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Engagement of Fusiform Cortex and Disengagement of Lateral Occipital Cortex in the Acquisition of Radiological Expertise

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The human visual pathways that are specialized for object recognition stretch from lateral occipital cortex (LO) to the ventral surface of the temporal lobe, including the fusiform gyrus. Plasticity in these pathways supports the acquisition of visual expertise, but precisely how training affects the different regions remains unclear. We used functional magnetic resonance imaging to measure neural activity in both LO and the fusiform gyrus in radiologists as they detected abnormalities in chest radiographs. Activity in the right fusiform face area (FFA) correlated with visual expertise, measured as behavioral performance during scanning. In contrast, activity in left LO correlated negatively with expertise, and the amount of LO that responded to radiographs was smaller in experts than in novices. Activity in the FFA and LO correlated negatively in experts, whereas in novices, the 2 regions showed no stable relationship. Together, these results suggest that the FFA becomes more engaged and left LO less engaged in interpreting radiographic images over the course of training. Achieving expert visual performance may involve suppressing existing neural representations while simultaneously developing others.

Keywords: diagnosis, expert, FFA, radiology, vision

Introduction

Human visual cortex contains many distinct regions that respond more strongly to images of objects than to more simple patterns (for reviews, see Grill-Spector 2003; Op de Beeck et al. 2008). These include the lateral occipital cortex (LO) and more ventrally, the posterior fusiform cortex. Together, these areas have been termed the lateral occipital complex. The ventral surface of the anterior occipital lobe and posterior temporal lobe is also object selective and includes a region that is highly responsive to images of faces, the fusiform face area (FFA, Kanwisher et al. 1997).

Object processing in human cortex appears to be hierarchical. Neurons in anterior regions show responses that are more closely tied to conscious recognition of object identity than neurons in LO (Bar et al. 2001; Grill-Spector et al. 2004). Conversely, neural responses in LO are more affected by stimulus transformations that do not affect object identity such as image size and retinal location (Grill-Spector et al. 1999; Eger, Kell, and Kleinschmidt 2008). Neurons in LO also integrate information over a smaller portion of the object than neurons in more anterior areas (Lerner et al. 2001, 2002), and LO neural responses are most closely related to physical measures of similarity between objects, whereas fusiform responses are more closely related to subjective measures of similarity (Haushofer et al. 2008). LO responses do not distinguish between real and "nonsense" objects, whereas anterior responses do (Vuilleumier et al. 2002). Developmentally, LO is relatively stable from ages 7–16, while areas on the fusiform gyrus specialized for faces and places increase in size (Golarai et al. 2007; Scherf et al. 2007; Grill-Spector et al. 2008). Together, these results suggest that LO may contain a representation of the shape of objects (Vinberg and Grill-Spector 2008), and the more ventral and anterior areas explicitly encode object identity.

Object selective cortex retains considerable plasticity in the adult, but the precise nature of this plasticity remains unclear. Training subjects in the laboratory to recognize briefly presented objects or to make fine discriminations between artificial stimuli generally increases neural response strength to the trained stimuli in both parts of fusiform cortex and parts of LO (Gauthier et al. 1999; Grill-Spector et al. 2000; Op de Beeck et al. 2006; Jiang et al. 2007; but see Yue et al. 2006). Shape discrimination training also appears to narrow neural tuning in LO (Yue et al. 2006; Jiang et al. 2007). Complementing these relatively short-term training studies (in which subjects received about a week of practice) are examinations of real-world experts with years of experience in a given domain. Expertise in birds, cars, and butterflies produces increased activity for objects of expertise primarily in ventral cortex (Gauthier et al. 2000; Rhodes et al. 2004; Xu 2005; but see Grill-Spector et al. 2004). Most of these studies, however, focused upon the FFA and did not localize a priori regions of interest in LO, and one study that examined LO responses post hoc actually found a decrease in activity with expertise (Gauthier et al. 2000).

The goal of the present work is to examine responses in both fusiform cortex and LO across the development of real-world expertise. We conducted a cross-sectional study of radiologists, who, in addition to their knowledge of disease processes, have documented visual expertise in detecting features of radiographic images (e.g., Sowden et al. 2000). We used functional magnetic resonance imaging (fMRI) to compare neural activity in first-year radiology residents ($n = 7$), fourth-year radiology residents ($n = 6$), and practicing expert thoracic or general radiologists ($n = 5$ and 2, respectively) as they detected abnormalities in chest radiographs. We first identified regions of interest in cortex, including the FFA, the part of LO that responded to chest radiographs, and retinotopic visual areas (see Fig. 1*A*,*B* and Materials and Methods, below). We then acquired a separate data set in which participants performed a diagnosis task, judging whether a specified location in a radiograph contained an abnormality or "nodule" (Fig. 1*C*). We averaged fMRI activity within each region of interest (ROI) and compared that activity with behavioral performance in the diagnosis task. We hypothesized that more

