

Object Representations for Multiple Visual Categories Overlap in Lateral Occipital and Medial Fusiform Cortex

Gilles Pourtois^{1,2}, Sophie Schwartz¹, Mona Spiridon¹, Roberto Martuzzi³ and Patrik Vuilleumier^{1,2}

¹Laboratory for Behavioral Neurology and Imaging of Cognition, Department of Neuroscience and Clinic of Neurology, 1211, ²Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland, 1205 and ³Department of Radiology, University Hospital, Lausanne, Switzerland, 1011

How representations of visual objects are maintained across changes in viewpoint is a central issue in visual perception. Whether neural processes underlying view-invariant recognition involve distinct subregions within extrastriate visual cortex for distinct categories of visual objects remains unresolved. We used event-related functional magnetic resonance imaging in 16 healthy volunteers to map visual cortical areas responding to a large set (156) of exemplars from 3 object categories (faces, houses, and chairs), each repeated once after a variable time lag (3–7 intervening stimuli). Exemplars were repeated with the same viewpoint (but different retinal size) or with different viewpoint and size. The task was kept constant across object categories (judging items as “young” vs. “old”). We identified object-selective adaptation effects by comparing neural responses to the first presentation versus repetition of each individual exemplar. We found that exemplar-specific adaptation effects partly overlapped with regions showing category-selective responses (as identified using a separate localizer scan). These included the lateral fusiform gyrus (FG) for faces, parahippocampal gyrus for houses, and lateral occipital complex (LOC) for chairs. In face-selective fusiform gyrus (FG), adaptation effects occurred only for faces repeated with the same viewpoint, but not with a different viewpoint, confirming previous studies using faces only. By contrast, a region in right medial FG, adjacent to but nonoverlapping with the more lateral and face-selective FG, showed repetition effects for faces and to a lesser extent for other objects, regardless of changes in viewpoint or in retinal image-size. Category- and viewpoint-independent repetition effects were also found in bilateral LOC. Our results reveal a common neural substrate in bilateral LOC and right medial FG underlying view-invariant and category-independent recognition for multiple object identities, with only a relative preference for faces in medial FG but no selectivity in LOC.

Keywords: category selectivity, face recognition, fusiform face area, fusiform gyrus, lateral occipital cortex, object recognition, repetition priming, unfamiliar objects, view invariance, viewpoint sensitivity, viewpoint transformation

Introduction

Visual objects in the environment are defined by 3-dimensional (3-D) cues. However, visual objects are rarely viewed from the exact same viewpoint, thus leading to important changes in the visual appearance of the same object. Despite these large variations in 2-dimensional retinal inputs, the human visual recognition system can rapidly and efficiently extract invariant properties of objects in a scene (Marr 1982; Biederman 1987; Riesenhuber and Poggio 2002; Vuilleumier 2007).

An important alteration in the retinal image occurs when a given object undergoes a rotation in depth across 2 consecutive views, sometimes unfolding a completely novel contour for this object. Although such a transformation is computationally demanding (Shepard and Metzler 1971; Ullman 1998; Riesenhuber and Poggio 2002), it hardly challenges recognition performance (Biederman and Bar 1999). Viewer-centered (Bulthoff and Edelman 1992; Ullman 1998) versus object-centered (Biederman 1987) models of visual object recognition in human have been proposed to explain the formation of stable object representations across variations in viewpoint. These competing theories suggest distinct roles for viewing specificities (i.e., central for viewer-centered theories vs. accidental for object-centered theories). Monkey neurophysiology studies also demonstrate the importance of viewpoint information by showing that the same neurons in the inferotemporal cortex may code both angular rotation and object type itself (see Perrett et al. 1998; Wang et al. 1998; Logothetis 2000), possibly providing a neural mechanism to identify an object across different views (Bulthoff and Edelman 1992; Wang et al. 1996). However, although some neurons have been found to show a remarkable selectivity for individual views of synthetic objects (e.g., artificial 3-D structures that can be rotated in depth around an arbitrary axis), other neurons were found to be tuned to different views of the same object with the peaks of view-tuning curves being spread up to 40–50° apart (Logothetis and Pauls 1995). These observations suggest the existence of “fuzzy” neurons, which respond to different (and possibly nonadjacent) views of the same object. Thus, these neurophysiological results highlight a complex organization of neural populations in inferotemporal cortex underlying visual object recognition, with a mixture of view-selective and view-invariant processing even at the level of single neurons.

The human visual cortex contains a mosaic of different areas, some of which seem differentially sensitive to distinct object categories (Spiridon and Kanwisher 2002; but see also Haxby et al. 2001). Faces preferentially activate a lateral region of the fusiform gyrus (FG) (i.e., fusiform face area [FFA] Kanwisher et al. 1997), whereas visual scenes or houses activate the parahippocampal gyrus (Epstein and Kanwisher 1998) and other man-made objects (e.g., artifacts) primarily activate lateral occipital complex (LOC; Malach et al. 1995; Grill-Spector et al. 2001). The degree to which these “category-selective” regions encode object identity in a view-dependent or view-independent manner is still unclear. Recent imaging studies have shown that these regions are differentially affected by changes in viewpoint (or other dimensions), suggesting some generalization across views in some areas and not in

others (Grill-Spector et al. 1999; Gauthier et al. 2002; Epstein et al. 2003; Ewbank et al. 2005). However, whether view-invariant activations in occipitotemporal cortex reflect category-selective representations or more general visual recognition processes remains unresolved because, to our knowledge, no imaging study directly compared invariant recognition mechanisms across multiple object categories. Here, we used functional magnetic resonance imaging (fMRI) to identify brain regions holding stimulus-specific and view-invariant representations of visual object for unique or multiple categories by comparing brain responses to 3 homogenous object types (faces, houses, and chairs) seen with different viewpoints in 2 different occurrences.

Prior exposure to a visual stimulus improves its subsequent identification, a phenomenon known as behavioral priming (Tulving and Schacter 1990; Schacter and Buckner 1998; Schacter et al. 2007). At the brain level, a reduction in neuronal activity is observed for repeated exposures relative to initial presentations, a phenomenon known as neural priming (Schacter et al. 2007), adaptation (Grill-Spector and Malach 2001), or repetition suppression (Desimone 1996). Although the exact nature and functional relationship between behavioral and neural priming is still debated (Grill-Spector et al. 2006; Krekelberg et al. 2006; Sayres and Grill-Spector 2006; Schacter et al. 2007), these implicit memory effects have been successfully used to unravel brain areas coding for invariant physical features of visual stimuli (as produced by changes in viewpoint). Neural priming is particularly valuable to explore stimulus-specific visual representations (e.g., 2 different views of the same object) in occipitotemporal cortex (Grill-Spector et al. 1999; Koutstaal et al. 2001; Vuilleumier et al. 2002). Several brain imaging studies have compared brain responses when one particular stimulus was repeated many times in the same format or repeated with some variation along one visual dimension. Although early studies used blocked adaptation paradigms (Grill-Spector and Malach 2004; Kanwisher and Yovel 2006; Schacter et al. 2007; Grill-Spector et al. 1999), more recent studies took advantage of event-related designs to measure neural priming after a single (immediate or distant) repetition of objects with or without change in a visual dimension of interest (Kourtzi and Kanwisher 2001; Naccache and Dehaene 2001; Vuilleumier et al. 2002; Pourtois et al. 2005a). Unlike blocked adaptation paradigms where participants are aware of the repeated dimension, event-related designs can elicit reliable neural priming without awareness or anticipation of the repetition manipulation (Naccache and Dehaene 2001; Henson and Rugg 2003; Pourtois et al. 2005a).

