Cerebral Cortex October 2010;20:2304–2318
doi:10.1093/cercor/bhp316
Advance Access publication February 4, 2010

FEATURE ARTICLE
Top-Down Engagement Modulates the Neural Expressions of Visual Expertise

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Perceptual expertise is traditionally associated with enhanced brain activity in response to objects of expertise in category-selective visual cortex, primarily face-selective regions. We reevaluated this view by investigating whether the brain activity associated with expertise in object recognition is limited to category-selective cortex and specifically whether the extent of expertise-related activity manifests automatically or whether it can be top-down modulated. We conducted 2 functional magnetic resonance imaging studies comparing changes in hemodynamic activity associated with car expertise in a conventional 1-back task (Experiment 1) and when the task relevance of cars was explicitly manipulated (Experiment 2). Whole-brain analysis unveiled extensive expertise-related activity throughout the visual cortex, starting as early as V1 and extending into nonvisual areas. However, when the cars were task irrelevant, the expertise-related activity drastically diminished, indeed, becoming similar to the activity elicited by cars in novices. We suggest that expertise entails voluntary top-down engagement of multiple neural networks in addition to stimulus-driven activation associated with perceptual mechanisms.

Keywords: fMRI, object recognition, top-down effects, visual cortex, visual expertise

Introduction

Developing perceptual expertise with a particular category of objects enhances one's ability to identify subtle differences between its members and, therefore, improves the expert's ability to distinguish among the different exemplars of the category at subordinate levels. This improvement is most probably associated with developed changes in the cortical representation of objects of expertise as well as the way these representations are activated and manipulated. Consequently, perceptual expertise provides the opportunity to study the effects of experience on the cortical representations of objects and, in a more general sense, the principles of plasticity in the mature human brain.

The most common example of perceptual expertise is the outstanding human ability to easily identify individual faces despite their high structural homogeneity. Therefore, it is not surprising that the study of the neural substrates of visual expertise focused frequently on face perception (Gauthier et al. 1999; Gauthier, Skudlarski, et al. 2000; Kanwisher 2000; Tarr and Gauthier 2000; Grill-Spector et al. 2004), and the exploration of expertise-related effects in the brain was largely confined to face-selective regions such as the fusiform face area (FFA; Puce et al. 1996; Kanwisher et al. 1997) or employing stimuli resembling faces in their computational demands (e.g., Gauthier and Tarr 1997; Gauthier et al. 1999; Yue et al. 2006). Neuroimaging studies along this line showed enhanced activation for different objects of expertise in the FFA. Moreover, this preferential activation of the FFA to objects of expertise was also correlated with the level of expertise (Gauthier et al. 1999; Gauthier, Skudlarski, et al. 2000; Xu 2005; but see Grill-Spector et al. 2004, for a lack of a correlation between expertise level and FFA response magnitude). In addition, event-related potential (ERP) studies showed that the face-selective N170 component (Bentin et al. 1996) might arguably be modulated by expertise with nonface objects (Tanaka and Curran 2001; Gauthier et al. 2003; Rossion et al. 2007).

Although providing important insights about the consequences of expertise in the brain, the above studies do not treat object expertise as an end of itself and instead view it through the prism of face recognition. Consequently, expertise is considered to be expressed in the brain in a "face-like" manner, which confined its exploration to restricted areas of interest (e.g., FFA; Harley et al. 2009), time windows (e.g., 170 ms) and to objects that resemble faces (e.g., Yue et al. 2006). Thus, additional work is required to shed light on brain activity associated with expertise independent of face perception and to elaborate the factors that account for the changes in neural activation associated with acquired expertise. For example, because objects of expertise are probably more salient and engaging for the expert than for the novice, expertise-related neural activity might also reflect controlled top-down modulation of activity in object-selective regions rather than reflecting only the operation of a stimulus-driven automatic expert perceptual mechanism (Wojciulik et al. 1998; Kanwisher 2000; McKone et al. 2007). In fact, the effect of top-down factors on the manifestation of expertise in the brain was addressed in only 2 studies (Gauthier, Skudlarski, et al. 2000; Xu 2005), and critically, the task relevance of the stimuli (putatively modulating top-down control) was insufficiently manipulated. Furthermore, these studies focused primarily on the FFA, ignoring the possibility that expertise effects may be expressed across the entire cortex, reflecting a wider cortical network.

Two recent functional magnetic resonance imaging (fMRI) studies investigated the manifestations of expertise in brain regions additional to the FFA (Op de Beeck et al. 2006; Yue et al. 2006). These studies reported effects of expertise in the lateral occipital complex (LOC: Malach et al. 1995), which is a set of cortical regions that responds preferentially to objects and plays an important role in object recognition (Grill-Spector et al. 2001). However, in both these studies, expertise was operationalized as short-time training in the discrimination of artificial laboratory-created objects. Thus, it is not evident that their findings can be generalized to real-world objects of expertise, which have richer representations and are much more salient to skilled experts with years of experience. In addition, both studies applied a functional region of interest (ROI) approach (Saxe et al. 2006) and like most previous studies do not provide a detailed account of real-world object expertise across the entire cortex.

In contrast, the present study was designed to examine the influence of long-term, acquired expertise (for objects other than faces) on blood oxygenation level–dependent (BOLD) activity throughout the entire cortex in a manner that is not restricted to face-selective or category-selective regions, as well as to investigate whether top-down controlled factors might modulate this expression of expertise. In the first experiment, using a block-design paradigm and comparing between car experts and novices, we found that the manifestation of expertise for cars was not restricted to face-selective regions but rather evident throughout the visual system starting as early as V1. In the second experiment, using an event-related design, we controlled for task relevance effects and found that when the category of expertise (cars) was not task relevant, the expertise effects were considerably reduced, indeed, almost undistinguished from the activation found in novices. These results provide a new perspective on the neural manifestations of visual expertise. We suggest that changes in neural activation associated with expertise do not entail only changes in perceptual processing (associated perhaps with corresponding changes in neural tuning) but could also reflect top-down control on the activity of neural networks required for the detection and evaluation of salient task-relevant stimuli.

Materials and Methods

Subjects

Thirteen car experts (all males, 20–39 years, M = 24.8) and 15 volunteers (all males, 24–33 years, M = 26.5) matched in age and education participated in each of the 2 fMRI experiments. One subject from the novice group participated only in the event-related experiment (Experiment 2). All the participants were healthy and had normal or corrected-to-normal vision. Written informed consent to participate in the experiments was obtained from all the subjects according to the Tel-Aviv Sourasky Medical Center ethics committee that approved the experimental protocol.

The car experts were recruited among volunteers who responded to messages posted in car forums on the Internet. To assess their expertise, the expert candidates performed a perceptual discrimination task (see details below) inspired by Gauthier, Skudlarski, et al. (2000). Experts for the current study were determined according to an accuracy level of 83% or above in the car discrimination task. Novices also performed this task for control purposes.

Assessment of Expertise

The car experts' selection procedure was inspired by Gauthier, Skudlarski, et al. (2000). In each trial, candidates had to determine whether 2 cars presented sequentially (for 500 ms each and 500-ms Inter stimulus interval [ISI]) were of the same model (e.g., "Honda Civic" or not). The 2 cars in each trial were always of the same make (e.g., Honda) but differed in year of production, color, angle, and direction of presentation. Overall, the task consisted of 80 pairs of cars (half same, half different) and all of the car images were of frequently encountered models from recent years. Expertise was defined at 83% accuracy on this task. To assure that the car expertise displayed by the car experts was category specific, all participants performed an analog task with passenger airplanes. Due to changes in testing versions, we report here the expertise assessment data for 8 experts and 9 novices (for further details, see Supplementary Material).

fMRI Procedure and Experimental Design

Experiment 1

A 1-back memory task was used in a block-design experiment consisting of 2 scans. In each scan, subjects were presented with blocks of face, car, and airplane images. A scan consisted of 27 blocks presented in a random order with 9 blocks for each category. A block consisted of 9 stimuli (different for each block) and lasted 9 s. Each stimulus was presented for 500 ms followed by 500-ms blank. The blocks were separated by a fixation period of 6 s during which a fixation point was presented at the center of a gray screen. Each block contained 1 or 2 repetitions in which an identical stimulus was presented consecutively. The stimuli were grayscale photographs of faces, cars, and airplanes presented at the center of a uniform gray background, sized 360 × 360 pixels, subtending a visual angle of 14° × 14°. Subjects were instructed to fixate at the center of the screen and indicate by buttons whether a stimulus was the same as the previously seen or different. Responses were collected via a response box. All subjects underwent a short training session of 2 min outside the scanner prior to the experiment.

Experiment 2

In this experiment, we used an event-related fMRI design with an adapted 1-back memory task in which the task relevance of different object categories (hence the relevance of each event) varied across blocks. This manipulation allowed the assessment of the level of engagement of the observer with different categories, and consequently, of a putative influence of the level of engagement on the expertise-related BOLD activity. Images of cars and airplanes were presented in both an "attend cars" and an "attend airplanes" task so that the stimuli could be task relevant or not. In the "attend cars" task, the participants were instructed to detect repetition of car images while ignoring both repeated and unrepeated airplane images and vice versa in the "attend airplanes" task. Each task was presented in a separate block while cars and airplane images were mixed within each block (see Fig. 5*A*). A scan comprised of 4 blocks, in 2, the cars were task relevant, and in the other 2, the airplanes were task relevant. Each participant was tested in 2 scans, each with a different permutation of the blocks' order. The order of the 2 scans was also counterbalanced across participants.

In each block, there were 30 stimuli, 15 cars, and 15 airplanes with 1 or 2 cars and 1 or 2 airplanes repeated. Repetitions occurred for both categories within a block, so the repetition itself was not diagnostic of task relevance. Across 4 blocks in each scan, there were 30 events in each of the 4 experimental conditions: cars-Attend cars (Cars High Engagement), cars-Attend-airplanes (Cars Low Engagement), airplanes-Attend-airplanes (Airplanes High Engagement), and airplanes-Attend-cars (Airplanes Low Engagement). Each experimental event lasted 3 s: 200 ms of image presentation and an ISI of 2800-ms fixation. In addition, 30 null events, each consisting of 3 s of fixation, were included in each scan as baseline condition. Hence, with 2 scans per participant, each condition consisted of 60 events. To complete the design, note that cars were the objects of expertise in one group but not in the other. We deliberately did not include faces in this experiment, as we wanted to isolate the effect of expertise in object (rather than face) recognition. Particularly, face expertise may interact with expertise for other objects (Bukach et al. 2006), making it harder to interpret any possible results.