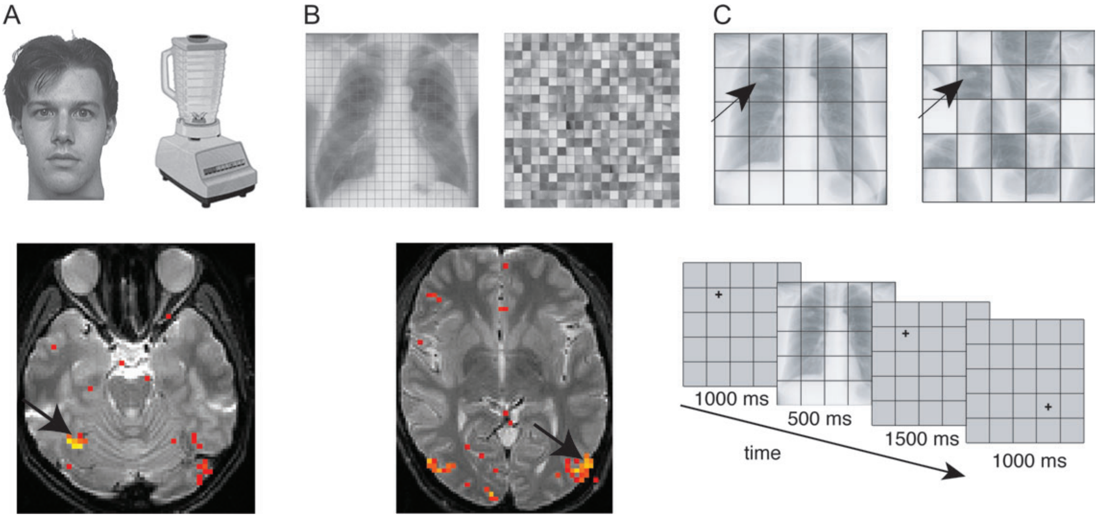

Figure 1. Experimental methods. (*A*) Example face and object used in face localizer scan and sample results from one participant. Arrow indicates the FFA; voxels were thresholded at $r > 0.25$. (*B*) Example images used in radiograph localizer scan and results from one participant. Arrow indicates left LO; voxels were again thresholded at $r > 0.25$. (*C*) Upper: example intact and scrambled radiographs used in the diagnosis scan; arrow (not seen by subject) indicates location of lung nodule. Lower: stimulus sequence in diagnosis scans: 500 ms stimulus presentations were preceded by 1000 ms and followed by 1500 ms fixation periods.

anterior areas of ventral cortex would show greater activity in experts.

Materials and Methods

Participants

Participants were recruited at the Department of Radiology at University of California, Los Angeles (UCLA) Medical Center from 3 volunteer subject populations: practicing thoracic radiologists ($n = 7$; 3 females; mean age = 51.6), fourth-year radiology residents ($n = 7$; 3 females; mean age = 30.9), and first-year radiology residents ($n = 7$; 2 females; mean age = 28.6). Practicing radiologists had at least 10 years experience postresidency (mean = 18.9 years). One fourth-year resident had large uncorrectable motion artifacts in his fMRI data and was excluded from all further analyses. In general, attrition rates are low across residency in Radiology. All participants had normal or corrected-to-normal vision. Informed consent was received from each participant, and all experimental procedures were approved by the UCLA Office for the Protection of Research Subjects.

Apparatus

Data were collected inside a magnetic resonance imaging (MRI) device while participants underwent functional scans of their brains. Stimuli were displayed on MR-compatible goggles controlled by a Macintosh frame buffer. The goggle display subtended 31 degrees of visual angle horizontally and 23 degrees vertically. While viewing stimuli, participants indicated their responses with an MR-compatible button box equipped with 4 buttons.

Stimuli

Stimuli were normal and abnormal chest radiographs obtained from a commercially available CD published by the Japanese Society of Radiological Technology (JSRT) in cooperation with the Japanese Radiological Society. Each abnormal radiograph contained a single lung nodule, a potentially malignant round lesion located in the lung field. The abnormal radiographs were further divided by the JSRT publishers into 3 difficulty levels. An expert thoracic radiologist independently evaluated each image and excluded images with the most difficult-to-detect nodules and those of poor image quality. This resulted in a usable set of 92 normal and 100 abnormal radiographs.

Two versions of each radiographic image were used in the main part of the experiment: intact and scrambled (Fig. 1*C*). The 2 radiograph types, normal and abnormal, were crossed with the 2 image types, intact and scrambled, to yield 4 total stimulus conditions. Scrambled radiographs were created by dividing each image into 25 squares and randomly shuffling the location of all but one of those squares. The one square that remained in its original location in each image was, for the abnormal radiographs, the square that contained the lung nodule and, for the normal radiographs, the square that was cued as a possible nodule location. Cue locations for the normal radiographs were matched to actual nodule locations in the abnormal radiographs. To ensure that each cue was a plausible nodule location, cue location assignment for the normal radiographs was determined by a postresidency radiologist at UCLA Medical Center who did not participate as a subject in the study.

Because scrambling the radiographs introduced vertical and horizontal lines in the images, grids were drawn on all stimuli, both intact and scrambled. Each lung nodule was entirely contained within a square and never obscured by the grid. For sample intact and scrambled nodule-containing radiographs, see Figure 1. All images were square and subtended a visual angle of approximately 19 degrees.

fMRI Procedures

Each participant completed one 80-min scanning session followed by an expertise posttest completed outside of the scanner. The scanning session contained several anatomical scans, 3 localizer scans, and 3 rapid event-related scans. Localizer scans were used to define regions of interest. Examples of images used in the localizer scans are shown in Figure 1.