In a pioneering fMRI study, Grill-Spector et al. (1999) used adaptation blocks with either cars, animals, or human faces and found a high degree of stimulus specificity for changes in viewpoint (or illumination, size, and position) in posterior regions of LOC, whereas more anterior portions of LOC showed greater invariance across changes (Grill-Spector et al. 1999; Grill-Spector and Malach 2001). This finding was subsequently extended by Kourtzi and Kanwisher (2001) who demonstrated, using short-term adaptation, that LOC did not code low-level features of perceived objects, but high-level shape information, with reliable adaptation effects in LOC when object shapes remained unchanged even if contours actually differed between study and test (see also Kourtzi and Kanwisher 2000). James et al. (2002) also reported that repetition effects in LOC had the same magnitude for identical

versus depth-rotated images of man-made objects, corroborating the notion that LOC may hold view-invariant representations (see also Epstein et al. 2003; Ewbank et al. 2005). However, Ewbank et al. (2005) showed that repetition of man-made objects produced adaptation effects not only in LOC but also in parahippocampal and FG, suggesting that adaptation may not necessarily be restricted to category-selective regions, but more distributed within the occipitotemporal cortex. Using man-made objects in a long-term repetition-priming paradigm, Vuilleumier et al. (2002) found a gradient of stimulus specificity along the occipitotemporal pathway, from poorly specific posterior LOC regions (showing adaptation for both real and nonsense objects) to more specific medial FG (showing size and/or viewpoint invariance for meaningful objects only). These results suggested item-specific representations in fusiform cortex, coding for specific visual form information in the right hemisphere and more abstract visual or functional properties in the left hemisphere (for similar findings, see Simons et al. 2003). However, several fMRI studies investigating face processing across different viewpoint transformation demonstrated that the (right) FFA does not hold a view-independent representation of individual faces (Grill-Spector et al. 1999; Andrews and Ewbank 2004; Pourtois et al. 2005a, 2005b). Using a long-term event-related priming paradigm (similar to Vuilleumier et al. 2002) and a large set of unfamiliar faces, we also observed view-specific adaptation to individual (and novel) identities in the FFA (Pourtois et al. 2005a, 2005b), but found another more medial region in the FG, adjacent to but not overlapping with FFA, that showed view-independent adaptation effects. However, we could not establish that this region was face selective (Pourtois et al. 2005a), and a similar region in medial fusiform was previously reported to respond to objects and houses (Ishai et al. 1999). It is therefore possible that this area may hold abstract/invariant representations of individual visual entities irrespective of category (Damasio et al. 1990). Alternatively, this area could include fuzzy neurons that respond to different views of the same object (even if these views are not directly adjacent; see Logothetis and Pauls 1995), without the need to postulate the existence of fully 3-D/object-centered representations. In any case, because our previous study used face stimuli only, it remains unsettled whether view-invariant effects could also be found in the medial FG with the repetition of objects from other visual (nonface) categories.

The main goal of the present fMRI study was to use a long-term event-related repetition-priming paradigm to determine the anatomical commonalities and specificities in view-independent visual processing across 3 distinct object categories with well-established neural substrates in extrastriate cortex; namely, faces, houses, and man-made objects (chairs). In particular, we sought to verify and better characterize the role of the medial fusiform region in viewpoint-independent coding of individual object exemplars. By comparing repetition-priming effects for multiple object types in the same experiment, our fMRI design enabled us to delineate for the first time both separate and shared neural representations for processing novel exemplars from different visual object categories. Based on previous findings, we expected that the face-selective region in right lateral FG (FFA, see Kanwisher et al. 1997) may show category-selective but view-dependent priming effects between first presentation and repetition of the same individual face (Andrews and Ewbank 2004; Pourtois et al.

2005a; Fang et al. 2007). By contrast, we hypothesized that repetition-priming effects may occur irrespective of viewpoint change and possibly regardless of visual category in an anatomically distinct (nonoverlapping) and more medial region of the FG (Vuilleumier et al. 2002; Pourtois et al. 2005a). Finally, we could also compare viewpoint- and size-invariant repetition-priming effects in LOC and parahippocampal cortex, as a function of the preferred or nonpreferred object category for each of these regions (Grill-Spector et al. 1999; Kourtzi and Kanwisher 2001; James et al. 2002; Epstein et al. 2003; Ewbank et al. 2005; Fang et al. 2007).

Materials and Methods

Subjects

Sixteen healthy paid volunteers (9 females, mean age 26, range 23–30, all right handed) gave informed consent to participate in a study approved by the local ethical committee. All had a normal or corrected to normal vision and no past of neurological or psychiatric history.

Stimuli and Procedure in Main Experiment

In the main adaptation experiment, participants were scanned while viewing pictures of unfamiliar faces, houses, and chairs (Fig. 1A). Face stimuli were identical to those used in our previous study (Pourtois et al. 2005a) and could have 2 different head orientations: full front or depth rotated (~30° to 40°), with the head turned to either the left or the right (50% each). House and chair stimuli matched as close as possible the orientations used for the face stimuli. None of these items was previously familiar to the participants (as further ensured by debriefing after scanning).

Each object identity ($N = 156$, 52 per object category) was repeated only once either with the same viewpoint (same view but different size) or with a different viewpoint (different size and view). This resulted in 4 possible event types for each visual category (face, house, or chair): 1) first presentation of objects later repeated with the same view, 2) first presentation of objects later repeated with a different view, 3) repetition of objects with the same view, and 4) repetition with different view. We systematically changed object size between first and second presentation in order to avoid mere image-based repetition effects and to tap into higher level mechanisms of object processing (see Vuilleumier et al. 2002). The image size either increased (600 × 600 pixels) or decreased (400 × 400 pixels) compared with a standard size (500 × 500 pixels). The trial order (object identities and viewpoints) as well as the direction of size change (increase or decrease) were counterbalanced across participants.

Each exemplar was repeated once only, but after a variable time lag, with 3–7 intervening stimuli, in a pseudorandom order. This procedure minimized a possible confound of repetition and time elapsed because the trial ranks largely overlapped for first and second presentations. Furthermore, additional “singleton” items (i.e., objects presented only once during the sequence, $N = 30$, 10 per visual category) were also included at the end of the scanning session to circumvent a correlation of repetition with time or more general habituation effects (in addition to including time-dependent regressors in our statistical analysis, see below). In this manner, the overall trial-ranks for first and second presentations (including singleton items) were 1–342 (median 180) and 5–312 (median 163), respectively. Thus, this procedure ensured that the average trial history preceding and following a given trial was equivalent for all trial types (for similar method, see Vuilleumier et al. 2002; Pourtois et al. 2005a, 2005b). The singleton items were averaged together with the first presentations of object exemplars ($N = 186$) (and compared with repetitions, $N = 156$). Because singletons represented only a small number of extraitems among first presentations (16%) and were

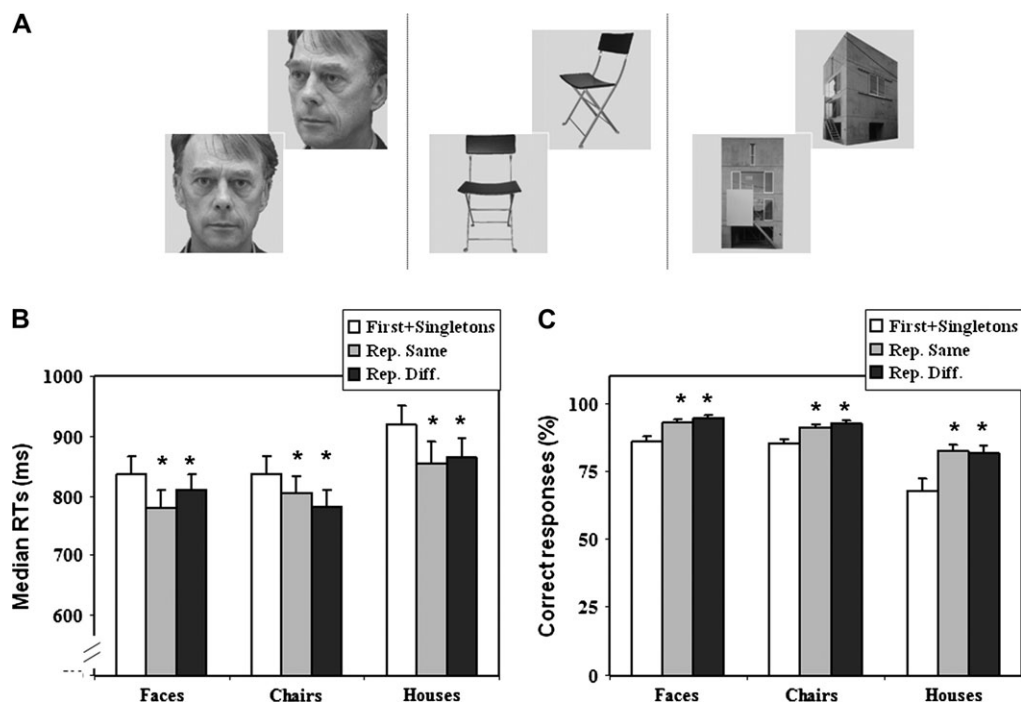


Figure 1. (A) Examples of face, chair, and house stimuli used in the repetition-priming experiment. Stimuli were shown either with a front or three-quarter view, with an equal probability of left versus right views. In the viewpoint change condition, the direction of change between first presentation and repetition (from front to three-quarter or vice versa) and the specific viewpoints were counterbalanced across participants. In both conditions (same viewpoint vs. different viewpoint), the size of the picture was also systematically changed between first presentation and repetition to avoid image-based repetition-priming effects (see Materials and Methods). (B) Behavioral results during scanning. Priming in RTs (median RTs for correct responses \pm 1 standard error of the mean) for the “younger” versus “older” judgments was significant ($P < 0.001$) but not modulated by object category or the viewpoint changes. There was also a main effect of category, with slower RTs to houses than either faces or chairs. Asterisks indicate significantly faster RTs ($P < 0.001$) for repetitions relative to first presentations. (C) Priming effects on accuracy (% of correct responses) were also found for all 3 categories (and larger for houses than faces or chairs) but not modulated by viewpoint changes. Asterisks indicate significant improvement in performance ($P < 0.001$) for repetitions relative to first presentations.

counterbalanced across subjects, they were unlikely to produce any systematic differences in image or identity properties between conditions but helped cancel out nonspecific effect of time or fatigue in the repetition-priming experiment. Moreover, accessory data analyses comparing statistical results with versus without the inclusion of singleton items showed a quantitatively larger magnitude of repetition-priming effects (at both the behavioral and brain imaging levels) when excluding the singletons, but with similar loci and qualitative differences between conditions, confirming that singletons were efficiently contributing to purify genuine exemplar repetition-priming effects from nonspecific habituation effects.