Each scan began with an 18-s fixation period and ended with a 16.5-s fixation period, and within a scan, the 4 blocks were separated by 3 nonequal fixation periods of 10.5–19.5 s each (e.g., 16.5, 10.5, and 13.5 s), summing to 75 s of between-blocks fixation periods in a scan. Each block began with a 3-s "instructions screen" indicating the target category and ended with a 1.5-s "end-of-block" instruction. The 30 null events were distributed among the blocks so that in 2 blocks per scan there were 7 null events and in the other 2 there were 8 null events. Consequently, 2 blocks in each scan lasted for 111.5 s and the other 2 118.5 s. Overall, each scan lasted 543 s.

Images were 300 × 300 pixels (12° × 12° of visual angle) grayscale photographs of cars and airplanes presented in three-quarter view. Throughout the experiment, each image (car or airplane) appeared twice, once as a task-relevant event, once as a task-irrelevant event but only once within a scan. The subjects were instructed to press a button each time a stimulus from the predesignated category repeated itself. Accuracy and speed of responses were recorded.

Category Localizer Experiment

An external localizer experiment was aimed at delineating category-selective regions in high-order visual cortex as well as differentiating between low-level retinotopic regions and higher-level visual areas in a manner that is independent of the experimental scans. This block-designed fMRI experiment included 4 stimulus conditions (faces, houses, objects, and simple textures). Each condition was repeated 7 times in pseudorandom order. Blocks lasted 9 s and were interleaved with 6-s fixation periods. The entire experiment lasted a total of 452 s. Blocks consisted of 9 images of the same category, each displayed for 800 ms followed by a 200-ms blank screen. All stimuli were grayscale photographs of 300 × 300 pixels each, subtending a visual angle of 12° × 12°. The task was a traditional one-back memory task without overt responses. An image repetition occurred once or twice in each block.

Magnetic Resonance Imaging Setup

fMRI

In the blocked-designed Experiment 1 and in the external localizer experiment, subjects were scanned in a 1.5-T Signa Horizon LX 8.25 GE scanner equipped with a standard head coil. The BOLD contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence: time repetition (TR) = 3000 ms, time echo (TE) = 55 ms, flip angle = 90°, field of view (FOV) 24 × 24 cm^2, and matrix size 80 × 80 (in-plane resolution of 3 × 3 mm^2). The scanned volume consisted of 27 nearly axial slices of 4-mm thickness and 1-mm gap covering the entire cortex.

In the event-related designed Experiment 2, subjects were scanned in 3-T G3 GE scanner. BOLD contrast was obtained with gradient-echo EPI sequence: TR = 1500 ms, TE = 33 ms, flip angle = 90°, FOV 24 × 24 cm^2, matrix size 64 × 64 (in-plane resolution of 3.75 × 3.75 mm^2), the scanned volume consisted of 24 oblique slices of 4-mm thickness and 1-mm gap in order to cover the entire cortex.

Structural MRI

A whole-brain spoiled gradient sequence was acquired for each of the subjects to allow accurate cortical segmentation, reconstruction, and volume-based statistical analysis. Twenty-four of the 28 subjects were scanned in the 3-T scanner (FOV 250 × 250 mm^2, matrix size 256 × 256, slice thickness 1.0 mm, and 146 axial slices), and 4 subjects were scanned in the 1.5-T scanner (FOV 240 × 240 mm^2, matrix size 256 × 256, slice thickness 1.2 mm, and 124 axial slices). In addition, high-resolution (1.1 × 1.1 mm^2) T1-weighted anatomic images of the same orientation and thickness as the EPI slices were also acquired to facilitate the incorporation of the functional data into the 3D Talairach space (Talairach and Tournoux 1988).

fMRI Data Preprocessing and Analysis

fMRI data were analyzed with the BrainVoyager software package (Brain Innovation, Maastricht, The Netherlands) and additional in-house software. The first 3 images of each functional scan were discarded. The functional images were superimposed on 2D anatomic images and incorporated into the 3D normalized Talairach space (Talairach and Tournoux 1988) through trilinear interpolation. Preprocessing of functional scans included 3D motion correction, slice scan time correction, linear trend removal and filtering out of low frequencies up to 3 cycles per experiment. No spatial smoothing was applied to the data.

Statistical Analysis—Block Design Experiments

A general linear model (Friston et al. 1994) was fit separately to the time course of each individual voxel in each experiment according to the experimental protocol. The model coefficients for each voxel were determined so that the error term between the model's prediction and the measured voxel time course was minimized (least squares method). The analysis was performed independently for each individual voxel. *t*-Test between coefficients of different conditions was applied to determine the voxel's activation pattern. Voxel's *P* value was determined as the "*P*" corresponding to the resulting significance level of the *t*-test.

Statistical Analysis—Event-Related Experiment

For each subject, after the time courses of the 2 scans were transformed into Talairach space and preprocessed (see fMRI data preprocessing and analysis), they were *z*-normalized and concatenated, and the statistical tests were performed on the concatenated time course.

For the multisubject whole-brain analysis a general linear model was fitted to the data (as described above), and the analysis was performed independently for each individual voxel. For the ROI time course analysis, the data were deconvolved using the deconvolution analysis for rapid-event-related paradigms that consists of a general linear model analysis (Friston et al. 1994) in BrainVoyager software package (Brain Innovation, Maastricht, The Netherlands) in order to extract the estimated hemodynamic response in each voxel for each condition. The analysis was done separately for each subject on a voxel-by-voxel basis.

Multisubject Analysis

To obtain the multisubject group activation maps, for each experiment, the time courses of subjects from the 2 groups were *z*-normalized. This was achieved using a random effect (RE) procedure (Friston et al. 1999) and for display purposes the maps were projected on a flattened Talairach normalized brain. Experiment 1′s car-selective visual activation maps were obtained for each group separately. For each group, they were obtained by the conjunction of activations to cars relative to airplanes and cars relative to baseline ($P < 0.0001$, RE, corrected, minimum cluster size of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 14$).

The car-selective visual activation maps for each group in Experiment 2 were obtained by the conjunction of activations to cars over airplanes and cars over baseline. This was performed separately for each of the engagement levels ($P < 0.0001$, RE, corrected, minimum cluster size of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 15$).

The category-selective and early visual borders displayed in Figures 2 and 6 (faces in red, objects in blue, early visual areas demarcated with black dotted line) were obtained by comparing the activations in response to one category with the activation in response to another category and the conjunction of the response to that category relative to the response at baseline (face-selective by [face > house] and [face > baseline], object-selective by [objects > textures] and [objects > baseline], early visual areas by [textures > objects] and [textures > baseline], $P < 0.0001$, RE, corrected). For visualization purposes, the borders were projected on a flattened Talairach normalized brain.

Statistical significance levels were calculated taking into account the individual voxel significance, a minimum cluster size of 10 functional voxels, and the probability threshold of a false detection of any given cluster within the entire cortical surface (Forman et al. 1995). This was achieved using a Monte Carlo simulation (AlphaSim by B. Douglas Ward, software module in Cox, 1996). For visualization purposes, the maps were projected on a flattened Talairach normalized brain.

ROI Analysis

ROIs were identified in each subject separately based on the category localizer experiment as described above. They were defined on the basis of a minimum cluster size of 6 contiguous functional voxels that exhibited selective activations in response to a specific category (e.g., faces > houses, $P < 0.05$). FFA ROIs were defined as regions within the posterior aspect of the fusiform gyrus that showed a preferential activation to faces relative to houses. Parahippocampal place area (PPA; Epstein and Kanwisher 1998) ROIs were defined as regions residing in the parahippocampal gyrus (PHG) or the adjacent collateral sulcus (CoS) that showed a preferential activation to houses relative to faces. LOC ROIs were defined as regions in the lateral occipital aspect of the cortex in the vicinity of the inferior occipital sulcus or gyrus that showed a preferential activation to objects relative to textures. Early visual areas were defined as regions in striate and extrastriate cortex in the medial aspect of the cortex that showed a preferential activation to textures relative to objects (Grill-Spector et al. 1999; Lerner et al. 2001; Levy et al. 2001; Hasson et al. 2003). We sampled the time courses of activation in Experiment 1 and Experiment 2 separately in the FFA, PPA, LOC, and the early visual areas for each subject. In some subjects, the FFA was found in only one hemisphere (right FFA: 6 of 13 experts and 1 of 14 novices; left FFA: 3 of 13 experts and 1 of 14 novices), all other subjects showed bilateral activation. One novice subject did not show any reliable FFA activity in either hemisphere and was thus excluded from the analysis. In Experiment 1, we then computed the percent of BOLD signal change compared with the fixation period preceding it. Because no hemispheric difference were found for any of the ROIs, the right and left hemisphere ROI time courses were combined by a weighted average. Finally, for each ROI and for each condition, the time courses were averaged across the participants of each group (Experiment 1: Fig. 4, Experiment 2: Fig. 9). These were later subjected to a factorial analysis of variance (ANOVA). All simple effects reported here are Bonferroni corrected for multiple comparisons. In Experiment 2, we followed the same procedures as for Experiment 1 except for the estimation of the hemodynamic response, which was different to account for the rapid event-related design. For that purpose, we applied the deconvolution analysis for rapid event-related paradigms in BrainVoyager software package (Brain Innovation, Maastricht, the Netherlands) to each time course of each voxel in each of the ROIs in order to extract the estimated hemodynamic response, and then the estimated responses at 4.5, 6, and 7.5 s after stimulus onset were averaged. We followed the above-described procedures of averaging across hemispheres (because no hemispheric differences were found for any of the ROIs), averaging across participants of each group, for each ROI.

Results

Performance of Car Experts and Novices in the Expertise Assessment Task

Expertise for cars was assessed using a perceptual discrimination task. This task was inspired by Gauthier, Skudlarski, et al. (2000) and was used for the selection of experts (see Materials and Methods). The stimuli and results are displayed in Figure 1.