Localizer Scans

To define visual cortical areas selective for processing faces, participants viewed 8 blocks of faces in alternation with 8 blocks of objects. Note that rest or fixation blocks were not placed between the blocks of faces and objects. Nine images were shown per stimulus block; 72 faces and 72 objects were displayed in total. Each image was presented for 1.7 s with 0.3-s interstimulus intervals yielding a block duration of 18 s. To control for attention, participants performed a 1-back task. On one in every 9 stimulus presentations, on average, the same image was shown on successive trials. Participants were instructed to press a button when an image repeated in this fashion. Performance on the one back task was 81% correct for novices and 85% correct for experts; these means did not differ reliably.

To identify regions of object selective cortex, including LO, that might be specialized for processing radiographs, participants viewed

8 blocks of intact radiographs in alternation with 8 blocks of scrambled radiographs. Note again, that rest or fixation blocks were not placed between the blocks of intact and scrambled radiographs. Scrambled radiographs for the localizer scan were finely scrambled; each image contained 100 equal-size squares (Figure 1*B*). Nine images were shown per stimulus block; 32 unique radiographs were shown during the localizer scan, repeated as necessary to yield a total of 72 intact presentations and 72 scrambled presentations. Each image was presented for 1.7 s with 0.3-s interstimulus intervals yielding a block duration of 18 s. Radiographs shown in the localizer scan were not shown in any event-related diagnosis scans. To control for attention, participants performed a 1-back task as described above for the face localizer scan (note that participants did not perform a diagnosis task on these images). Performance on the one back task was 96% correct for novices and 99% correct for experts; these means did not differ reliably.

We also employed standard retinotopic mapping procedures (Engel et al. 1994; Sereno et al. 1995; DeYoe et al. 1996) to identify retinotopic visual areas (e.g., V1, V2, and V3). Participants fixated on a square positioned in the center of the display. A wedge filled with a high contrast temporally reversing checkerboard pattern rotated around fixation, completing one rotation every 30 s. To keep participants fixated and attending, the fixation square intermittently changed from black to white or vice versa. Participants were instructed to press a button as rapidly as possible each time fixation changed color.

Experimental Scans

The diagnosis scans were event-related scans in which participants viewed intact and coarsely scrambled radiographs and judged whether a cued region in each radiograph contained a lung nodule (Fig. 1*C*). A new trial occurred every 3.0 s. The sequence of a single trial was as follows: 1) a grid the same size as the radiographs was displayed for 1000 ms. The grid contained a fixation cross in the unit of the grid that the subject was to judge. Participants were instructed to move their eyes to the fixation cross and then to remain fixated at that location for the remainder of the trial. 2) The grid, but not the fixation cross, remained on the screen and a radiograph was displayed for 500 ms. 3) The radiograph was removed, but the grid and fixation remained for 1000 ms.

Each scan consisted of 124 trials composed of 25 radiographs in each of the 4 stimulus conditions: 1) intact, normal; 2) scrambled, normal; 3) intact, abnormal; 4) scrambled, abnormal, and 24 rest trials in which no radiograph was presented. Condition order was counterbalanced using an m-sequence (Buracas and Boynton 2002).

Functional MRI data were acquired using a blood oxygen level–dependent contrast-weighted echo-planar pulse sequence (3T; time echo = 25; time repetition = 3 s; flip angle = 90; field of view = 20 × 20 cm; voxel size = 3.125 × 3.125 × 4 mm; 36 slices parallel to the anterior-posterior commissure line). High-resolution conventional anatomical images were acquired coplanar to the functional data, and T_1-weighted volumetric scans were acquired for cortical flattening.

fMRI Data Analysis

Localizer scans were analyzed by simple correlation of each voxel's time series with a sinusoid at the stimulus frequency. Because the face localizer and radiograph localizer scans did not include rest blocks, this correlation effectively measured the reliability of the difference between activity in the 2 conditions (faces vs. objects or intact vs. scrambled localizers). Active pixels were identified as those with a correlation above a threshold whose activity was in-phase with the stimulus. Different threshold levels were tested for area identification; the overall pattern of results did not depend upon threshold.

Event-related scans were analyzed using the general linear model and the "Finite Impulse Response" approach. The design matrix contained regressors for each time point in the response for each condition. Estimates for each regressor were computed using ordinary least squares from the average timecourse of active voxels in each visual area. The amplitude of the response for each condition was computed as the peak of the estimated impulse response, excluding the first and last time points. This peak was computed independently for each subject, and so the time point at which it occurred varied slightly between subjects. Other estimates of response amplitude (e.g., area under the curve and fit model hemodynamic response) yielded similar results.

ROI Identification

Following standard techniques, the FFA was identified as voxels in the mid-fusiform gyrus that were active in the face localizer scan (Kanwisher et al. 1997). The occipital face area (OFA) was identified as voxels on the posterior lateral surface of the occipital lobe that were active in the face localizer scan. Areas on the lateral aspect of the occipital lobe that were consistently active in the radiograph localizer scan were defined as LO. Additional contiguous areas on the ventral surface of the occipital lobe were also identified; this region corresponds to the posterior fusiform gyrus and has been annotated pFus as in other studies. Note that the regions in LO and pFus identified in this way correspond to only a subset of the larger lateral occipital complex that is often identified by comparing images of other types of objects to textures (Malach et al. 1995).