Stimuli were projected and viewed through a screen-box placed on the head coil. All images were presented centrally, against the same homogenous gray-level background and covered approximately 8×6 degrees of visual angle. Stimuli were shown for a duration of 400 ms, preceded by a 500 ms fixation cross, in an event-related design with a constant stimulus onset asynchrony of 2.4 s. These presentation parameters were selected as they provided an optimal sampling of the hemodynamic brain response (time repetition [TR] of 2 s). A short over a longer stimulus presentation was preferred to minimize the use of different task strategies (or eye movements) across the 3 object categories (see below) and to yield optimal repetition suppression effects in the visual cortex (see Zago et al. 2005). Eighty null trials were also randomly intermixed with visual stimuli to provide good baseline estimate in this rapid event-related design.

The task required participants to categorize the vintage style of each object (young/recent vs. old/ancient 2-alternative forced choice) by pressing 1 of 2 buttons with their dominant hand. This discrimination allowed us to keep the task constant across the different object categories. Seventy-eight "younger" items (26 per visual category) and 78 "older" items (26 per visual category) were presented (with these responses being orthogonal to the object categories and the repetition factors of interest). Behavioral data from one subject were lost due to technical reasons.

Stimuli and Procedure in Functional Localizer Scan

Following the main repetition-priming experiment, we performed a separate fMRI scan to map house-, object-, and face-selective areas in each participant, using a standard block design with different object categories (Malach et al. 1995; Kanwisher et al. 1997; Grill-Spector et al. 2004; Spiridon et al. 2006). A different set of photographs (32 faces, 32 houses, 32 objects/artifacts, and the 32 corresponding scrambled objects/artifacts) was presented in 16 alternating blocks (4 per stimulus category, 16 stimuli in each block). Face stimuli did not include exemplars with different viewpoints and appeared with a generally straight orientation, as used by face localizer in many previous studies (Kanwisher and Yovel 2006). Each stimulus identity was repeated once during the localizer scan, to match the procedure used in the main repetition-priming experiment. Scrambled images were created by cutting the intact image into a 20×20 grid of square subimages, then randomly exchanging the positions of each subimage (see Spiridon et al. 2006).

Each stimulus was presented for 750 ms with an intertrial interval of 500 ms. Subjects performed a one-back repetition-detection task, pressing a button for any immediate repetition (one per block). Participants correctly detected such immediate repetitions in 92% for scrambled artifacts, 100% for intact artifacts, 93% for houses, and 97% for faces (none of the 6 pairwise comparisons was statistically significant; all $P > 0.1$).

MRI Scanning

MRI data were acquired at the Lemanic Bio-Medical Imaging Center using a 3-T Trio system (Siemens, Munich, Germany) with parallel imaging (GRAPPA) from an 8-channel head coil. For each participant, structural images were acquired with a T_1 -weighted 3-D sequence (160 contiguous sagittal slices, field of view [FOV] = 256 mm, TR/time echo [TE]/flip angle = 1480 ms/2.63 ms/15°, matrix = 256×256 , slice thickness = 1 mm) and functional images with a gradient-echo EPI sequence (TR/TE/flip angle = 2000 ms/30 ms/90°, FOV = 211 mm, matrix = 64×64). Each functional image comprised 36 axial slices (voxel size: 2×2 mm; thickness 3 mm; gap 0.3 mm) oriented parallel to the

inferior edge of the occipital and temporal lobes. For the main experiment, a total of 725 functional images were acquired across 3 runs, separated by a brief pause. In the localizer scan, 165 images were acquired using identical imaging parameters.

Data Analysis

Functional images were analyzed using the general linear model (Friston et al. 1998) for event-related designs using SPM2 software (www.fil.ion.ucl.ac.uk/spm/). All images were realigned, corrected for slice timing, normalized to the Montreal Neurological Institute (MNI) template (resampled voxel size of $3 \times 3 \times 3$ mm), spatially smoothed (8 mm FWHM Gaussian kernel), and high-pass filtered (cutoff 120 s). We selected this standard 8-mm smoothing value because the signal in our images was likely to correspond to a Gaussian distribution and spatial spreading matching this FWHM kernel and ensured a good probability to detect overlapping regions at the group level (i.e., random effects) despite interindividual variability in functional cortical anatomy after spatial normalization (see Henson et al. 2003; Eger et al. 2005; Rotshtein et al. 2005). Accessory analyses using a smaller smoothing size did not reveal more selective activations but generally reduced the statistical strength of responses at the group level (data not reported). For spatial normalization, we used the MNI average of 152 scans, as routinely provided in SPM2. Statistical analyses were performed on a voxel-wise basis across the whole brain.

For the main repetition-priming experiment, individual events were modeled by a standard synthetic hemodynamic response function (HRF). Four conditions were defined for each of the 3 object categories (2 views \times 2 presentations), resulting in 12 event types. We also modeled a parametric modulation by time for each of the 12 regressors of interest in such a way to covariate out from the fMRI data any variance accounted by linear (and potentially unspecific) decreases of the hemodynamic response over time (in addition to our inclusion of singleton items at the end of scanning runs, see above). For the localizer scan, blocks with faces, houses, objects, and scrambled images were modeled by a boxcar function with 4 epoch types, corresponding to these 4 categories, convolved with the standard HRF. Movement parameters from spatial realignment (3 translations, 3 rotations) were also entered as covariates of no interest in all statistical analyses to account for residual movement artifacts.

The general linear model was then used to generate parameter estimates of activity at each voxel, for each condition in each participant. Statistical parametric maps were generated from linear contrasts between parameter estimates from the different conditions. We then performed random-effect group analyses on the contrast images using one-sample t -tests (Friston et al. 1998). For the repetition-priming experiment and the functional localizer experiment, we report regions that survived $P < 0.05$ FDR corrected (Genovese et al. 2002), with a cluster size of more than 5 contiguous voxels. For regions of interest (ROIs) such as the medial part of the FG (see Pourtois et al. 2005a), we also report statistical effects at a conventional $P < 0.001$ uncorrected threshold with a cluster size of more than 20 contiguous voxels (Worsley et al. 1996; Henson et al. 2003).

Results from the main repetition-priming experiment were first examined using whole-brain SPM analysis. Statistical maps of the repetition-priming experiment and of the functional localizer experiment were directly compared using both inclusive masking and conjunction analyses (Friston et al. 1999; Nichols et al. 2005). Finally, we also performed ROI analyses using peaks of category-selective areas, as independently defined by the localizer scan. To better account for anatomical variations in individual activation peaks, even after normalization, we extracted parameters of activity (betas) from ROIs defined in each individual subject, and then submitted these values to repeated-measure analyses of variance (ANOVAs). All stereotactic coordinates are reported using the MNI template.

Results

Behavior

Systematic debriefing postscanning confirmed that none of the 16 participants were aware that individual objects were

systematically shown twice. Nevertheless, although our instructions did not stress speed for young/old judgments, we found highly significant repetition-priming effects in both reaction times (RTs) (Fig. 1B) and accuracy.

A 3 (face, house, or chair category) \times 3 (first presentation averaged across views, repetition with same view, or repetition with different view) ANOVA on median RTs for correct responses (Fig. 1B) revealed a significant main effect of object category ($F_{2,28} = 22.11, P < 0.001$) and a significant main effect of priming ($F_{2,28} = 13.10, P < 0.001$). Participants were slower to make vintage judgments for houses (mean: 879.2 ms) than faces (mean: 808.8 ms) or chairs (mean: 807.5 ms). There was no RT difference between these 2 latter categories ($t(14) = 0.17, P = 0.86$). More importantly, the significant main effect of priming indicated faster RTs to repeated relative to initial presentations, irrespective of repetition type. The amount of priming in RTs was comparable for faces (first minus repeated: 41.6 ms; $t(14) = 5.02, P < 0.001$), chairs (43.2 ms; $t(14) = 3.97, P = 0.001$), and houses (59.6 ms; $t(14) = 4.32, P < 0.001$) and similar for the same and different view conditions within each object category (faces: $t(14) = 1.67, P = 0.12$; chairs: $t(14) = 1.73, P = 0.11$; houses: $t(14) = 0.34, P = 0.74$), suggesting a robust view-independent coding of object identity regardless of the specific visual object category. Importantly, this view-invariant repetition-priming effect in RTs could not be attributed to unspecific effects of time elapsed (e.g., habituation or fatigue, see Grill-Spector et al. 2006) because trial ranks overlapped for first and second presentations and several items were presented for the first time at the end of the scanning session (singleton items, see Materials and Methods).