Formal comparison of the experts' performance with that of novices was based on mixed-model, 2-way ANOVA with expertise (experts/novices) as a between-subjects factor and object category (airplanes/cars) as a within-subjects factor. Accuracy level of discrimination (d') was the dependent variable. This analysis showed a significant interaction between the 2 factors ($F(1,15) = 29.00$, $P < 0.001$). As expected, experts were highly more accurate when recognizing cars (Mean d' = 2.40, range = 1.90–3.58) compared with airplanes (Mean d' = 0.57, range = 0.19–1.24) (see Fig. 1). Novices, on the other hand showed similar performance to both of the categories (cars: mean d' = 0.58, range = 0.12–1.15; airplanes: mean d' = 0.57, range = 0.20–1.31, respectively), which was also in the same range of the experts' performance to airplanes.

Experiment 1

Whole-Brain Analysis

The consequence of object expertise on BOLD activity across the whole brain is evident in Figure 2, which presents the

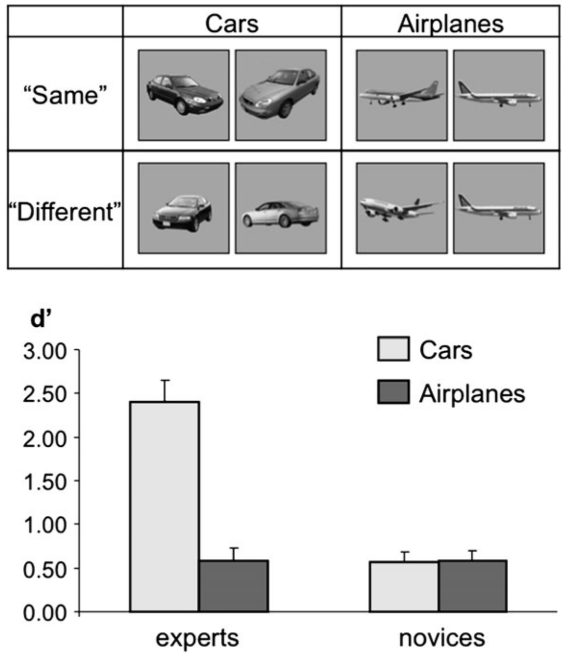

Figure 1. Behavioral performance in the expertise assessment task. Top: examples of the stimuli viewed in the expertise assessment experiment are presented. In each trial, subjects viewed a pair of sequentially presented private cars or passenger airplanes and had to indicate whether the 2 stimuli were of the same model or of a different model (examples for an expected "same" response are presented in the top row and for expected "different" response in the bottom row). Trials consisted of 500-ms image presentation followed by 500-ms fixation image after which the second image appeared for 500 ms. Bottom: mean performance (d') of the car experts and the car novices in the expertise assessment task. Car performance is indicated in light gray, airplane performance in dark gray. Note the low level of performance of the car novices in both the car and airplane conditions, similar to the performance of the car experts in the airplane condition and in comparison the car experts' superior performance in the car condition. Error bars indicate standard error of the mean (SEM).

average response to cars relative to airplanes in car experts (Fig. 2*A*; $P < 0.0001$, corrected, RE, $n = 13$) and car novices (Fig. 2*B*; $P < 0.0001$, corrected, RE, $n = 14$). In the novices, preferential activation to cars was confined mainly to low-level visual areas (delineated in the figure by the black dotted line).

In contrast to novices, in car experts, extensive preferential activation to cars was evident throughout the visual cortex extending over object-selective visual cortex bilaterally. These areas included mainly the fusiform gyrus, the CoS and the PHG with a minor extension into the LOC. Moreover, the car-selective activation only partially overlapped face-selective representations in the experts (namely, the FFA, and the occipital face area [OFA; Gauthier, Tarr, et al. 2000] as denoted in Fig. 2*A* by red borders). Additional foci beyond the occipitotemporal cortex included posterior cingulate, precuneus, and the hippocampus. In addition, predominantly left-lateralized foci of activation were found in prefrontal cortex, particularly in inferior frontal gyrus and middle frontal gyrus, regions that are known to participate in attentional networks (Corbetta and Shulman 2002).

To directly assess the difference in the extent of car-selective activation between the car experts and the car novices, we conducted a whole-brain analysis contrasting the cars relative to airplanes contrast between the 2 groups. A group contrast was specified in which the comparison (cars > airplanes) was contrasted between experts and novices (i.e., $[\text{cars} > \text{airplanes}]_{\text{experts}} > [\text{cars} > \text{airplanes}]_{\text{novices}}$). In other words, we

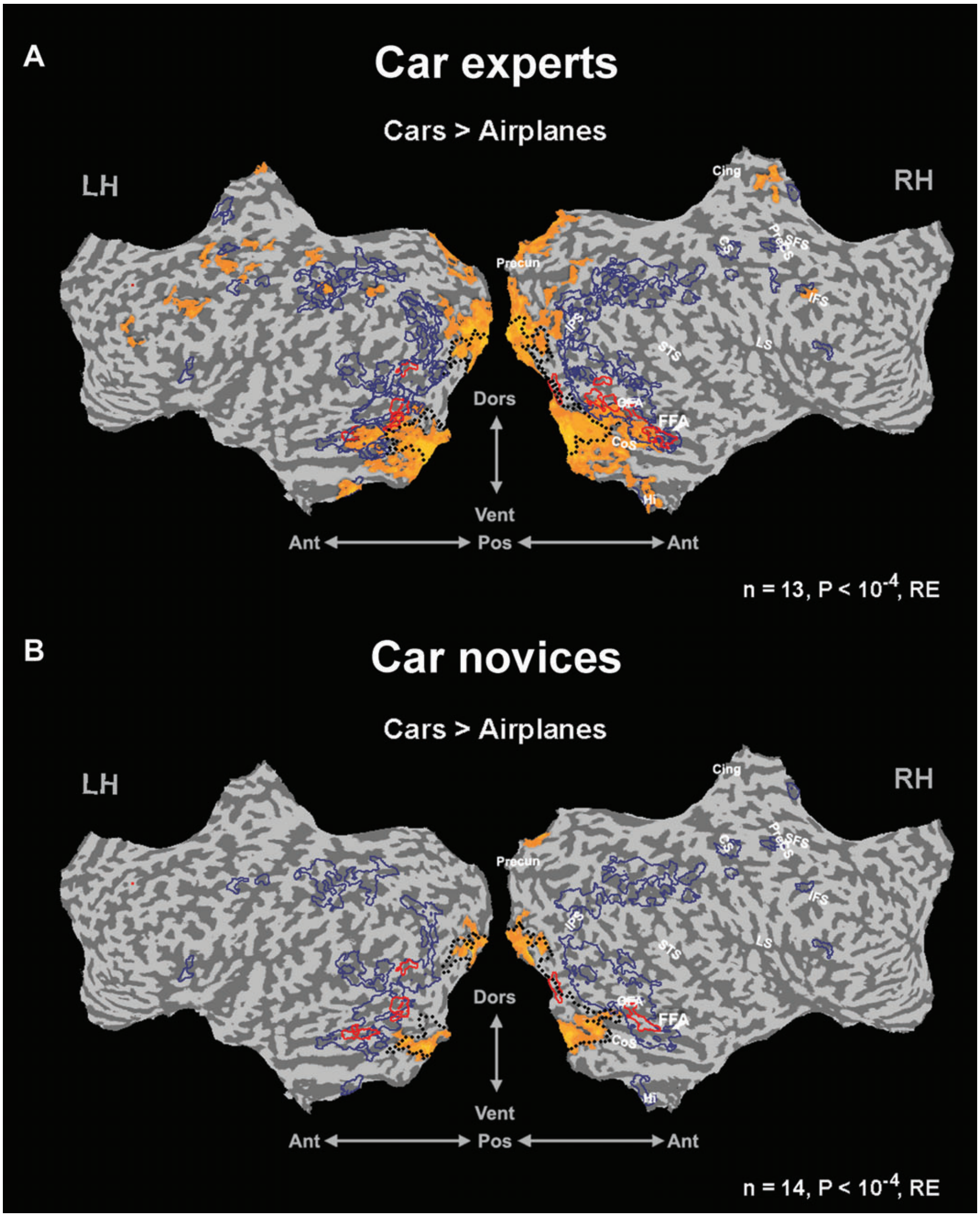

Figure 2. Experiment 1 car-selective activation maps. Experiment 1 multisubject activation maps of car experts and car novices displayed on flattened cortical surfaces. Yellow to orange patches denote regions that were activated above baseline and showed car-selective activation (compared with airplanes) defined by the contrast (cars > airplanes and cars > baseline). The light blue patches denote regions exhibited negative results to that contrast. Face-selective regions are indicated by red contours (defined by above baseline preference to faces over houses in the category localizer experiment). Black dotted lines denote the approximated borders of early visual areas showing preference to textures over objects ("low-level visual areas," defined separately by the category localizer experiment). The blue contours represent borders of high-level visual object areas (defined as areas showing above baseline preference to objects over textures). Note that in car experts (*A*), the car-selective activation extends extensively beyond early visual regions (black dotted line) into far peripheral visual representations and face and object-selective regions, whereas in novices (*B*), the car-selective activation is confined to early visual regions. FFA—fusiform face area, OFA—occipital face area, CoS—collateral sulcus, IPS—intraparietal sulcus, CS—central sulcus, PreCS—precentral sulcus, SFS—superior frontal sulcus, IFS—inferior frontal sulcus, LS—lateral sulcus, Hi—hippocampus, Precun—precuneus, Cing—cingulate, RH—right hemisphere, LH—left hemisphere, Dors—dorsal, Vent—ventral, Pos—posterior, Ant—anterior. All the statistical contrasts were obtained with corrected $P < 0.0001$, RE analysis, $n = 13$ experts in the experts' maps, $n = 14$ novices in the novices' maps.

