise areas, however, were not identified in one car expert and in one bird expert (who actually showed the highest behavioral bird expertise), suggesting that the existence of an expertise area in the ventral cortex may not be necessary in achieving behavioral expertise. It is possible that in future studies, with a more powerful localizer scan, the 'car' and 'bird' areas may be identified in every subject. This would allow a better examination of the amount of overlap between an expertise area and the FFA and that between a nonexpertise area and the FFA.

ERP/MEG Studies on Visual Expertise

Besides studies in fMRI, studies that measured event-related potentials (ERPs) have also reported a visual expertise effect. In ERPs and magnetoencephalography (MEG) studies, a face-selective response component, termed the N170 response in ERP or the M170 response in MEG, has been identified over the occipito-temporal region and is believed to be originated from the FFAs (Halgren *et al.*, 2000). N170/M170 occurs ~170 ms after stimulus onset, and is much higher for faces than for nonface stimuli such as hands, houses or animals (Bentin *et al.*, 1996; Jeffreys, 1996; Sams *et al.*, 1997; Liu *et al.*, 2002). Tanaka and Curran (2001) reported that the face-selective N170 response to birds and dogs was higher in experts than in novice subjects. Rossion *et al.* (2002) found that after extensive training on 'greebles', the N170 latency delay for inverted versus upright 'greebles' was comparable to the inverted versus upright latency delay for faces. Rossion *et al.* (2002) also observed a small N170 amplitude modulation similar to that reported by Tanaka and Curran (2001). In a third study, Gauthier *et al.* (2003) studied holistic processing of faces and cars in novices and car experts. They found that car perception interfered with concurrent face perception in the car experts using both behavioral and ERP measures. Moreover, the amount of interference correlated with the degree of car expertise in the car experts. These results therefore seem to be consistent with the Expertise Hypothesis and suggest that the same neural mechanisms may be involved in the processing of both faces and non-face expertise visual stimuli.

As Xu *et al.* (2005) pointed out, however, these three prior ERP studies all suffered from various degrees of weakness. In Tanaka and Curran (2001), sensors that showed the expertise effect in bird and dog experts were not tested for face selectivity. As the authors themselves noted, 'the N170 for objects of expertise may be distributed slightly more superiorly and posteriorly than the N170 for faces' (p. 45). Moreover, dog and bird have faces. As such, showing an expertise effect with 'facelike' stimuli may reflect the ability of face mechanisms to be recruited for facelike stimuli after training rather than addressing whether the face mechanisms can be recruited for the processing of non-facelike stimuli after acquisition of visual expertise. The greebles used in Rossion *et al.* (2002) resemble faces in their structure. In fact, even before training, the N170 amplitude to these stimuli was 84% as high as for faces, whereas prior studies have reported no

N170 response for nonfaces (Bentin *et al.*, 1996). These data suggest that either the sensors examined by Rossion *et al.* were not very face-selective, or even before training, greebles naturally evoked some of the same mechanisms used in face processing. Either possibility renders the results of this study unhelpful in distinguishing between the Face Specific and the Expertise Specific Hypotheses. As in Tanaka and Curran (2001) and Rossion *et al.* (2002), face-selective sensors were again not independently localized in Gauthier *et al.* (2003). In fact, the N170 response reported was not much higher for faces than for cars even in novices (fig. 3a of Gauthier *et al.*, 2003), raising the question of whether the sensors examined by Gauthier *et al.* were face selective. In addition, although Gauthier *et al.* reported a strong correlation between the amount of car interference on face perception and the degree of behavioral car expertise, if the amount of car interference on face perception by subject group was examined, there was actually no difference between experts and the controls (if anything, the effect was in the opposite direction as predicted by the expertise hypothesis — see table 1 of Gauthier *et al.*, 2003). This inconsistency raises serious questions about the behavioral results reported by Gauthier *et al.* As such, prior ERP studies have not unambiguously established that the face-selective N170 response is also expertise specific. It is possible that the expertise-selective N170 response reported (Tanaka and Curran, 2001; Rossion *et al.*, 2002; Gauthier *et al.*, 2003) might have originated from occipito-temporal sensors that were not face selective.

When independently localized face-selective sensors were used with stimuli that did not resemble faces (side-view cars), Xu *et al.* (2005) failed to observe any expertise effect in the amplitude of the M170 face-selective response to car stimuli in car experts. Moreover, in a second task in Xu *et al.*, while the M170 response correlated with success and failure of face identification as previously reported (Liu *et al.*, 2002), it did not correlate with car identification performance in the car experts. Results from Xu *et al.* thus suggest that the face-selective M170 response is face specific and not expertise specific. Although Xu *et al.* failed to find an expertise effect in other occipital-temporal sensors that were not face-selective, it is possible that the expertise effect may originate in cortical tissue oriented parallel to the MEG sensors (Hamalainen *et al.*, 1993), and thus the expertise effect may not be detectable by the MEG sensors. Nonetheless, if the FFA is indeed the source of the N170 and M170 face-selective responses, results from Xu *et al.* suggest that certain portion of the right FFA may be face selective and not expertise selective. It is also possible given that the M170/N170 face-selective response occurs at an early stage of face processing, the expertise effect reported in the present fMRI study and in Gauthier *et al.* (2000) may come from later components of expertise visual stimulus processing (although more evidence is need to support this). Further research is necessary to fully understand how expertise non-face visual stimulus is processed in the brain.

To summarize, the present study reported a strong expertise effect in the right FFA. The results are overall consistent with those of Gauthier *et al.* (2000) and suggest the involvement of the right FFA in the processing of non-face expertise visual stimulus.

Notes

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