An ANOVA performed on error rates with the same factors as above also confirmed the presence of significant repetition-priming effect ($F_{2,28} = 55.06, P < 0.001$), with higher accuracy

for repetitions than first presentations (Fig. 1C). Young/old judgments were worst with houses (mean 22.68% errors) compared with faces (mean 8.88%) or chairs (mean 10.41%; main effect ($F_{2,28} = 10.68, P = 0.003$). This increased accuracy with repetition was significant for each of the 3 visual categories (faces: 7.79%, $t(14) = 6.17, P < 0.001$; chairs: 6.61%, $t(14) = 5.24, P < 0.001$; houses: 14.59%, $t(14) = 6.80, P < 0.001$), but larger for houses than faces or chairs, reflected by a significant interaction between visual category and priming ($F_{4,56} = 8.35, P = 0.001$). Repetition-related gain in accuracy did not statistically differ for same versus different view conditions when tested for each category separately (faces: $t(14) = 0.72, P = 0.49$; chairs: $t(14) = 0.95, P = 0.36$; houses: $t(14) = 0.38, P = 0.71$).

Taken together, these behavioral repetition-priming effects clearly suggest that the participants formed robust memory traces for unfamiliar object exemplars, equally so for all categories.

Brain Imaging

Functional Visual Localizer

We identified face-selective regions by comparing blocks with faces to blocks with houses, man-made objects, and scrambled images. This contrast revealed a widespread network of brain regions (Ishai et al. 1999), including the lateral FG (FFA, see Kanwisher et al. 1997), superior temporal sulcus (STS), amygdala, orbitofrontal cortex, and precuneus/posterior cingulate cortex (see Fig. 2 and Table 1). All these regions have been associated with face processing in previous fMRI studies (Kanwisher et al. 1997; Halgren et al. 1999; Haxby et al. 2000; Downing et al. 2006; Spiridon et al. 2006). However, we failed to reliably identify the occipital face area (OFA) on either side,

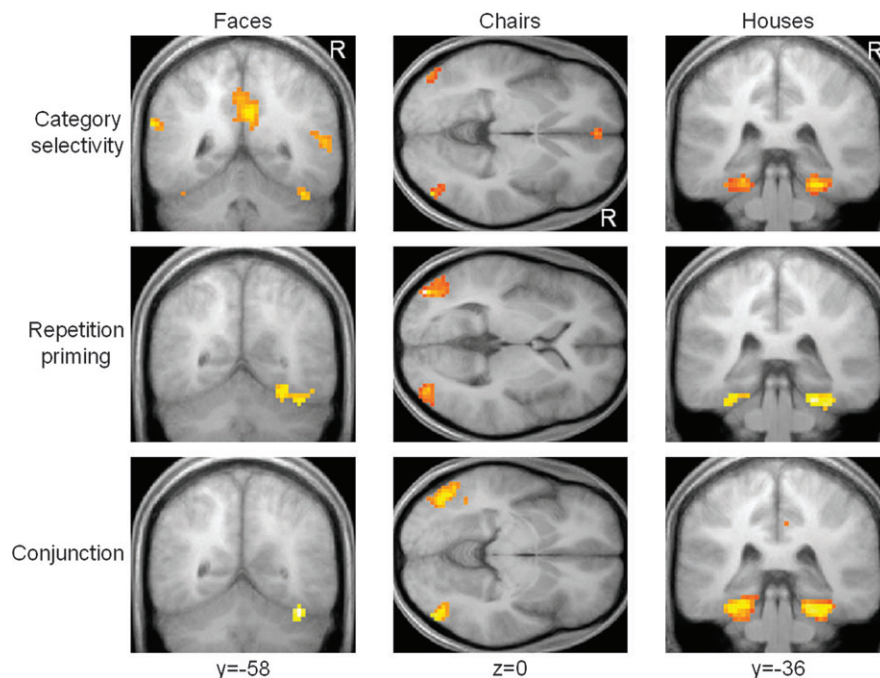


Figure 2. Brain areas showing category-selective preference in the functional localizer scan (top row) and exemplar-specific repetition decreases in the main experimental scan (middle row) for each object category separately, overlaid on the mean anatomical scan of participants. A precise anatomical overlap was observed (bottom row) between the category-selective preference and exemplar-specific repetition decreases, as shown by a conjunction analysis for each category. These overlapping effects arose in the right FFA for faces, bilateral LOC for chairs, and bilateral parahippocampal gyrus for houses. All SPMs thresholded at $P < 0.05$ FDR corrected; random-effect analyses.

Table 1

Localizer scan.

| Brain areas | Side | Coordinates | | | <i>T</i> | <i>Z</i> -score |
|--|------|-------------|----------|----------|----------|-----------------|
| | | <i>x</i> | <i>y</i> | <i>z</i> | | |
| Faces > houses + objects + scrambled objects | | | | | | |
| Amygdala | R | 27 | -3 | -24 | 8.14 | 4.96 |
| Amygdala | L | -21 | -9 | -21 | 4.22 | 3.38 |
| Anterior fusiform gyrus | R | 39 | -57 | -21 | 6.79 | 4.52 |
| Anterior fusiform gyrus | L | -42 | -48 | -24 | 5.25 | 3.89 |
| Superior temporal sulcus | R | 60 | -63 | 18 | 6.39 | 4.38 |
| Superior temporal sulcus | L | -57 | -63 | 24 | 6.15 | 4.28 |
| Orbitofrontal cortex | R | 3 | 39 | -18 | 7.00 | 4.60 |
| Posterior cingulate cortex/precuneus | R | 3 | -66 | 33 | 7.78 | 4.85 |
| Objects > scrambled objects | | | | | | |
| Lateral occipital complex | R | 48 | -81 | -6 | 8.03 | 4.93 |
| Lateral occipital complex | L | -48 | -81 | 0 | 5.30 | 3.92 |
| Transverse occipital sulcus | L | -39 | -84 | 30 | 4.60 | 3.57 |
| Posterior cingulate cortex/precuneus | L | -3 | -63 | 27 | 10.64 | 5.60 |
| Anterior fusiform gyrus | R | 39 | -45 | -30 | 4.78 | 3.67 |
| Anterior fusiform gyrus | L | -36 | -45 | -24 | 7.05 | 4.62 |
| Parahippocampal gyrus | L | -27 | -39 | -24 | 6.75 | 4.51 |
| Houses > faces + objects + scrambled objects | | | | | | |
| Parahippocampal gyrus | R | 24 | -39 | -15 | 8.50 | 5.07 |
| Parahippocampal gyrus | L | -27 | -45 | -9 | 8.40 | 5.04 |
| Anterior fusiform gyrus | R | 30 | -57 | -12 | 10.59 | 5.59 |
| Anterior fusiform gyrus | L | -27 | -54 | -9 | 7.74 | 4.84 |
| Lingual gyrus | R | 30 | -72 | -12 | 7.42 | 4.74 |
| Lingual gyrus | L | -24 | -75 | -6 | 9.48 | 5.33 |
| Transverse occipital sulcus | R | 36 | -84 | 21 | 8.28 | 5.00 |
| Transverse occipital sulcus | L | -33 | -90 | 18 | 8.19 | 4.98 |
| Cuneus | R | 18 | -54 | 18 | 6.81 | 4.53 |
| Cuneus | L | -12 | -60 | 18 | 7.55 | 4.78 |

Note.—All $P < 0.05$ FDR corrected (random-effect analysis).

both at the single-subject and group level, even when using a more liberal statistical threshold (i.e., $P < 0.01$ uncorrected) and using different contrasts from the localizer scan (faces > houses or faces > objects instead of faces > all 3 other image types). This is consistent with other observations suggesting less systematic effects in the OFA than FFA during face recognition (see Kanwisher and Yovel 2006).