asked which brain regions distinguish between the car-selective activity of the car experts and the car novices. These results are presented in Figure 3*A*. As can be seen, the distribution of car-selective activity that was more responsive in the car experts relative to the car novices was widespread and extended beyond early visual regions into far peripheral visual representations and face and object-selective regions and was also evident in regions outside of occipitotemporal cortex, such as the precuneus, intraparietal sulcus (IPS) and prefrontal cortex ($P < 0.0001$, RE, corrected, minimum cluster size of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 14$). As a control, we compared the face-selective activation in the car experts and the car novices (i.e., $[\text{faces} > \text{airplanes}]_{\text{experts}} > [\text{faces} > \text{airplanes}]_{\text{novices}}$; $P < 0.0001$, RE, corrected, minimum cluster size

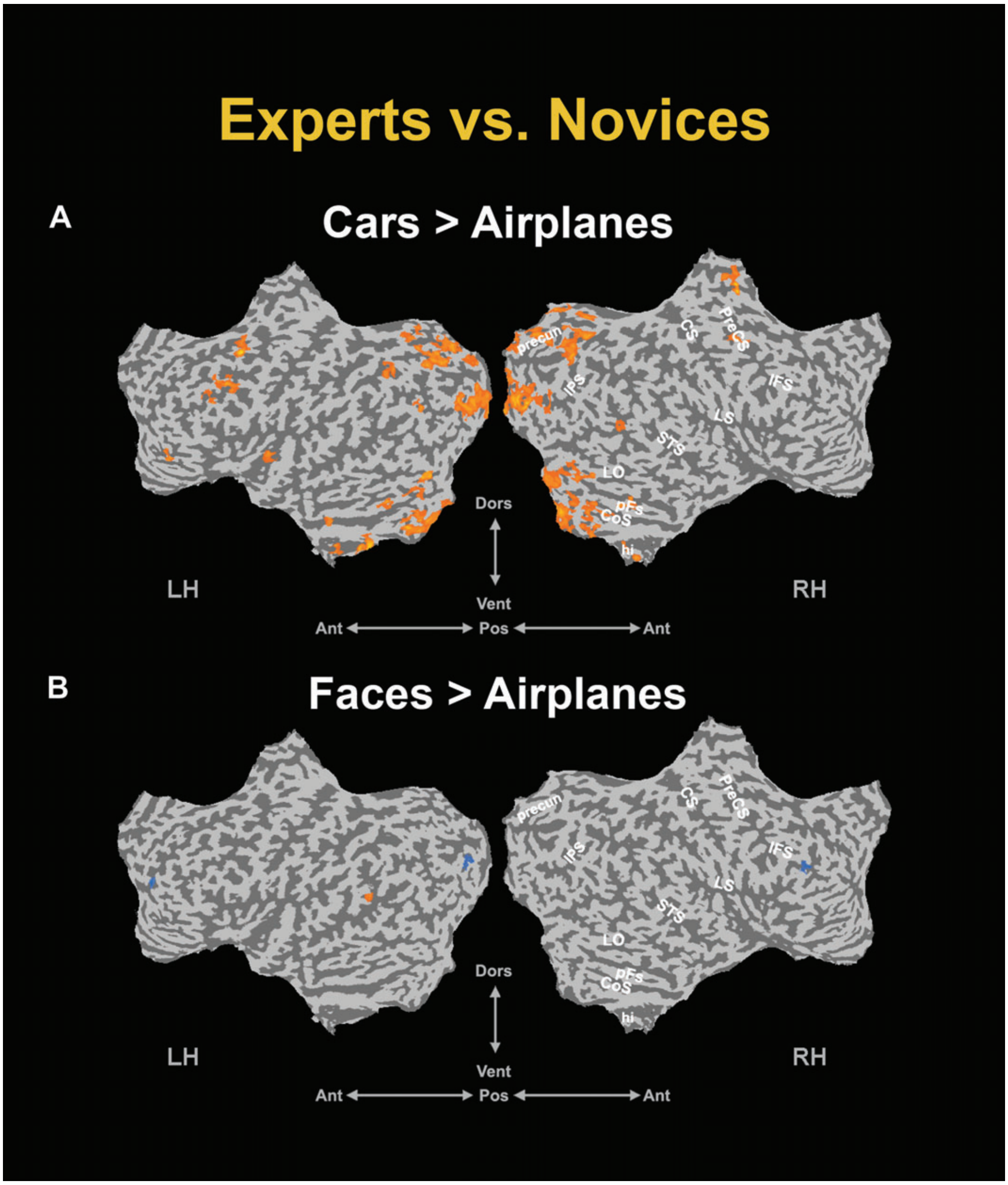

Figure 3. Experiment 1 intergroup comparisons. Experiment 1′s group contrast (Experts vs. Novices) multisubject maps for the cars versus airplanes contrast (*A*) and the faces versus airplanes contrast (*B*), displayed on flattened cortical surfaces. These statistical maps show up the significant difference between the groups for the contrast specified ($P < 0.0001$, RE, corrected, minimum cluster size of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 14$). Hence,yellow to orange patches denote in (*A*) car-selective regions that were more activated in experts than in novices (i.e., defined by the contrast $[\text{cars} > \text{airplanes}]_{\text{experts}} > [\text{cars} > \text{airplanes}]_{\text{novices}}$) and in (*B*) face-selective regions that were more activated in experts than in novices (i.e., defined by the contrast $[\text{faces} > \text{airplanes}]_{\text{experts}} > [\text{faces} > \text{airplanes}]_{\text{novices}}$). The light blue patches denote regions exhibited negative results to these contrasts. Presentation format and anatomical landmarks as in Figure 2.

of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 14$). Because both groups had the same expertise with faces, we did not expect any differences in activation. Indeed, this contrast yielded almost no significant group difference, indicating that there was no difference in the general pattern of BOLD activation between the 2 groups (Fig. 3*B*).

ROI Analysis

Because earlier studies of visual expertise focused on the FFA (e.g., Gauthier, Skudlarski, et al. 2000; Grill-Spector et al. 2004; Xu 2005) and because our whole-brain analysis provided evidence that car expertise and face expertise may have different cortical manifestations, we further examined the actual time course of activation for each object category during the experimental scans within 4 ROIs: (FFA, PPA, LOC, and early visual cortex). The ROIs were defined individually based on an external localizer experiment. Figure 4 displays the average activation levels across subjects in each of the groups (experts and novices) for each of these ROIs.

The first region examined was the FFA (Fig. 4*A*), which is known for its face selectivity (Kanwisher et al. 1997) and argued by many authors to play a role in object expertise as well (Gauthier, Skudlarski, et al. 2000). ANOVA with Group (experts and novices) as between-subjects factor and Category (faces, airplanes, and cars) as within-subjects factor showed no significant main effect of Group ($F(1,21) = 1.15$, $P > 0.25$), and

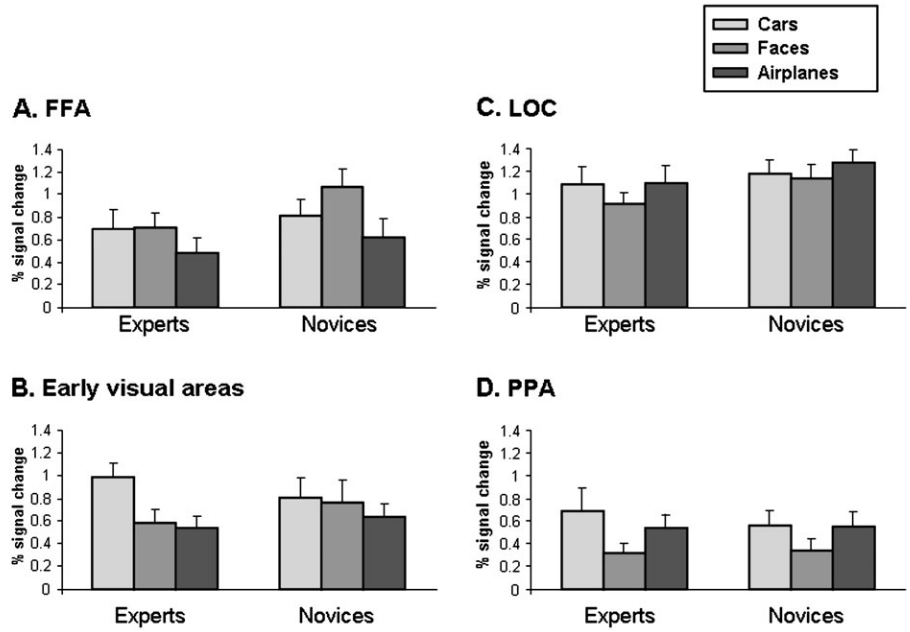

Figure 4. Experiment 1 ROI analysis. Mean activation levels in Experiment 1 to the different categories (cars in light gray, faces in medium gray, and airplanes in dark gray) in both experts and novices in the 4 ROIs (which were defined independently, see Materials and Methods for more details). (*A*) FFA, (*B*) Early visual areas, (*C*) LOC, and (*D*) PPA. The *y*-axis denotes fMRI BOLD percent signal change relative to the fixation blocks. In LOC and PPA, no significant difference was found between experts and novices. In FFA and early visual areas, significant differences were observed between the experts and the novices (see Results for further details). Error bars, SEM.

a significant Category effect ($F(2,42) = 15.33$, $P < 0.001$), which was further qualified by a trend of a Category by Group interaction ($F(2,42) = 2.52$, $P = 0.09$) (see Supplementary Table 1 for full details on all statistical analyses). For novices, as expected, faces were found to activate FFA more than both airplanes ($P < 0.001$) and cars ($P < 0.001$). In contrast, for experts, although faces elicited a higher response than airplanes in the FFA ($P < 0.04$), the magnitude of response to cars was equal to that in response to faces ($P > 0.80$). Although prima facie this pattern should have been expected reflecting an effect of expertise in the FFA, further analysis revealed that, surprisingly, the magnitude of activation in the FFA to cars and airplanes was actually comparable across novices and experts; indeed, the Category by Group interaction reflected reduced activation in car experts relative to novices in response to faces but not relative to cars or airplanes (cars: $t(21) = -0.51$, $P > 0.60$; airplanes: $t(21) = -0.72$, $P > 0.45$; faces: $t(21) = -1.29$, $P < 0.07$). This pattern suggests that in the current experimental setting car expertise was manifested not as an "increase" in FFA activation for cars but rather as a "decrease" in FFA activation for faces. This manifestation is consistent with previous studies showing a decrease in N170 amplitude to faces in car experts when faces were processed in the context of cars (Gauthier et al. 2003; Harel and Bentin, unpublished data; Rossion et al. 2007).