Correlating Behavior and Neural Activity

We computed Pearson correlation coefficients between participants' estimated response amplitudes and behavioral performance on the diagnosis task. Corresponding Student's t values were also computed. To test whether our results were due to low-performing subjects, we removed subjects from the analysis when their performance was below a d' of 0.75. Two subjects were below this threshold for scrambled radiographs only; these data were removed from the correlation analysis and only data for intact radiographs (both activity and performance) were used. One subject was below d' of 0.75 for both intact and scrambled objects, and their data were completely removed from the analysis.

To compare correlations between groups, we conducted a randomization analysis in which participants were assigned to groups at random, and the correlation between behavior and FFA activity was computed for each group. The difference between group correlations was then computed. This randomization was repeated 1000 times, yielding a null distribution of group correlation differences from which p values were computed.

General Expertise Posttest

To provide a measure of general radiology expertise, each participant completed a posttest outside of the scanner. The posttest consisted of 15 chest radiographs selected from radiology board certification training images. Test items ranged in degree of diagnosis difficulty, for example, pneumopericardium, aortic aneurysm, and mitral valve calcification. Participants were allowed to view each image freely under no time constraints and were asked to provide a written diagnosis for each. An expert radiologist at UCLA Medical Center who was not a participant in the study scored expertise posttests.

Results

Practicing radiologists and fourth-year residents performed better than first-year residents on the test of general radiological expertise, conducted after scanning (see Materials and Methods). Group average scores were 86.67%, 70.00%, and 38.10% correct, respectively. Four years of intense training appears to have allowed the fourth-year residents to approach knowledge levels of the practicing radiologists. Because the difference between fourth-year residents and practicing radiologists was relatively small, we combined these 2 into one group, called "experts." Experts reliably outperformed novices on the test of general radiological expertise ($t = 6.96$, $p < 0.001$).

Visual expertise, measured using the diagnosis task performed in the scanner, showed a similar pattern (see Fig. 2). Practicing and fourth-year radiologists' performance was again relatively close and above that of first-year radiologists ($d' = 1.26$, 1.19, and 0.97 for the 3 groups, respectively). The difference between experts and novices was reliable ($t = 2.1$, $p < 0.03$).

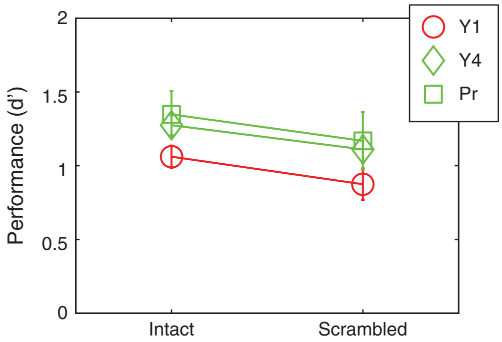

Figure 2. Average performance (d') on nodule detection task in intact and scrambled radiographs for 3 subject group expertise levels: practicing radiologists, fourth-year residents (Y4), and first-year residents (Y1). Error bars are ±1 standard error of the mean.

Table 1
Average ROI sizes (mm^3)

	First years (n = 7)	Fourth years (n = 6)	Practicing (n = 7)
Right FFA	505	539	402
Left FFA	318	344 (1)	345 (1)
OFA	758 (1)	518	313 (1)
Left LO	1422	789	783 (2)
Left pFus	1170	625 (3)	827 (1)
Right LO	960	1084	940
Right pFus	1957	1016	1537

Note: Entries are the average ROI sizes for each group. The numbers in parenthesis indicate the number of participants from each group for whom no ROI could be identified; these participants were not included in the averages. Except for the left LO, ROI sizes did not differ reliably between groups.

On average, performance on the diagnosis task was lower when radiographs were scrambled compared with intact; this scrambling effect was small but reliable (d' = 1.05, 1.23 for scrambled and intact, $F_{1,17} = -13.49$, $p < 0.01$). Scrambling the images did not affect the groups differently ($F_{2,27} = 0.02$), and so most analyses combine data from intact and scrambled trials.

Fusiform Face Area

A discrete region of activity in the right fusiform gyrus was identified in all subjects (see Fig. 1 and Table 1). Corresponding activity in the left hemisphere was evident in all but 2 subjects, and this region was on average much smaller than in the right hemisphere. During the radiograph diagnosis scans, overall activity was moderate in the right FFA (hereafter, simply FFA) and did not differ reliably between novices and experts (Fig. 3).

To examine in detail the relationship between visual expertise and neural activity, we correlated performance during diagnosis scans with the amplitude of the FFA response, across participants. The fMRI response amplitude (hereafter referred to as activity) in the FFA correlated reliably with visual expertise as measured by diagnosis performance ($r = 0.55$, $p < 0.01$). Figure 3 shows the scatter plot of FFA activity against expertise.