Pictures of objects (including chairs) compared with scrambled stimuli selectively activated LOC bilaterally (Fig. 2), also consistent with previous findings showing the involvement of this posterior occipital region in shape processing (Malach et al. 1995; Grill-Spector et al. 2001; Kourtzi and Kanwisher 2001; Hayworth and Biederman 2006). A detailed inspection of peak activations confirmed that these shape-selective effects in bilateral LOC did not encompass the locations previously described for OFA, which is typically located more ventral and lateral (see Rotshtein et al. 2005; Gilaie-Dotan and Malach 2007) as compared with these LOC responses. Other regions responding to shapes included the bilateral anterior FG, left parahippocampal gyrus, and posterior cingulate cortex. In addition, we performed a comparison between pictures of objects and the 3 other visual categories (faces, houses, and scrambled objects) to identify not only shape-selective regions (objects > scrambled objects) but also object-selective regions. This contrast disclosed a single cluster in the left posterior parahippocampal gyrus in a region close to the collateral sulcus ($-30x, -36y, -21z$; $T = 6.91$, $Z = 4.57$, $P < 0.05$ FDR corrected). These data are consistent with previous fMRI studies using multivoxel pattern analyses that found distributed and overlapping representations of different object categories within ventral occipital cortex, including the left posterior parahippocampal gyrus for man-made objects (Haxby et al. 2001).

Finally, houses compared with faces, objects, and scrambled images activated a network of regions previously associated with scene perception (Fig. 2), including the medial parahippocampal gyrus (Epstein and Kanwisher 1998) and a region near the transverse occipital sulcus (TOS, see Nakamura et al. 2000; Grill-Spector 2003; Hasson et al. 2003; Epstein et al. 2005). Other occipitotemporal regions also responded to houses, including the anterior medial FG, cuneus, and lingual gyrus (Table 1).

Repetition-Priming Experiment

First, for each visual object category, we identified repetition-priming effects by contrasting first presentations (including singleton items, see Materials and Methods) to repetitions and then compared these effects to the category-selective activations identified in the separate visual localizer scan (see Fig. 2). Next, we determined regions showing repetition-priming effects across changes in viewpoint regardless of the specific visual object categories (face, chair, and house) using a stringent conjunction analysis.

Faces Repetition of face identities (collapsing across both the same and different viewpoints) produced a selective decrease of responses in the face-selective region of the right lateral FG ($39x, -57y, -24z$; Fig. 2 and 3A). This contrast also revealed reliable decreases in a separate, more medial part of the right FG ($27x, -51y, -21z$; Fig. 3A), an area that was not face selective and did not overlap with the visual localizer results used as an inclusive mask (Fig. 3B), unlike the more lateral peak whose coordinates corresponded to the classical FFA location (see Kanwisher et al. 1997).

This anatomical segregation between the right lateral FFA and the medial FG was further established by inspection of fMRI data in individual subjects. For each participant, we determined the x , y , and z coordinates of the right FFA obtained from the localizer scan and those of the right medial fusiform peak that showed significant repetition decreases for faces irrespective of viewpoints change in the repetition-priming experiment. Notably, the right medial FG activity was not seen in the localizer scans for any subject. Individual coordinates of these 2 peaks were directly compared by paired t -tests. This confirmed a highly significant difference for the mean x coordinates [$t(15) = 7.60$, $P < 0.001$], reflecting a systematic lateral shift (see also Pourtois et al. 2005a), but there was no significant difference for the mean y coordinates [$t(15) = 1.42$, $P = 0.18$] and mean z coordinates [$t(15) = 1.48$, $P = 0.16$]. This pattern of results thus replicates our previous fMRI findings and confirms repetition-priming effects for faces occurring in 2 adjacent and nonoverlapping clusters in the right anterior FG (Pourtois et al. 2005a, 2005b). In addition, repeating face identities also produced reliable repetition decreases in a posterior part of the right medial FG ($30x, -69y, -9z$), with symmetrical effects on the left side ($-36x, -69y, -12z$), as well as in a ventral portion of the left LOC and the right precuneus (see Table 2).

We next tested whether, in addition to be anatomically distinct (Fig. 3A), the FFA and the more medial region were also functionally dissociable (Fig. 3C,D). We extracted parameters of activity from these 2 areas in all 16 participants (see Materials and Methods) and submitted these data to a 2 (Region: FFA vs. medial FG) \times 2 (viewpoint condition: same view vs. different view) \times 2 (repetition: first presentation vs.

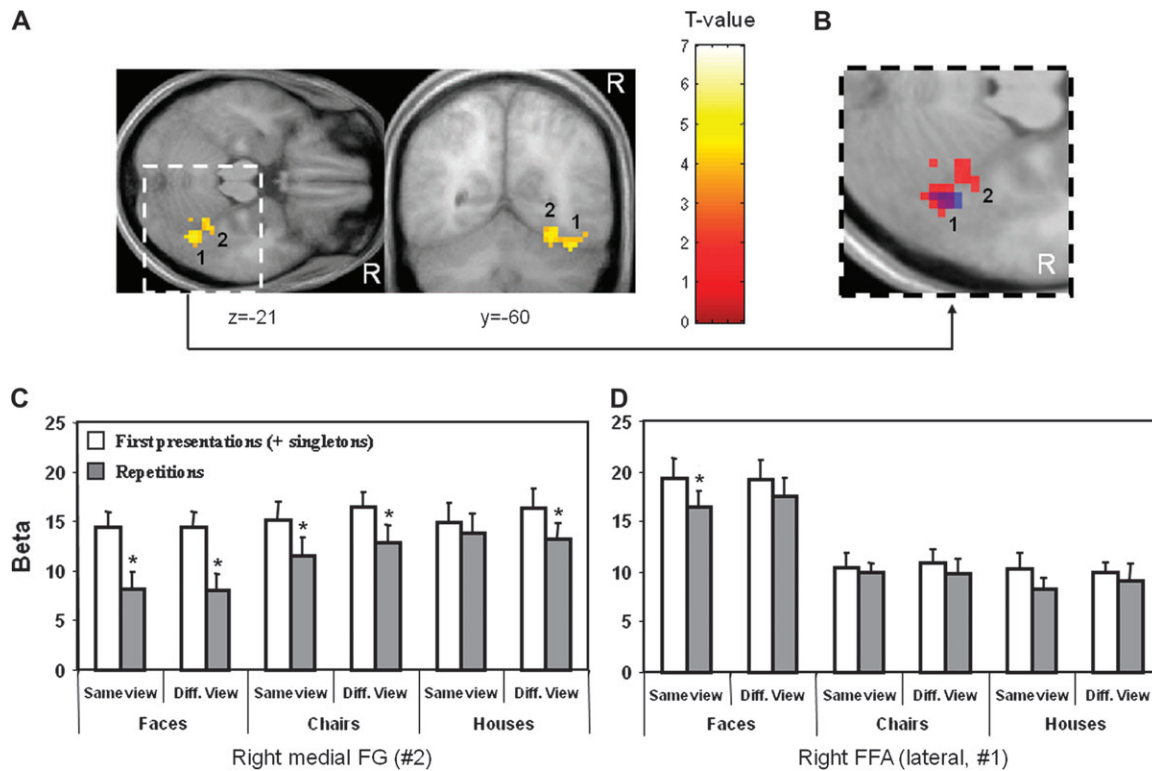


Figure 3. (A) Repetition-priming effects for faces in the right anterior FG overlaid on the mean anatomical scan of participants. Two distinct and adjacent regions (labeled #1 and #2) showed significant repetition decreases for the second versus first presentation of the same face identities (SPMs thresholded at $P < 0.001$ uncorrected). (B) Inclusive masking analysis at the group level showing that only the lateral region overlapped with the right FFA identified by the separate visual localizer scan (faces > objects contrast, in blue). The more medial region was not included in face-selective areas. Repetition-priming effects for faces are shown in red. (C, D) Mean parameter estimates (beta, proportional to percentage of signal change) ± 1 standard error of the mean for the right medial FG (area #2; left panel) and right FFA (area #1; right panel). Whereas the right FFA response was category selective and viewpoint dependent, the adjacent medial FG region was neither category selective nor viewpoint dependent but showed a gradient in the amount of repetition-priming effects as a function of the specific visual object category (with larger effects for faces than either chairs or houses). Asterisks indicate significantly reduced responses ($P < 0.01$) for repetitions relative to first presentations.

repetition) ANOVA that revealed a significant interaction of region \times repetition ($F_{1,15} = 21.44$, $P < 0.001$), reflecting larger repetition-priming effects for faces in the medial than lateral FG region (FFA, see Fig. 3C,D). Both regions also differed in their sensitivity to viewpoint manipulation. Although the medial region of the right FG showed comparable repetition-priming effects for same and different viewpoint conditions [$t(15) = 4.77$ and 6.52 , respectively, both $P < 0.001$], this pattern was not seen in the right FFA, which only showed significant repetition-priming effects for the same viewpoint condition [$t(15) = 2.90$, $P = 0.011$] but not for the different viewpoint condition ($t(15) = 1.68$, $P = 0.113$). The same trend for view-dependent repetition effects was also observed in the left FFA, as defined by the functional visual localizer (same view: $t(15) = 1.82$, $P = 0.09$; different view: $t(15) = 0.12$, $P = 0.91$) (for similar pattern of results and asymmetry between left and right FFA, see Gilaie-Dotan and Malach 2007; Fang et al. 2007). These statistical comparisons thus corroborate a dissociation between the lateral and medial right FG, supporting the notion of distinct functional subregions. In addition, note that we found the same magnitude of neural responses in right FFA to faces seen in full frontal or 3/4 views, further demonstrating that this functionally defined region was truly category selective (i.e., with a clear face preference) and did not respond to some “canonical” views only (see Pourtois et al. 2005a).