Early visual areas, which during the external localizer were more responsive to simple textures than to objects, showed a differential response to cars in car experts (Fig. 4*B*). A significant Category by Group interaction ($F(2,44) = 5.07$, $P < 0.01$), followed by post hoc analyses (see Supplementary Table 1 for full details of the statistical analyses) showed that the activation in the early visual areas of car experts in response to cars was significantly higher compared with the response of either faces or airplanes (for both categories, $P < 0.001$), with no difference between the latter 2 categories ($P = \sim1.00$). In contrast, the early visual areas of the novices did not reveal any object selectivity, that is, that there was no significant effect of Category ($F(2,20) = 1.50$, $P > 0.20$).

Finally, as can be seen in Figure 4*C*,*D*, expertise did not modulate the other 2 object-related ROIs that we examined, LOC and PPA. ANOVA showed neither overall Group differences (LOC: $F(1,22) < 1.00$, PPA: $F(1,22) < 1.00$) nor Category by Group interaction (LOC: $F(2,44) < 1.00$, PPA: $F(2,44) = 1.32$, $P > 0.25$) (Supplementary Table1).

Experiment 2

The extent of cortical regions that were apparently modulated by car expertise in Experiment 1 suggest that this effect is not restricted to a specific "hot spot"; rather, it is manifested in a multitude of brain areas ranging from nonspecific low-level visual cortex, to higher-level, object-selective regions, all the way to prefrontal regions. However, because Experiment 1 was designed in a standard block-design paradigm and the task relevance of the stimuli was not manipulated, the extensive preferential car activation observed in car experts could, in fact, reflect the level of top-down engagement that experts naturally have with objects within their domain of interest, in addition to the consequences of pure perceptual expertise. It is important to note that enhanced engagement may denote many observer-based factors, such as specific recognition goals, depth of processing, task-based attention, and arousal.

In order to disentangle the effects of perceptual expertise and enhanced engagement with a specific object category on cortical activation, in Experiment 2, we manipulated the level of engagement with the stimuli (see Fig. 5*A* for design and examples of stimuli). We hypothesized that if expertise is an automatic stimulus-driven perceptual skill, that is, if objects of expertise trigger extensive perceptual processing regardless of task, then car experts should show a similar degree of preferential neural activation to cars irrespective of task relevance, whereas the activation elicited by airplanes should

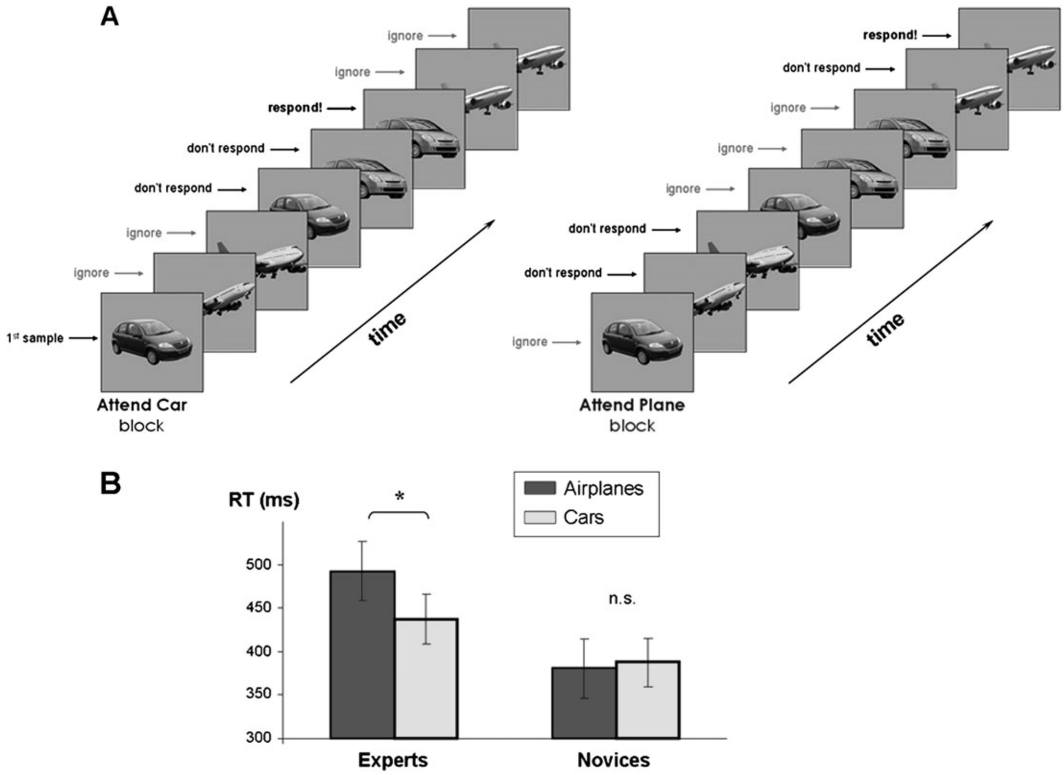

Figure 5. Experiment 2 design and behavior in the high engagement condition. (*A*) An illustration of Experiment 2's experimental design. For demonstration purposes, the same sequence is presented once appearing in the "attend-car" block (left) and once appearing in the "attend-airplane" block (right). The expected behavior of the subject is indicated on the left of the sequence. The subjects were instructed to attend a specific category throughout the block and press a button each time an image from the instructed category was immediately repeated, while ignoring the stimuli from the other category. (*B*) Mean RTs of the car experts and the car novices in response to task-relevant car images (indicated in light gray) and task-relevant airplane images (indicated in dark gray), as measured inside the scanner. In each block of Experiment 2, subjects performed a one-back memory task for a specific predesignated category, deeming one category as task relevant (requiring high level of engagement) and the other category as task-irrelevant (requiring low level of engagement). Note that although the novices show a similar performance for both attended categories, the experts show an enhanced performance for cars compared with airplanes, even though both categories required high engagement.

be modulated by the level of engagement induced by the task. Alternatively, if the neural activity, which has been commonly associated with expertise, reflects top-down controlled high level of engagement of experts with their category of expertise, then the preferential neural activation for cars should be reduced when the car experts need to ignore the cars.

Task-Related Behavior during Scanning

The task-related reaction times (RTs) to correct responses in the magnet are presented in Figure 5*B*. A Wilcoxon signed-ranks test comparing the RT differences in response to cars and airplanes within each group revealed that car experts responded significantly faster to cars than to airplanes ($P < 0.05$, 11 of 13 experts showed the effect), whereas car novices responded equally fast to both stimulus categories ($P > 0.60$, 6 of 15 novices showed faster RTs to cars compared with airplanes). (The nonparametric Wilcoxon signed-ranks test was used due to the small number of data points [8 or less data points per condition per participant]. Accuracy was at ceiling in this task and is thus not reported here.) This finding demonstrates that although both types of objects required similar engagement when they were task relevant, car experts showed a bias for cars compared with airplanes.

Whole-Brain Analysis

Similar to Experiment 1, we assessed car-preferential activations in car experts and in novices by looking in each group for areas that were activated by cars more than by airplanes while being activated by cars significantly above baseline. Importantly, in this experiment, we were able to examine category-selective activation under different levels of engagement, as has been defined above by the conditions: "high engagement" (when the category was "task relevant," similar to Experiment 1), and "low engagement" (when the category was "task irrelevant").

High Engagement Conditions

Contrasting cars with airplanes, both presented in the high engagement conditions, we found once again that the activation patterns differed between the 2 groups, even though the signals in the current event-related design were weaker relative to the block design used in Experiment 1. As can be seen in Figure 6*A* ($P < 0.0001$ corrected, RE, $n = 13$), the car-preferential activity in experts extended beyond the early low-level visual regions, and into high-order object-selective cortex, and it overlapped to some extent face-selective regions. Additional car-selective regions in the experts outside the unimodal visual cortex were observed, including left precuneus, the posterior cingulate, hippocampus, and prefrontal cortex. Note that even in this event-related design (rather than the block design used in Experiment 1) the preferential activation to cars in experts was not confined to a specific hot spot in the visual cortex, and extended beyond the ventral visual cortex. In contrast to the experts, in novices, no