The correlation between visual expertise and FFA activity was stable. It was evident for correlations conducted separately on intact and scrambled images ($r = 0.49$, 0.54). The correlation was also not due to subject age. To test this, we first correlated performance with age and then correlated the residuals from this regression with FFA activity. The FFA activity correlated reliably with the residuals ($r = 0.56$, $p < 0.01$). The correlation was additionally not explainable by general responsiveness of the FFA. Regressing out activity in the FFA localizer scans revealed a reliable residual correlation with performance ($r = 0.55$, $p < 0.01$).

Because our measure of expertise was performance during scanning, it was important to verify our results did not simply reflect experts' greater success at the task. To control for this, the radiographs were chosen from 3 levels of difficulty determined a priori. For each subject, we examined FFA activity for the set of trials at the single level of difficulty where performance was closest to d' = 1.25. For experts, this tended to be the more difficult levels, whereas for novices, it tended to be the easier levels. Even for these trials, where the groups' success at the task was matched (average d' = 1.1 for novices and 1.09 for experts), activity in the FFA correlated with our behavioral measure of visual expertise, overall performance in the scanner ($r = -0.50$, $p < 0.02$).

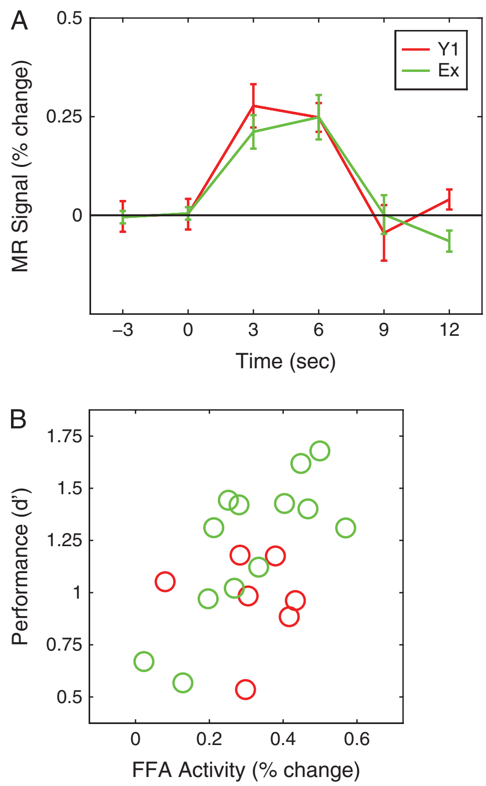

Figure 3. Activity in the FFA during diagnosis scans. (*A*) Average fMRI time courses for each group; the expert group consisted of both fourth-year residents and practicing radiologists. Error bars indicate one standard error of the mean. (*B*) Scatter plot of the amplitude of fMRI response with performance of the diagnosis task during scanning for first years and experts. Colors are as in subplot (*A*).

Three subjects—2 experts and 1 novice—performed relatively poorly on the diagnosis task. This may have been due to difficulty with the speeded task, the visual display apparatus, or the scanner environment, all of which differed from traditional diagnosis. Regardless, the relationship between FFA activity and performance was not due to these potential outliers, as can be seen by inspecting Figure 3*B*. Removing data when performance was below a threshold d' of 0.75 still yielded a reliable correlation ($r = 0.47$, $p < 0.02$).

Responses in the FFA were not reliably affected by stimulus condition. Activity did not reliably differ between images that contained nodules and those that did not. It also did not differ reliably between intact and scrambled radiographs. This pattern held for all ROIs examined.

Activity in the left FFA during the diagnosis scans was weak and did not differ between groups. It also did not correlate with expertise.

Occipital Face Area

The OFA was identifiable reliably only in the right hemispheres of our subject population. Weak activity was seen in the left hemisphere generally, but clear ROIs were identifiable in less than half of our participants. The right OFA was more active in first-year residents than in experts during the diagnosis scans ($F_{1,16} = 5.99$, $p < 0.05$). This activity did not correlate with expertise ($r = -0.08$).

LO and Posterior Fusiform Gyrus

All participants showed activity in LO during the radiograph localizer scan (Fig. 1; Table 1). We identified separable foci of activity in LO and the posterior fusiform gyrus and analyzed the data separately for each region in each hemisphere. The focus in left LO was larger in novices than in experts (Table 1; $F_{1,16} = 5.88$, $p < 0.05$) and showed a trend toward higher activity in novices than in experts in the diagnosis scans ($F_{1,16} = 2.8$, $p < 0.11$; Fig. 4).

Activity in left LO showed a negative correlation with visual expertise (Fig. 4; $r = -0.53$, $p < 0.02$). This correlation held for both intact and scrambled stimuli ($r = -0.57, -0.44$). The correlation also could not be accounted for by age ($r = -0.47$ on residuals, $p < 0.05$). The correlation also remained after removing potential outlier data below a d' of 0.75 ($r = -0.49$, $p < 0.05$).

The negative correlation between left LO activity and visual expertise was not due to general effort or attention. It is in theory possible that subjects who performed better on the task did so with less effort or attention, which in turn led to reduced activity in left LO. Such an explanation, however, would predict a similar pattern in other visual areas that are known to be modulated by attention. Our findings of an opposite pattern in FFA and no relationship between performance and robust activity in right LO (see below) argue against a general effort account.