We further confirmed the view sensitivity of the right FFA by performing additional masking analyses, to test the degree of overlap between face-selective regions identified in the functional visual localizer (defined by contrasting faces > houses + objects + scrambled objects; $P < 0.001$ uncorrected) and those regions showing repetition priming for face identities in the main experiment (all first presentations > repetition, $P < 0.001$ uncorrected). Two inclusive masking analyses were conducted separately for repetition of same views and different views. Whereas the latter analysis did not reveal any overlap, the former analysis disclosed a single cluster precisely corresponding to the right FFA ($42x$, $-57y$, $-21z$; $T = 4.21$, $Z = 3.37$, $P < 0.001$ uncorrected). Because the right FFA was the only region showing such view-dependent responses to face identity repetitions, this area is likely to be critically involved in the early perceptual encoding of faces (Kanwisher and Yovel 2006).

Chairs Repetition of pictures of the same chair (collapsing across same and different viewpoints), relative to their first presentations, produced significant decreases along the object-selective ventral occipitotemporal cortex, including bilateral TOS, LOC (Fig. 2), lingual gyrus, anterior and posterior FG, plus parahippocampal gyrus (see Table 2). Importantly, the repetition of chair exemplars also produced decreases in the right medial FG ($33x$, $-54y$, $-27z$) in a region very close to that

Table 2

Brain regions showing repetition-priming effects.

| Brain areas | Side | Coordinates | | | <i>T</i> | <i>Z</i> -score |
|--|------|-------------|----------|----------|----------|-------------------|
| | | <i>x</i> | <i>y</i> | <i>z</i> | | |
| First > repeated (faces) | | | | | | |
| Anterior fusiform gyrus (lateral) ^a | R | 39 | -57 | -24 | 6.60 | 4.45 |
| Anterior fusiform gyrus (medial) | R | 27 | -51 | -21 | 4.53 | 3.54 ^b |
| Posterior fusiform gyrus (medial) | R | 30 | -69 | -9 | 6.97 | 4.59 |
| Posterior fusiform gyrus (medial) | L | -36 | -69 | -12 | 4.73 | 3.65 ^b |
| Lateral occipital complex | R | 39 | -87 | -6 | 4.92 | 3.74 ^b |
| Lateral occipital complex | L | -36 | -78 | -3 | 6.17 | 4.29 |
| Precuneus ^a | R | 3 | -72 | 27 | 4.69 | 3.63 ^b |
| First > repeated (chairs) | | | | | | |
| Transverse occipital sulcus ^a | L | -36 | -90 | 21 | 7.56 | 4.78 |
| Transverse occipital sulcus | R | 42 | -84 | 21 | 6.92 | 4.57 |
| Lateral occipital complex ^a | L | -42 | -87 | 3 | 10.72 | 5.61 |
| Lateral occipital complex ^a | R | 42 | -78 | -12 | 5.94 | 4.20 |
| Lingual gyrus | L | -24 | -69 | -12 | 4.77 | 3.66 |
| Lingual gyrus | R | 36 | -72 | -12 | 6.46 | 4.40 |
| Anterior fusiform gyrus (medial) ^a | R | 33 | -54 | -27 | 5.13 | 3.84 |
| Anterior fusiform gyrus (medial) | L | -27 | -54 | -15 | 5.25 | 3.90 |
| Posterior fusiform gyrus | L | -51 | -63 | -9 | 5.81 | 4.14 |
| Posterior fusiform gyrus | R | 42 | -60 | -15 | 7.30 | 4.70 |
| Parahippocampal gyrus | L | -12 | -45 | -6 | 5.55 | 4.03 |
| Parahippocampal gyrus | R | 30 | -45 | -9 | 7.22 | 4.67 |
| First > repeated (houses) | | | | | | |
| Parahippocampal gyrus ^a | R | 27 | -33 | -24 | 6.91 | 4.56 |
| Parahippocampal gyrus ^a | L | -33 | -39 | -18 | 5.25 | 3.90 |
| Anterior fusiform gyrus (medial) ^a | R | 30 | -48 | -15 | 6.77 | 4.51 |
| Anterior fusiform gyrus (medial) ^a | L | -24 | -51 | -9 | 4.70 | 3.63 |
| Lateral occipital complex | R | 45 | -72 | -3 | 5.24 | 3.89 |
| Lateral occipital complex | L | -39 | -80 | -3 | 5.60 | 4.05 |
| Transverse occipital sulcus ^a | L | -45 | -75 | 12 | 5.99 | 4.22 |
| Transverse occipital sulcus ^a | R | 36 | -81 | 21 | 5.52 | 4.02 |

^aCategory-selective activation observed in the same region during the localizer scan.^b $P < 0.001$ uncorrected (random-effect analysis) or all $P < 0.05$ FDR corrected.

showing repetition priming for faces across different viewpoints (27*x*, -51*y*, -21*z*; see above). In addition, using the objects > scrambled objects contrast from the separate visual localizer scan as an inclusive mask, we found that these repetition effects for chair exemplars in the left TOS and LOC and in the right anterior medial FG were also shape selective (Table 2). However, only repetition-priming effects for chair exemplars in the left posterior parahippocampal gyrus (-30*x*, -36*y*, -21*z*) were found to be object selective, as confirmed by their inclusion in the objects > faces, houses, and scrambled objects contrast from the separate localizer scan.

We did not find any reliable difference in any of these regions for repetition-priming effects as a function of viewpoint conditions, suggesting that these regions might be involved in abstract-/viewpoint-invariant coding of chair exemplars. Only at a lower statistical threshold, repetition-priming effects in the anterior right parahippocampal were found to be larger in the same view condition, relative to the different viewpoint condition (18*x*, -42*y*, -6*z*; $T = 3.34$, $Z = 2.84$, $P = 0.002$ uncorrected; see Epstein et al. 2003).

Houses Repetition of the same house exemplars (collapsing across same and different viewpoints) compared with their initial presentations revealed decreases in a network of regions typically involved in scene perception (Epstein et al. 1999, 2003; Grill-Spector 2003) and found to be house selective when the repetition effects were masked by results from our visual localizer scan. These regions included the parahippocampal gyrus (Fig. 2) plus a region near the TOS, the LOC, and the medial anterior FG. We did not find any significant difference in viewpoint sensitivity in any of these regions,

including in the parahippocampal gyrus. Importantly, the repetition of house exemplars across different viewpoints produced repetition decreases in a region of the medial FG (30*x*, -48*y*, -15*z*), close to where both faces (27*x*, -51*y*, -21*z*) and chairs (33*x*, -54*y*, -27*z*) also elicited reliable repetition-priming effects across view conditions.

All regions showing reliable repetition priming for house exemplars except LOC were included within house-selective areas defined by the visual localizer scan. This suggests a tight anatomical overlap between repetition-priming effects for house exemplars and house-selective effects.

Category-independent repetition priming One of our main goals was to establish whether visual regions subserving viewpoint-invariant recognition overlapped at least partly across the 3 distinct object categories. We formally tested for category-independent and viewpoint-independent repetition effects by performing a whole-brain conjunction analysis on repetition decreases arising equally for faces, chairs, and houses. Statistical parametric maps were thresholded ($P < 0.05$ FDR corrected) according to a conjunction null hypothesis (Nichols et al. 2005). This analysis revealed a selective involvement of LOC bilaterally (left: -42*x*, -84*y*, 3*z*; right: 36*x*, -78*y*, -12*z*; all $P < 0.05$ FDR corrected) and of the right medial FG (33*x*, -45*y*, -24*z*; $T = 5.90$, $Z = 4.18$, $P < 0.05$ FDR corrected).

Parameters of activity extracted from the LOC cluster (across all 16 participants) were submitted to a 3 (category) × 2 (repetition) × 2 (viewpoint manipulation) ANOVA, separately for the left and right side. Results revealed a significant effect of repetition ($F_{1,15} = 27.49$, $P < 0.001$), but no interaction with other factors (all $F < 1.7$, all $P > 0.21$) for both the left and right LOC. The left-sided region was also more generally “shape selective” (Malach et al. 1995) as evidenced by its precise overlap (see Fig. 4) with the objects > scrambled objects contrast from the localizer scan (see Table 1); whereas, the right-sided region was close to but not precisely overlapping with this general shape-selective response (see Fig. 4*B* and Table 1). Altogether, these results are consistent with a crucial role of this LOC region in extracting viewpoint-invariant features of object exemplars, shared across different visual object categories.