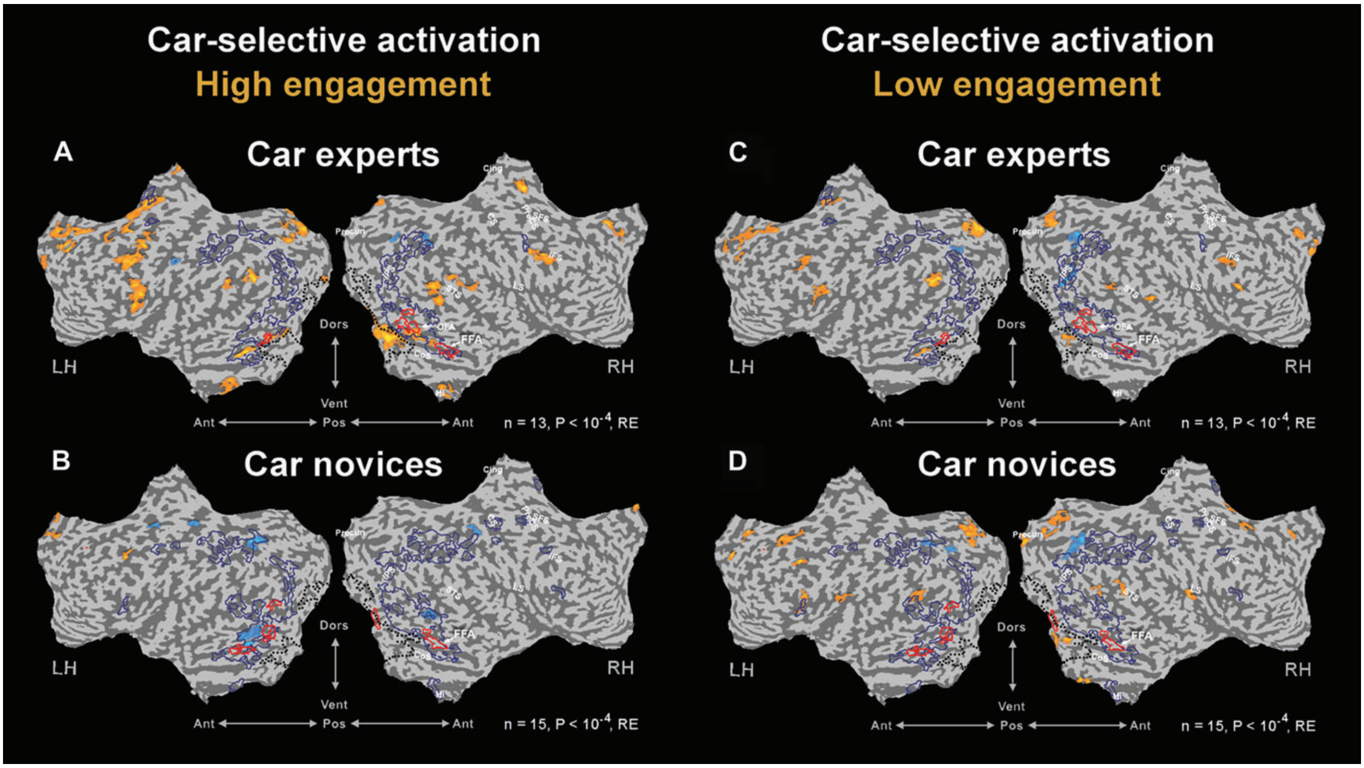

Figure 6. Experiment 2 high and low engagement car-selective activation maps. Experiment 2 multisubject activation maps of car experts and car novices' are displayed on flattened cortical surfaces. Presentation format, anatomical landmarks, and functional borders (black dotted line, red and blue delineation) as in Figure 2. Left column: high engagement (task-relevant) condition of the car experts (*A*) and car novices (*B*). Right column: low engagement (task-irrelevant) condition of the car experts *(C)* and of the car novices (*D*). Yellow to orange patches denote car-selective activation (compared with airplanes) defined by the contrast (cars > airplanes and cars > baseline). The light blue patches denote the negative to that contrast. All the statistical contrasts were obtained with corrected $P < 0.0001$, RE analysis, $n = 13$ experts in the experts maps, $n = 15$ novices in the novices maps.

significant car-preferential foci were detected when both cars and airplanes were task relevant (Fig. 6*B*; $P < 0.0001$, corrected, RE, $n = 14$).

Low Engagement Conditions

The critical question was whether the widespread activation pattern that was associated with car expertise (shown in Experiment 1 as well as in the high engagement condition of Experiment 2) would still be evident when the experts are instructed to ignore the objects of expertise. As can be seen in Figure 6*C*, when car experts were "not" actively engaged with cars, the car-selective activation (contrasted with airplanes) was extensively reduced (compare with Fig. 6*A*).

Car-selective activation was evident in the early visual areas and the left fusiform gyrus, as well as nonvisual areas including the angular gyrus, posterior cingulate cortex, insula and prefrontal regions. However, these regions were also activated in the car novices in this condition (Fig. 6*D*). Indeed, in the absence of intentional engagement, there were no conspicuous differences in activation patterns between experts and novices (see below). In other words, when car experts were instructed to ignore the cars (i.e., with low engagement) the neural expression of expertise was drastically reduced. The behavioral data acquired during scanning (in conjunction with the expertise assessment experiment) indicate that the novices did not have an inherent bias to process either cars or airplanes. (We verified that the airplane and car stimuli were comparable in their general activation patterns by contrasting each 1 of the 4 experimental conditions with a fixation baseline in each group of subjects [see Supplementary Figs. 1–8]).

Similar to Experiment 1, we assessed in Experiment 2 the difference in the extent of car-selective activation between the car experts and the car novices by directly comparing the cars versus airplanes contrast between the 2 groups ($P < 0.0001$, RE, corrected, minimum cluster size of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 15$). This was done separately for the high engagement condition and the low engagement condition. In the high engagement condition, expertise car-selective activity was evident throughout the cortex (Fig. 7*A*). Activated areas included early visual areas, the fusiform gyrus, IPS, precuneus, and precentral sulcus (preCS). Critically, in the low engagement condition this widespread pattern of activation was almost completely absent with the only activated region in left anterior IPS (Fig. 7*B*). This implies that almost no car-selective brain region was differentially activated in the experts compared with novices when the experts were required to direct their attention away from their objects of expertise. Altogether, the results of the direct comparisons between the experts and the novices confirm our findings that high engagement with cars lead to widespread expertise-related activity and that this expertise-related activity was almost completely diminished in the low engagement condition.

In sum, the whole-brain analyses showed that changes in BOLD activity associated with expertise can be top-down modulated by the level at which the experts are engaged in processing objects from their domain of expertise. Similar to

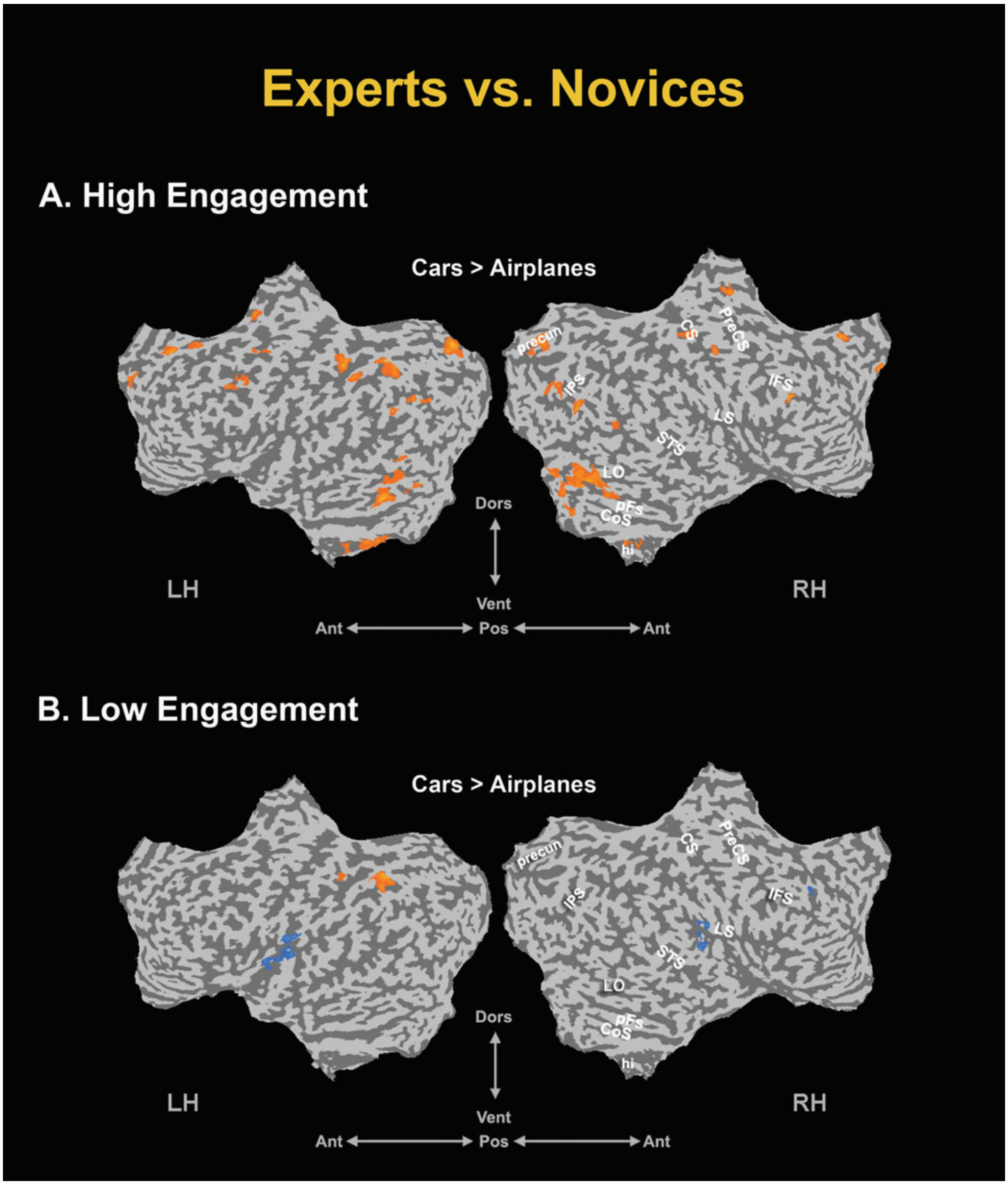

Figure 7. Experiment 2 intergroup comparisons. Experiment 2′s group contrast (Experts vs. Novices) multisubject maps for the cars versus airplanes contrast in the high engagement condition (*A*) and the cars versus airplanes contrast in the low engagement condition (*B*), displayed on flattened cortical surfaces. These statistical maps show up the significant difference between the groups for the contrast specified ($P < 0.0001$, RE, corrected, minimum cluster size of 10 contiguous functional voxels. Experts: $n = 13$, Novices: $n = 14$). Yellow to orange patches denote in (*A*) car-selective regions that were more activated in experts than in novices in the high engagement condition (i.e., defined by the contrast [cars High Engagement > airplanes High Engagement]$_{experts}$ > [cars High Engagement > airplanes High Engagement]$_{novices}$) and in (*B*) car-selective regions that were more activated in experts than in novices (i.e., defined by the contrast [cars Low Engagement > airplanes Low Engagement]$_{experts}$ > [cars Low Engagement > airplanes Low Engagement]$_{novices}$). The light blue patches denote regions exhibited negative results to these contrasts. Presentation format and anatomical landmarks as in Figure 2.

Experiment 1, when the car experts were actively engaged in the processing of cars they differed from novices showing preferential activation for cars in many more brain areas (Fig. 7*A*). The difference between experts and novices was particularly conspicuous in the visual cortex with widespread preferential activity, from visual areas as early as V1 and into high-level object areas. However, when the car experts viewed the same pictures of cars but were not required to actively process them (indeed, they were required to ignore them), the overall preferential car activation was reduced to the extent of activation in novices and the characteristic expertise-related visual activity diminished (Fig. 7*B*).