Nevertheless, to rule out both effort and task success as an account for our results, we again analyzed a subset of our data that were matched for task performance. The data were chosen using the 3 levels of difficulty assigned to the stimuli; for each subject, we examined LO activity in the subset of trials at the single level of difficulty where performance was closest to $d' = 1.0$. Even for these trials, where presumably effort was greater for novices than experts (average d' was 0.874 for novices and 0.868 for experts), activity in left LO correlated with visual expertise ($r = -0.51$, $p < 0.02$).

Although active left LO was larger in novices than in experts, this difference did not account for the observed correlation between expertise and activity. A control analysis that used data only from the most active voxels in each subject still found a reliable correlation between expertise and performance ($r = -0.50$, $p < 0.02$; 40 most active voxels).

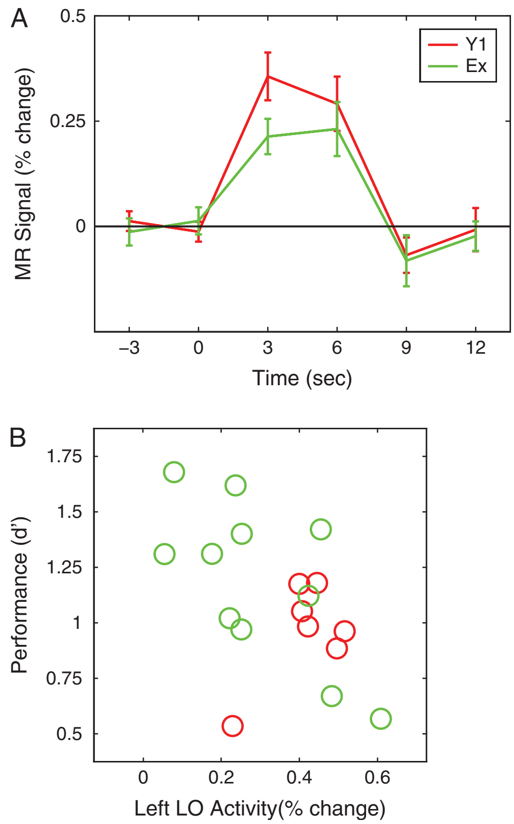

Figure 4. Activity in left LO during diagnosis scans. (*A*) Average fMRI time courses for each group; error bars indicate one standard error of the mean. (*B*) Scatter plot of activity with performance of the diagnosis task during scanning for first years and experts. Colors are as in subplot (*A*).

Activity in left LO was also negatively correlated with activity in the FFA (Fig. 5; $r = -0.47$, $p < 0.05$). Subjects in which LO activity was relatively high showed FFA activity that was relatively low and vice versa.

Left pFus showed a weak negative correlation with visual expertise ($r = -0.18$, n.s.). Right LO and pFus showed no correlation with expertise ($r = 0.10, -0.08$, respectively). None of these areas showed overall activity differences between novices and experts.

Retinotopic Visual Areas

Retinotopic areas did not show reliable correlations between activity and expertise; however, they generally did show trends for negative correlations and greater activity in novices than in experts during the diagnosis task. This latter difference was reliable only in V1 ($F_{1,18} = 4.475$, $p < 0.05$). V1 activity did not account for the negative correlation found in left LO ($r = -0.51$, $p < 0.02$ on residuals).

Discussion

Our results reveal a striking double dissociation between radiological visual expertise and cortical area activation. Activity in the FFA correlated positively with expertise, whereas activity in left LO correlated negatively. One interpretation of this pattern is that the acquisition of expertise

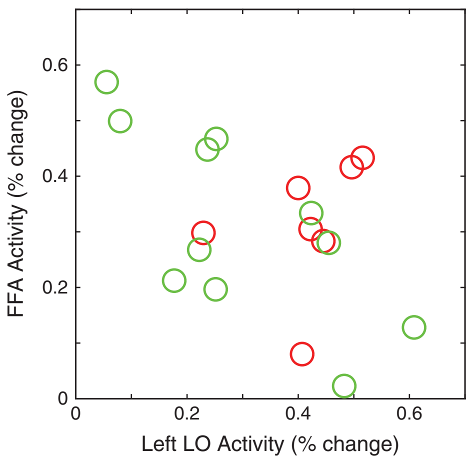

Figure 5. Scatterplot of activity in FFA versus activity in left LO during diagnosis scans. Colors are as in previous figures.

involves suppressing preexisting neural representations in LO as well as developing new ones in the FFA.

Expert Object Processing in LO and Fusiform Cortex

Our results agree with and extend prior studies of object-specific cortex. LO appears to contain a general representation of object shape; short-term adaptation there depends upon shape (Kourtzi and Kanwisher 2001), and LO responses are greater for closed shapes than for visual surfaces (Vinberg and Grill-Spector 2008). The spatial pattern of activity in LO correlates with physical shape (Haushofer et al. 2008) and distinguishes between members of an object category that differ in shape (Eger, Ashburner, et al. 2008). Consistent with this role, training to discriminate complex shapes increases the overall level of activity in LO, changes its spatial pattern, and narrows its tuning but does not lead to the development of category-specific regions of cortex (Grill-Spector et al. 2000; Op de Beeck et al. 2006; Yue et al. 2006; Jiang et al. 2007).