The conjunction analysis also revealed category- and viewpoint-independent repetition effects in a right medial FG region (see above). Again, parameters of activity from this region were extracted in all 16 participants and submitted to the same 3-way ANOVA as above. Results disclosed not only a main effect of repetition ($F_{1,15} = 47.16$, $P < 0.001$) but also a significant interaction between category and repetition ($F_{2,30} = 11.44$, $P < 0.001$), due to higher repetition-priming effects for face identities ($F_{1,15} = 75.08$, $P < 0.001$) and to a lesser extent for chair identities ($F_{1,15} = 21.77$, $P < 0.001$) and house identities ($F_{1,15} = 6.42$, $P = 0.02$) but without any modulation by the viewpoint manipulation ($F_{2,30} = 0.5$, $P = 0.61$). Direct pairwise comparisons demonstrated that repetition-priming decreases were indeed larger for face exemplars than either chair exemplars ($F_{1,15} = 11.33$, $P = 0.004$) or house exemplars ($F_{1,15} = 22.61$, $P < 0.001$). The amount of repetition priming was not statistically different between chairs and houses ($F_{1,15} = 2.39$, $P = 0.14$).

In sum, the pattern of responses in the right medial FG (but not LOC) displayed a significant gradient of repetition-related decreases according to the specific object category, maximal

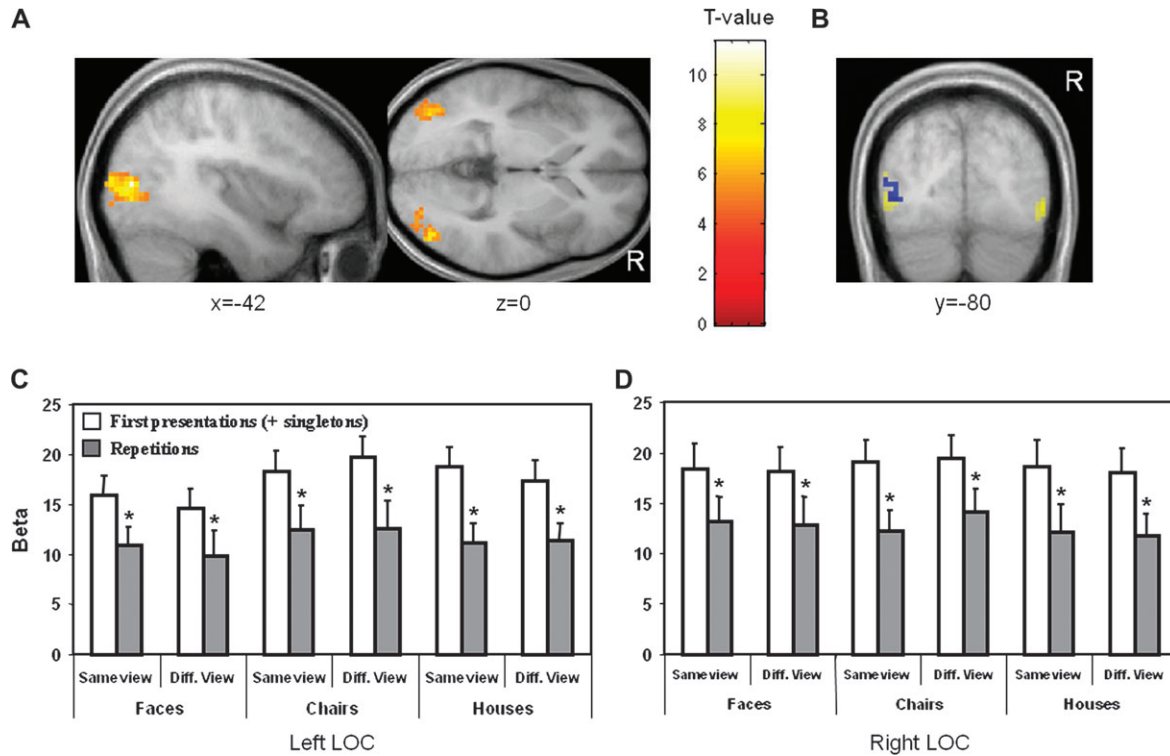


Figure 4. (A) Category-independent and viewpoint-independent repetition effects were primarily found in bilateral LOC (SPM thresholded at $P < 0.05$ FDR corrected; overlaid on the mean anatomical scan of participants). (B) Shape-selective areas of LOC (localizer scan; intact objects > scrambled objects contrast, $P < 0.05$ FDR corrected; shown in blue) overlapped only partly in the left hemisphere with category-independent and viewpoint-independent repetition effects (repetition-priming experiment; first > repeated contrast, $P < 0.05$ FDR corrected; shown in yellow). (C, D) Mean parameter estimates (beta, proportional to percentage of signal change) ± 1 standard error of the mean for left LOC (left panel) and right LOC (right panel). Both sides showed similar repetition effect irrespective of the object category (faces, chairs, or houses) or viewpoint change (same vs. different). Asterisks indicate significantly reduced responses ($P < 0.01$) for repetitions relative to first presentations.

for faces relative to the 2 other categories, despite a lack of significant category-selective preference observed in the separate visual localizer scan (see Table 1). This differential pattern of repetition-priming effects for right medial FG versus right LOC as a function of object category was further substantiated by a significant region \times visual category \times repetition-priming interaction ($F_{2,30} = 6.12$, $P = 0.006$; compare Fig. 3C and 4D).

Discussion

In this event-related fMRI study, we used a repetition-priming method to map regions of the human brain showing exemplar-specific adaptation effects across 3 different visual object categories, that is, faces, chairs, and houses. We used a large set of unfamiliar items (52 per category) that had not been encountered prior to scanning and were repeated in a pseudo-random, unpredictable order during the experiment. Critically, we systematically manipulated either the size or both the size and viewpoint between first presentations and repetitions for all these objects. This viewpoint transformation allowed us to identify brain regions showing view-independent adaptation effects, which are presumably responsible for the formation and long-term maintenance of invariant, exemplar-specific representations in extrastriate cortex (Schacter et al. 2007), based on relatively abstract or fuzzy coding of visual inputs (Logothetis and Pauls 1995). For the first time, our study directly compared such view-invariant processing for multiple visual object categories intermingled during the same task,

allowing us to extend previous findings derived from studies that focused on a single visual object category, such as man-made tools (Vuilleumier et al. 2002; Simons et al. 2003) or faces (Andrews and Ewbank 2004; Pourtois et al. 2005a; Fang et al. 2007).

Behaviorally, participants showed improved performance and faster RTs for repetitions relative to first presentations of the object exemplars, even though none of them reported being aware of the repetition-priming manipulation in post-scanning debriefing. These behavioral effects arose irrespective of viewpoint changes, consistent with the notion that an implicit but abstract viewpoint-independent memory trace may be formed after a single brief exposure to a novel object (Tulving and Schacter 1990). Such repetition-priming effects are in fact remarkable when considering that the retinal image of objects was substantially altered from the first exposure to the second one (see Henson et al. 2003; Pourtois et al. 2005a) and demonstrate the efficiency of neural processes by which the visual system may extract complex shape information and develop familiarity with new objects (see Bar et al. 2001; Gilaie-Dotan and Malach 2007).

At the neural level, we found that repeated object exemplars, relative to their first presentations, produced significant adaptation effects independent of viewpoint in distributed visual areas. For each object category, these repetition-priming effects overlapped partly with those regions showing category-selective responses in a standard visual localizer (including right lateral FG for faces, bilateral LOC for chairs, and bilateral parahippocampal gyrus for houses, see Fig. 2). In addition,

however, other extrastriate regions showed view-independent adaptation to repeated exemplars irrespective of the visual category, including the right medial FG and LOC. Furthermore, distinct effects of repetition for the same or different viewpoint conditions were observed only for face identities in the right FFA, but no viewpoint selectivity was found for other regions or other object categories in this study. This pattern of results replicates the segregation between 2 adjacent regions within the right FG reported in our previous study on view-invariant recognition of novel faces (Pourtois et al. 2005a) but provides new evidence for the implication of the medial FG in abstract-/view-independent coding of visual objects across different categories. Whereas the right lateral FG corresponding to the FFA is both category selective and viewpoint sensitive (see also Andrews and Ewbank 2004; Kanwisher and Yovel 2006; Fang et al. 2007), the nonoverlapping right medial FG appears to be viewpoint and category independent. Importantly, viewpoint- and category-independent repetition effects were also found in more posterior regions within bilateral LOC (Grill-Spector et al. 2001), suggesting that different view-invariant recognition processes might exist and subserve different functions, as discussed in more details below.