ROI Analysis

To examine the influence of the expertise and engagement on the BOLD signal in predetermined object-selective areas, we performed ROI analyses. As in Experiment 1, we examined the time courses of activation of Experiment 2 for each of the 2 groups within the FFA, the PPA, the LOC and the early visual areas. Of particular interest were the 2 ROIs that showed expertise effects in Experiment 1, namely, the FFA and the early visual areas.

In the FFA (Fig. 8*A*), ANOVA with Group (experts and novices), as between-subjects factor and Category (cars and airplanes) and Engagement Level (high and low) as within-subjects

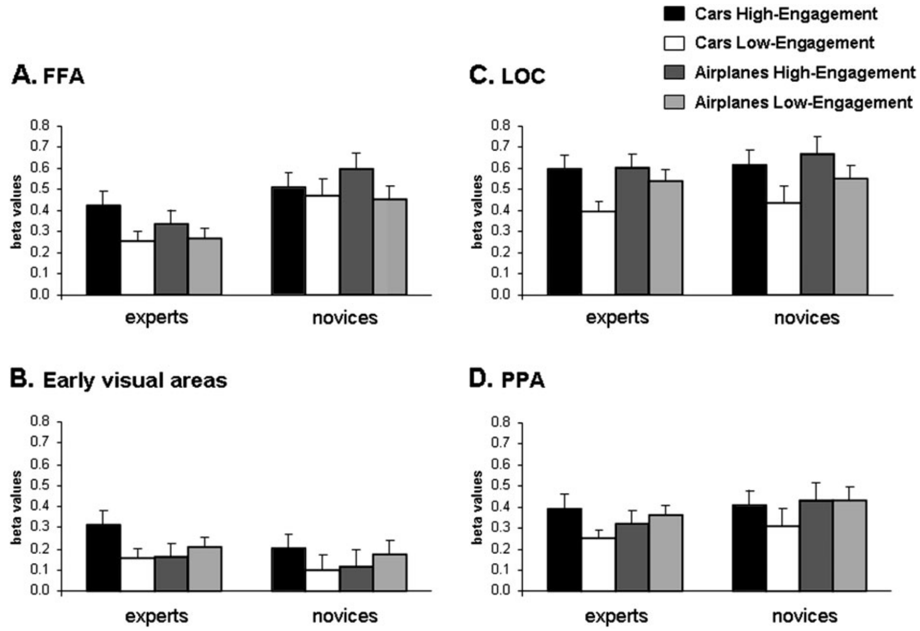

Figure 8. Experiment 2 ROI analysis. Mean activation levels in Experiment 2 to the 4 conditions (cars in the high engagement condition [black], cars in the low engagement condition [white], airplanes in the high engagement condition (dark gray), airplanes in the low engagement condition [light gray]) for the experts and novices in the 4 ROIs (as in Fig. 3, see Materials and Methods for further details). (*A*) FFA, (*B*) Early visual areas, (*C*) LOC, and (*D*) PPA. *Y*-axis denotes mean beta values compared with the fixation baseline condition. See Results for further details. Error bars, SEM.

factors showed that across objects and groups activation was, higher in the high than in the low engagement conditions ($F(1,21) = 10.00$, $P < 0.005$ and overall higher in novices compared with experts ($F(1,21) = 4.67$, $P < 0.05$, see Supplementary Table 2 for details). A significant Group by Category by Engagement Level interaction ($F(1,21) = 5.50$, $P < 0.03$) followed by separate 2-way ANOVA in each group revealed that although in car experts the Category by Engagement Level interaction in the FFA approached significance ($F(1,12) = 3.66$, $P = 0.08$), there was no trend of such interaction in novices ($F(1,9) = 2.06$, $P = 0.19$). In car experts, both categories of objects elicited higher activity in the high engagement than in the low engagement conditions (Cars: $F(1,12) = 8.36$, $P < 0.02$; Airplanes: $F(1,12) = 3.53$, $P = 0.08$). Although the Category by Engagement interaction in experts was not quite significant, it is important to note that the difference between the high engagement and the low engagement conditions was higher for cars (beta value = 0.16) than for airplanes (beta value = 0.07). Thus, the activity of FFA was reduced in experts when they were not actively engaged in the recognition of objects in general and objects of expertise in particular.

The other ROI that was modulated by expertise in Experiment 1 encompassed early visual cortex, functionally defined as regions in the extrastriate cortex, which are not object selective. In contrast to Experiment 1, in the current experiment we found no main effect of Group ($F(1,22) < 1.00$) and no significant interactions with Group in these areas (Category × Group: $F(1,22) = 1.18$, $P < 0.30$; Engagement × Group: $F(1,22) < 1.00$) (Fig. 8*B*, Supplementary Table 2). A significant Category × Engagement interaction effect ($F(1,22) = 9.40$, $P < 0.006$) revealed further that across the 2 groups of subjects airplanes were not influenced by the level of engagement ($F(1,23) = 1.58$, $P > 0.20$), whereas cars were ($F(1,23) = 7.16$, $P < 0.01$): In the high engagement condition, cars elicited a higher response than in the low engagement condition.

The LOC and PPA (Fig. 8*C*,*D*), which did not show any modulation by Group in Experiment 1, did not show any significant modulation by Group in Experiment 2 as well ($F(1,22) < 1.00$ for all interactions with Group in both the LOC and PPA) and no Group main effects ($F(1,22) < 1.00$ for both LOC and PPA) (Supplementary Table 2). Both areas, however, were sensitive to Category and Level of engagement. In the LOC, airplanes evoked a higher activity compared with cars ($F(1,22) = 8.37$, $P < 0.01$), and both object categories evoked greater activity when they were task relevant than when they were not ($F(1,22) = 15.07$, $P < 0.001$). A significant Category by Engagement interaction ($F(1,22) = 4.39$, $P < 0.05$) followed by simple comparisons showed that the effect of engagement was more pronounced for cars than for airplanes (cars: $F(1,23) = 20.49$, $P < 0.001$; airplanes: $F(1,23) = 4.06$, $P < 0.06$). Similarly, in the PPA an exploration of the significant Category by Engagement interaction ($F(1,22) = 10.65$, $P < 0.005$) showed that engagement in the recognition of objects affected cars ($F(1,23) = 7.74$, $P < 0.02$) but not airplanes ($F(1,23) < 1.00$).

To summarize, the ROI analysis of Experiment 2 shows that a combination of the object's category and level of engagement modulates the FFA activity differently in experts and novices. In contrast, the experts and the novices showed the same pattern of activity in early visual areas as well as object-selective areas (LOC and PPA).

Discussion

The goal of the present study was to explore the neural manifestations of acquired expertise in object recognition throughout the cortex and examine whether they could be top-down influenced. Unlike most previous studies, we assessed the distribution of expertise-associated activation across the entire cortex in addition to focusing on specific regions such as face and object-selective areas. In a block design and using a standard 1-back task (Experiment 1), we found extensive expertise-related activity that encompassed multiple brain regions, including low-level visual areas, high-order object and face-selective occipitotemporal regions, as well as parietal and frontal activations. Switching to an event-related design, in Experiment 2, we investigated the possibility that this extensive neural activity, putatively underlying object expertise, reflects (at least in part) the level of engagement that experts might naturally display for their category of expertise. Specifically, we examined whether the neural manifestations of expertise in car experts could be top-down controlled if the task requires the expert to ignore the object of expertise. Although complex in some ways, the results of Experiment 2 largely supported this hypothesis. In the high engagement (task-relevant) condition, the activation elicited by cars in car experts was widely distributed and in that sense reproduced the expertise effects of Experiment 1. In contrast, in the low engagement (task-irrelevant) condition, the extent of neural activation elicited by cars in car experts was diminished and resembled that observed in novices. Therefore, the current results suggest that the neural manifestations of visual expertise, when observed, reflect enhanced engagement of experts with their category of expertise and not necessarily a mandatory operation of perceptual, stimulus-driven expert recognition mechanisms.

Although the widespread car-selective activity in car experts included face-sensitive areas, the bulk of this activity did not fully overlap the FFA and extended much beyond. This pattern indicates that neural manifestations of object expertise are not confined to face-selective regions. One possible reason for this difference is that faces are stimuli for which expertise develops naturally in most people, reflecting their paramount ecological importance. In contrast, expertise for cars develops in some people "intentionally," probably as an outcome of a-priori special interest that these individuals have for cars. We hypothesized that under normal (unconstrained) circumstances, this special interest elevates the engagement that the car experts have with cars in general, which in turn is the main source of the neural activation that distinguishes the processing of cars in car experts from novices. This hypothesis was supported by the findings of Experiment 2. When the experts viewed cars, which they were instructed to ignore, the extent of car-related preferential activation decreased dramatically compared with the broad pattern of activation following high engagement with the same car stimuli. The widespread activation pattern in the high engagement condition appeared also in Experiment 1 where the level of engagement was not controlled. The effect of engagement on the neural expression of car expertise is particularly interesting because this pattern diverges from that observed with faces, a category of natural human expertise, which most probably also engage the observer. However, in contrast to the widespread preferential activation elicited by cars in car experts even in the unconstrained conditions of the present study, faces usually activate preferentially a discrete and selective set of brain regions (Haxby et al. 2000). (This of course does not mean to imply that object categories may not be represented in a distributed fashion across the ventral occipitotemporal cortex [e.g., Haxby et al. 2001; Spiridon and Kanwisher 2002]). Thus, one may ask why in unconstrained conditions faces do not elicit a distributed pattern of activation as wide as that observed in the car experts. Although the answer to this question is not clear and further research is needed, the present data suggest that expertise for faces is based on different principles than expertise for objects. Expert processing of faces is exerted automatically, engaging brain areas that are dedicated to the idiosyncratic aspects of facial information. It may even be the case, that due to their vital importance for humans, faces are neurally coded in a more efficient fashion (Reddy and Kanwisher 2006) even in comparison to other objects of expertise. Conversely, the current data suggest that expertise-related activity induced by intentionally acquired expertise, is less vital for the visual system and, therefore, more susceptible to top-down control and mediated by attentional networks (see also van der Linden et al. 2008).