Perhaps surprisingly, we found that both the size of and activity level in the part of left LO most responsive to radiographs were negatively correlated with expressed expertise. One prior study of expertise also reported greater activity in LO for novices than for experts (Gauthier et al. 2000). Our results extend this work to show a continuous correlation between LO activity and expertise. In addition, our results show that the negative correlation with expertise arises in the part of LO that is most active to radiographs generally. The simplest interpretation of our data is that the left LO's general representation of shape is less important for diagnosing radiographs in expert radiologists than it is for novices.

Neural representations of objects in more ventral cortex differ from those in LO in a number of ways. Responses in these regions are more invariant with respect to image size and image location and integrate information across a larger portion of objects (Grill-Spector et al. 1999; Lerner et al. 2001, 2002; Eger, Kell, and Kleinschmidt 2008). Responses also correlate better with subjective similarity of shapes than physical similarity (Haushofer et al. 2008). In addition, neurons in ventral cortex are closely tied to identification of objects in familiar categories (Gauthier et al. 1997; Bar et al. 2001; Grill-Spector et al. 2004). Areas specialized for the particular categories of letter strings, faces, and body parts all have been found anterior to LO (Downing et al. 2001; McCandliss et al. 2003; Rhodes et al. 2004).

Our data show a positive correlation of activity in ventral cortex during diagnosis as a function of expertise in radiology. These findings agree with prior findings that experts in cars, birds, and butterflies all show increased activation in ventral cortex for the objects of their expertise (Gauthier et al. 2000; Rhodes et al. 2004; Xu 2005, but see Grill-Spector et al. 2004). The simplest interpretation of our data is that more expert radiologists make use of specialized neural representations in anterior ventral visual cortex that are engaged in the diagnosis task.

Interactions between LO and Fusiform Cortex

One novel aspect of our results is the negative correlation between activity in the FFA and left LO, which suggests that training in radiology alters the interaction between cortical areas. Consistent with this idea, the negative correlation between activity in LO and the FFA was larger in experts than in novices and only reliable in experts (Fig. 5; for experts $r = -0.71$, $p < 0.01$; for novices $r = 0.35$, n.s.). To compare directly the group correlations, we conducted a randomization analysis in which we repeatedly randomly assigned participants to groups and recomputed the correlation between LO and FFA activity (see Materials and Methods). The observed difference in correlation between first-year residents and experts was reliable; differences of that magnitude or greater were obtained in less than 3.5% of randomized samples ($n = 1000$).

The negative correlation of LO and FFA activity may indicate a competitive interaction between different neural representations engaged in the task, as has been proposed for memory systems (e.g., Poldrack and Packard 2003). It is possible, for example, that left LO contains a more parts-based representation that is suppressed as a more "holistic," "global," or "configural" representation develops in the FFA (Gauthier et al. 1999; 2000; Lux et al. 2004; Busey and Vanderkolk 2005). Similarly, the left hemisphere may contain viewpoint invariant representations (Vuilleumier et al. 2002) that are less useful for diagnosis than viewpoint dependent ones in the right hemisphere.

Alternatively, the negative correlation could reflect "explaining away," in which higher level representations suppress corresponding lower level representations in order to aid processing of the remaining image regions (Murray et al. 2002). For example, the fusiform region may subserve recognition of normal anatomical features in the radiograph and suppress lower level representations of them in LO. This in turn would leave abnormal features of the radiograph isolated in LO, which could aid their identification.

Origins of the Correlations between Activity and Expertise

The correlations we observed between expressed expertise and neural activity (Figs 3*B* and 4*B*) have 2 possible origins. They could reflect the hypothesis that 1) as subjects became expert in radiology, mean activity levels during diagnosis increased in the FFA and decreased in left LO. Under this interpretation, training affected the mean level of activity in each region. Inspecting the figures closely, however, also reveals stronger correlations for experts than for novices. Thus, our results could also reflect the hypothesis that 2) as subjects became expert in radiology, activity became more correlated with expressed expertise in the FFA and more anticorrelated in left LO. Under this interpretation, training affected the relationship between expressed expertise and activity. Note that these 2 hypotheses are not mutually exclusive. Evaluating both hypotheses requires evaluating effects of training, rather than expressed expertise, on neural activity.

The first hypothesis predicts that training groups should differ in their mean levels of activity in the 2 regions, but our results did not show reliable differences in overall FFA or LO activity. This pattern has 2 likely causes. First, the novices in our study were already on their way to becoming expert, which could have moved some into the expert range. More critically, our measure of visual expertise was performance on the diagnosis task while in the scanner. The slightly unnatural nature of the task may have prevented some subjects from fully expressing their expertise, including the 3 subjects that were outliers in performance. Subjects with higher expressed expertise, as measured by performance on the diagnosis task, did show reliably higher activity in the FFA ($t = 2.3$, $p < 0.05$ for comparison of 10 highest performers to remainders) and a strong trend toward the opposite pattern in left LO ($t = 2.1$, $p < 0.06$). Additionally, removing outlier performance data yielded a trend toward greater activity for novices than experts in LO ($t = 1.7$, $p < 0.11$), though not the opposite trend in FFA ($t = 0.55$; n.s.). Given these suggestive patterns, it seems plausible that group differences in mean activity were at least one source of the correlations we observed between expertise and neural activity. But, because our data do not show overall group differences in neural activity, we cannot rule out that mean activity in the FFA and LO was unaffected by training.