One criticism regarding the current study could be that it did not include airplane experts. Aside from possibly finding double dissociations, including such a group might have circumvented the difficulty in interpreting how comparable are the car and airplane stimuli in the car experts and novices (but see Supplementary Material). However, comparing car experts and airplane experts might also be problematic, as different types of expertise might require different types of diagnostic information (Harel and Bentin 2009), which might be expressed in the recruitment of distinct brain regions (Bukach et al. 2006).

The suggestion that top-down influences and attention play a modulating role in the neural responses associated with expertise originated from a debate concerning the functional nature of the FFA. An ongoing debate revolves over the role of the FFA in object expertise and whether the face-preferential activity exhibited in this region is, indeed, face-specific or reflects detailed within-category visual processing automatized by expertise (see Bukach et al. 2006 vs. McKone et al. 2007). The current findings support the former view, as expressed in a recent review (McKone et al. 2007). To account for previously reported expertise effects in the FFA, McKone and her colleagues argued that experts pay more attention to their objects of expertise and that this augmented attention is reflected by corresponding increases in the response of the FFA (as well as other extrastriate regions). Only 2 previous fMRI studies investigated the "attentional" account. Gauthier, Skudlarski, et al. (2000) used 2 different types of tasks (location and matching) to show that expertise is not task dependent. However, the use of a block-design paradigm in that study prevents drawing strong conclusions because experts could have anticipated the category of the stimuli presented in the different blocks, and this might have increased their level of engagement with their objects of expertise compared with blocks of other objects. Although another study (Xu 2005) used, indeed, an event-related design in an experiment very similar to Gauthier et al., the task relevance of the different stimuli was not manipulated and, therefore, that study could not assess the effect of controlled engagement. We addressed both these limitations in the present study assuming that when a stimulus is not task relevant, the typical observer would not be highly engaged with it, and would not allocate resources to process it beyond basic level.

Although our findings point to the widespread nature of expertise-related activity in brain regions other than the FFA, they do not rule out the possibility that the FFA may also be involved in the manifestation of object as well as face expertise. Indeed, in Experiment 1, the magnitude of the FFA response was slightly modulated by expertise. However, car expertise was not expressed by increased activation for cars (Gauthier, Skudlarski, et al. 2000; Xu 2005) but rather by decrease in the FFA activation for faces. This result might reflect a competition between faces and nonface objects of expertise for neural resources within the FFA (Gauthier et al. 2003; Rossion et al. 2007). Supporting this conjecture, originated from ERP N170 studies, a previous study showed that training a prosopagnosic patient in discriminating between a highly homogeneous category of artificial objects ("Greebles") resulted in an increase in Greeble selectivity in FFA coupled with a concomitant decrease in face selectivity (Behrmann et al. 2005). The authors suggested that the neural systems that mediate face and Greeble recognition are shared and, therefore, if these systems turned to be fine tuned to the properties of Greebles, their tuning to the processing of face details is reduced. Unfortunately, although our results tend to support this interpretation, our experimental design does not allow a direct test of this hypothesis because it did not confront directly faces and cars. Future research utilizing, for example, interference paradigms (cf., Rossion et al. 2007) is needed to investigate the degree of overlap in tuning properties between faces and objects of expertise in FFA.

The influential role of top-down factors on the manifestation of expertise in the brain is further supported by the results of ROI analysis in Experiment 1. This analysis showed expertise-associated activity in early visual areas, which are not category specific but modulated by top-down attention (Moran and Desimone 1985; Luck et al. 1997; Watanabe et al. 1998; Martinez et al. 1999). Hence, the preferential activation observed in car experts in the early visual cortex when they were highly engaged with the stimuli might reflect top-down attentional enhancement initiated by experts while processing object of expertise without task constraints (see also Bar 2003; Ahissar and Hochstein 2004).

Intriguingly, in Experiment 2, the interaction between Expertise, Category, and Engagement level did not reach significance in the early visual areas. In fact, the findings of Experiment 1 might lead one to expect a difference in magnitude between cars and airplanes in car experts. Moreover, this difference should have been more conspicuous in the high-level engagement than in the low-level engagement. Not fulfilling this expectation, a similar Category by Engagement level interaction was found in both experts and novices. Although null results are difficult to interpret, these findings may stem from specific differences between the settings of Experiments 1 and 2. For example, Experiment 1 required detecting a repetition of a stimulus that was always presented among other exemplars of the same category. In contrast, Experiment 2 required from the subjects not only to detect repeated stimuli but also to actively ignore repeated and nonrepeated stimuli from a second, competing category. These differences may also explain why the novice car activation in the high engagement condition did not show the same pattern of activation as in Experiment 1. It is possible that the more taxing nature of the task in Experiment 2 relative to Experiment 1 resulted in equal level of processing of cars and airplanes in novices culminating in the almost lack of object selectivity (Fig. 6*B*). Experts on the other hand, due to their inherent bias to attend to cars were able to overcome this difficulty resulting in the extensive car-preferential activation (Fig. 6*A*). Perhaps even the need to ignore stimuli, which for experts could require more effort when the ignored stimuli are cars, actually raises the level of engagement/effort/attention needed for task performance. Future research should aim to quantify the specific effects of different task demands on the extent and nature of the expertise-related neural activation.

At a more theoretical level, it is important to note that perceptual expertise and engagement are not necessarily mutually exclusive. In fact, changes in brain activity induced by expertise might reflect either of these 2 factors or a combination of both. For example, certain computational models of expertise and category learning suggest that patterns of selective attention "can become manifest in the very perceptual representations that support categorization, perhaps to the level of neurons representing objects in inferotemporal cortex" (Palmeri et al. 2004, p. 383). However, these attentional accounts of the acquisition of expertise consider selective attention to operate on features or dimensions that are diagnostic for recognition (Sigala and Logothetis 2002; Palmeri et al. 2004) while we refer primarily to the consequences of intentional interest and/or "top-down task-based attention" (Reddy et al. 2007). Note that the latter is most often brought as an alternative account of the findings of object expertise studies. Based on the current outcome, we suggest that task relevance (or top-down task-based attention) has a major influence on the neural and perceptual expressions of expertise. Although expertise is, indeed, knowledge of relevant diagnostic features discriminating among individual objects of expertise, the application of this knowledge is optional and not mandatory. It may not manifest if the task leads the expert to ignore the objects of expertise or alternatively, it may be modulated by the expert's own goals in specific contexts.

Support for our interpretation of expertise and its consequence on perception comes from 2 sources: First, previous studies of the neural manifestations of task relevance showed that this factor modulates activation of a network of brain regions including the temporoparietal junction, precuneus, anterior insula, anterior cingulate cortex, and right thalamus (Downar et al. 2001). These areas were also identified as responsive to detection of stimulus changes in a neutral behavioral context (Downar et al. 2000, 2002). In the current study, when cars were task relevant, car experts showed preferential activation in areas similar or neighboring to the areas associated with task relevance. However, as noted above, cars in experts also preferentially activated additional areas when they were relevant; these were visual regions starting from V1, through extrastriate cortex and going into posterior fusiform gyrus, hippocampus, and dorsolateral prefrontal cortex (DLPFC). Therefore, we suggest that expertise interacts with or activates frontoparietal-cingulate attentional networks that are usually dedicated to identifying and evaluating salient sensory stimuli, which accounts for the widespread activity found in Experiments 1 and 2. However, task manipulations could overcome the seemingly inherent salience of objects of expertise and inhibit the expertise-associated neural response in car experts, as preferential activation was drastically reduced throughout and notably absent in the occipitotemporal cortex even in car experts when the cars were irrelevant for the task (see also Experiment 2′s FFA ROI analysis).

It may be argued that the extensive recruitment of the attentional frontoparietal network in experts compared with novices might be attributed at least in part, to eye movement control. This possibility would be a caveat for our interpretation of the results in Experiment 1 where the stimuli were presented for 500 ms. Although it is quite reasonable that car experts might have screened the car images differently than novices, the influence of this strategy on the frontoparietal network was diminished in Experiment 2 in which the stimuli exposure time was only 200 ms, which is commonly accepted as being too short to allow saccadic movements. Critically, the widespread expertise-related activity was still evident using this brief presentation time (see Figs. 6*A* and 7*A*). In addition, it is important to note that even if the expertise-related BOLD activity would be associated with differential eye movements, it was drastically reduced when the attention of the experts was diverted away from their objects of expertise, meaning that this activity indeed reflects the level of engagement of experts with their objects of expertise.

A second source of support comes from a recent study showing that encoding as well as maintenance of artificial objects of expertise in visual working memory activated areas outside the occipitotemporal cortex to a higher extent than novel objects (Moore et al. 2006). These areas were the IPS, DLPFC, the preCS, the posterior and anterior cingulate cortex, and the right thalamus, a network of areas overlaps to a great extent with the areas that were associated in our study with the enhanced activity for objects of expertise compared with regular objects as well as with the attentional network dedicated to identifying and evaluating salient sensory stimuli (Downar et al. 2002). Indeed, subjects in the present study were engaged in a one-back memory task, which demands explicit encoding and retention of objects in working memory. This encoding and retention activity was associated with a greater extent of activation in experts than in novices, pointing to the "differential" encoding (or engagement) of the objects of expertise by the experts compared with novices.

In conclusion, the 2 experiments in the present study show that object expertise under unconstrained engagement conditions has a distinct neural signature, which is different than the neural manifestation of face expertise. The neural areas that are preferentially activated by expertise for objects are not limited to a number of "hot spots," but rather constitute a large-scale distributed network, which operates when experts are highly engaged in the recognition of objects from their domain of expertise. The current findings support a new conceptualization of the cognitive and neural processes involved in object expertise. We propose that the preferential activation associated with object expertise is elicited only if the expert is voluntarily engaged in processing the diagnostic features either because these are task relevant or because there are no task constraints limiting this process. Specifically, reducing the engagement level of the expert experimentally reduces the selective cortical activity underlying the expert object recognition.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

Funding

National Institute of Mental Health (R01 MH 64458 to S.B.); Israel Foundations Trustees Program for the Advancement of Research in the Social Sciences (Research Grant for Doctoral Students in the Social Sciences to A.H.).

Notes

Conflict of Interest: None declared.

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