The second hypothesis, that training affects the correlation between activity and expertise, predicts that the expert group of subjects should show higher correlations than the novices. Visually inspecting the data suggested that this may be the case and computing correlations coefficients separately for each group yielded higher values for experts (FFA, $r = 0.77$; left LO, $r = -0.68$) than for novices (FFA, $r = -0.10$; left LO, $r = 0.61$). To test this more formally, we conducted additional randomization analyses. The differences in correlation between first-year residents and experts were reliable; for both regions, differences of that magnitude or greater were obtained in less than 3% of randomized samples ($n = 1000$). These results should be interpreted cautiously, however, because of the small sample size and limited variance of the novice group as well as the presence of potential outlier subjects in both groups. Future work with larger sample sizes can overcome these limitations and also examine potential differences between fourth-year residents and practicing radiologists.

Nevertheless, the current results are consistent with the hypothesis that training increased the correlation between expressed expertise and FFA activity and decreased the correlation between it and activity in left LO. These differences in correlation between training groups have several possible functional interpretations. One possibility is that the greater correlation for experts was simply due to greater effort and/or success at the task. This explanation was ruled out by our analysis that examined neural activity for a subset of trials on which performance was matched (see Results). In the performance matched trials, success was equated by definition, and novices were presumably putting forth even more effort than experts because the task was more difficult for them. Activity in both ROIs still correlated with overall expressed expertise even for these trials.

Our data are more consistent with the interpretation that training changed neural representations in FFA and LO that were important for the diagnosis task. These learning effects were stronger in some subjects than others, which produced the observed correlation between activity and expressed expertise in experts. The training-induced changes could have been "bottom-up," reflecting relatively permanent alterations in receptive fields in FFA and LO, though the low performance of some experts suggests that external factors were able to influence their expression. Alternatively, the learning could have occurred primarily in higher cortical regions and affected FFA and LO activity through "top-down" mechanisms. For example, experts may have learned a task strategy, such as focusing attention on particular learned feature combinations in the image. Such learning could also vary in strength between subjects and could have been disrupted by external factors; perhaps, the low-performing experts adopted a different strategy under the unusual conditions in the scanner. Our present data do not allow us to distinguish between top-down and bottom-up effects of learning, but they do identify the FFA and left LO as important targets of training.

The FFA and Expert Visual Processing

The overall questions of whether visual expertise for objects other than faces depends upon the FFA remain quite controversial. Differences in methods and results have left room for widely disparate overall interpretations of the literature (Bukach et al. 2006; McKone et al. 2007). Addressing this debate was not the primary goal of the present study, but its results are nevertheless relevant. Four previous studies have tested whether people with many years of expertise differ in their pattern of FFA activity from novices: Two found greater relative activity in the FFA for experts, as well as correlations between expertise and activity (Gauthier et al. 2000; Xu 2005), one found a nonsignificant trend for greater relative activity for experts (Rhodes et al. 2004), and one found no difference between experts and novices (Grill-Spector et al. 2004). Our results support the idea that the FFA is important for visual expertise for stimuli other than faces. Our study does have limitations, however. We (like all previous fMRI studies) cannot rule out that the expertise effects we see in the FFA are not instead due to spread of activity from some very nearby area that, for example, is specialized for body parts (Peelen and Downing 2005; Schwarzlose et al. 2005). Similarly, this study cannot determine whether the same neurons within the FFA are responding to both radiographs and faces.

It is also clear from prior work that not all expert visual processing depends upon the FFA (e.g., processing of letters and words). Determining when the FFA is involved in expert visual processing remains a challenge. Our scrambled stimuli were one attempt to do so; they were intended to disrupt "holistic" processing in which the FFA might play a selective role. Unfortunately, our scrambling manipulation had only a small effect on behavior and no reliable effect on FFA activity. It seems likely that the scrambling, which left relatively large-scale anatomical features intact, was too coarse to provide a strong test of the holistic hypothesis. Consistent with this idea, the finely scrambled images in the radiograph localizer scan did generate less activity in the FFA than the intact images ($p < 0.05$;

tested by measuring fit of sinusoid in-phase with the intact images).

The Role of LO and the FFA in Radiograph Diagnosis

Diagnosis of chest radiographs is a complex task, one that certainly depends upon specialized processing in other cortical regions beyond those localized here. This initial study focused on processing of the entire radiograph; we did not, for example, run a "nodule localizer" scan to identify regions containing neurons sensitive to the small variations in shape that indicate potential tumors and other abnormalities in medical images. The diagnosis task may depend heavily upon such areas, and whether they lie near the FFA or in LO (or both or neither) remains unknown. Our results do nevertheless constrain possible models of the neural bases of radiological expertise. What follows is one speculative account that is consistent with our data.

The activity in the FFA and LO measured here likely reflects the processing of anatomical features of radiographs. Activity in the right FFA could signal recognition of features that are common or normal, and in experts may cause suppression of a shape-based representation in left LO. This suppression in turn may aid task performance by reducing the strength of representations that are less useful for the task of identifying abnormalities. Visual expertise, then, might involve not only the growth of new knowledge but also the suppression of older forms of knowledge.

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