These new fMRI data for the right FFA accord with, but also extend, the well-established cognitive (Bruce and Young 1986) and neural (Haxby et al. 2000) models of face recognition as they indicate that perceptual encoding of faces may involve several distinct stages in visual cortical areas and further demonstrate that the initial representation of face identity information is viewpoint sensitive in the face-selective lateral FG (see also Gilaie-Dotan and Malach 2007; Fang et al. 2007). In addition, our data go beyond these models by showing parallel effects in right medial FG and bilateral LOC for view-invariant processing of both faces and objects (chairs and houses), which might make distinct contributions to view-invariant recognition (see below). It remains, however, to be determined (perhaps by using other brain imaging techniques with a better temporal resolution such as EEG or MEG) whether such processing of item-specific information in LOC and medial FG actually precedes or follows in time the viewpoint-dependent encoding of face identity within the lateral FG (FFA). Such data would not only refine cognitive models of face recognition (Bruce and Young 1986) but also provide important insights on visual properties or components that are shared between face and nonface stimuli during visual object processing in occipitotemporal cortex (Haxby et al. 2000).

Importantly, the present repetition-related decreases in cortical responses are unlikely to reflect any anticipation or expectation biases because all items were intermixed and randomized in an event-related design. They are also unlikely to result from unspecific effects of time elapsed or fatigue because not only did we carefully balance trial ranks between first and second presentations (see Vuilleumier et al. 2002; Pourtois et al. 2005a) but we also added several singleton items that were seen only once at the end of the experiment (hence pooled with the first presentations of other subsequently repeated items), and we included a specific parametric regressor for time in our SPM analysis (see Materials and Methods) such that altogether any effect of time should be covaried out in our results. However, even though we used a similar judgment of “vintage” to equate task demands across the 3 object categories (face, chair, and house; see Behavioral results), some task characteristics may produce substantial

changes in pattern of neural selectivity and invariant responses recorded from inferotemporal cortex (DiCarlo and Maunsell 2003; Murray and He 2006), and it remains to be determined to what extent our fMRI results depend on the current task demands. In line with this, a recent fMRI study (Murray and He 2006) investigated contrast-invariant responses in LOC using fMRI while subjects attended either toward or away from the contrast-varying shapes and found that this manipulation reliably changed contrast response function in LOC, although this represents a relatively low-level visual property. Accordingly, the nature and distribution of view-invariant repetition-priming effects in our study (in particular, in bilateral LOC) might potentially also vary as a function of specific task demands, and further fMRI studies would be useful to establish whether such factors might modulate the degree of view-invariant repetition-priming effects in LOC.

View-Independent Processing in Right Medial FG

A major result of our study concerns the functional subdivision between 2 adjacent regions within the right anterior FG. We found that the right face-selective FFA does not hold viewpoint-independent representations of face identities (Pourtois et al. 2005a) as repetition effects were significant only when a given person's face was repeated with the same viewpoint (yet with a different size). This result converges with previous fMRI results showing viewpoint-dependent representations of unfamiliar faces in the FFA (Andrews and Ewbank 2004; Pourtois et al. 2005a; Fang et al. 2007). Hence, this finding is consistent with the notion of rather narrow tuning for novel faces in right FFA, and emphasizes the relative distinctiveness of recognition processes subserved by this category-selective area (Kanwisher and Yovel 2006; Gilaie-Dotan and Malach 2007). These fMRI results for the FFA also accord with neurophysiological studies in the monkey showing that face-responsive neurons in the inferotemporal cortex or STS are viewpoint tuned (Perrett et al. 1998; Wang et al. 1998).

However, our new data reveal the existence of a more medial region within the right FG, showing the same magnitude of repetition effects for face identities in the same and different viewpoint conditions. Our detailed analysis of peak coordinates in each individual participant clearly demonstrates that this region is functionally distinct from, and nonoverlapping with, the more lateral FFA (see also Pourtois et al. 2005a). Moreover, the medial FG was not face selective because it showed similar repetition effects across viewpoint changes for chairs and houses and did not show category-specific responses in the visual localizer scan, suggesting a more general role in visual recognition. This region might hold some abstract-/view-invariant representations of visual objects, including novel face identities, allowing efficient generalization across changes in viewpoint (Biederman and Kalocsa 1997), unlike viewpoint-dependent computations performed by the right FFA (Pourtois et al. 2005a). The existence of neural populations underlying view-invariant recognition is further supported by monkey neurophysiological studies showing that some neurons in the inferotemporal cortex (or STS) may encode view-independent properties of face or object stimuli, sometimes with a high degree of invariance in their responses to a specific stimulus despite important changes in angle, size, contrast polarity, or spatial frequency content (Rolls 2000; Vogels et al. 2001). However, the view invariance of such neurons is rarely complete for all

possible views and they are often mixed with other neurons showing view-selective responses within the same cortical areas (Sawamura et al. 2005). Moreover, single cell studies have shown the existence of fuzzy neurons that preferentially respond to different views of the same object even when they are nonadjacent (Logothetis and Pauls 1995). It is therefore possible that the right medial FG area identified in this fMRI study mainly hosts a population of fuzzy neurons, which could be optimally tuned to frontal and three-quarter views of face identities, without the need to postulate more abstract or 3-D representations. Future fMRI studies using more than 2 views or transformations should be able to further characterize the view-tuning curves of right medial FG and other visual areas, so as to better understand the exact neural computations performed by different regions during face and object recognition (see Gilaie-Dotan and Malach 2007).

Nevertheless, by comparing different categories in the same experiment, we were able to show for the first time that neural activity in the medial FG area exhibited a gradient in the amount of repetition-priming effects as a function of the specific visual object category. Thus, repetition-related decreases across viewpoint changes in medial FG were significantly larger for faces than either chairs or houses, even though some decreases also arose for the 2 latter categories. Such gradient was not observed in LOC (see below). This pattern of responses points to differential view-invariant memory traces for novel objects identities in the medial FG, with better encoding of visual information from faces than houses or chairs. Such preference might relate to its anatomical proximity with the adjacent FFA and/or some general functional properties of right fusiform cortex well suited for processing objects defined by a particular configural or multipart structure (including but not exclusively restricted to faces). For instance, the medial FG might be critically involved in extracting view-invariant information about volumetric properties or relative metric relationships between internal features of objects, which might play an important role not only for face recognition (Bulthoff et al. 1995; Laeng and Caviness 2001; Maurer et al. 2002) but also objects seen across changing viewpoints (Biederman 1987). Alternatively, the medial FG might be particularly important to establish long-term view-invariant representations of visual entities at the subordinate level (Rhodes 1985; Damasio et al. 1990; Pourtois et al. 2005a), a recognition ability that may operate irrespective of category but is clearly more important for faces than other objects (Gauthier et al. 2000).

It is noteworthy that previous studies (Vuilleumier et al. 2002; Simons et al. 2003) found a hemispheric lateralization in fusiform responses suggesting preferential processing of view-invariant properties of objects (man-made and tools) in anterior left FG but processing of view-specific visual form information in right FG. Although this appears to contrast with the present finding of view-independent repetition-priming effects (for faces and other objects) in a right (but not left) medial FG region, we note that activated regions in FG did not exactly overlap across these studies, and we suspect that these differences may at least partly reflect different task demands (see also DiCarlo and Maunsell 2003; Murray and He 2006;). Our current task (judgments about the perceived vintage of stimuli) emphasized the processing of more perceptual/visual attributes as compared with previous categorization tasks (e.g., real vs. nonsense object decision),

which presumably required more elaborate processing of object identity and semantic properties and thus potentially induced a differential activation of the left FG (Vuilleumier et al. 2002; Simons et al. 2003; see also Damasio et al. 1990). The effect of task or attentional demands should be examined more systematically in the future, in order to test for any systematic modulation of hemispheric dominance and view-invariant processing.

View-Independent Processing in LOC

Several recent fMRI studies have shown adaptation or repetition effects for objects in LOC across changes in size or position (Grill-Spector et al. 1999, 2001; Kourtzi and Kanwisher 2001; James et al. 2002; Vuilleumier et al. 2002; Epstein et al. 2003; Hayworth and Biederman 2006). Repetition effects across changes in viewpoint have been less consistently found in LOC, being observed for faces in some studies (Grill-Spector et al. 1999; Pourtois et al. 2005a), but not for man-made objects in other studies (Vuilleumier et al. 2002). Ewbank et al. (2005) also reported size- and viewpoint-invariant adaptation effects in LOC to pictures of houses (outdoor places) but not to pictures of inanimate objects (e.g., couch). However, LOC encompasses a large cortical region that is likely to include functionally distinct areas (Grill-Spector et al. 2001). Another important outcome of the present study with different object categories was to demonstrate for the first time that viewpoint-independent repetition priming may arise in bilateral occipital regions within LOC, with the same magnitude regardless of the specific visual object category (faces, chairs, or houses). In contrast to the medial FG, LOC did not show any gradient in such effects as a function of the object category.

This result has important implications concerning the functional role of LOC in visual object processing, by revealing that the occipital regions identified here may hold exemplar-specific but category-independent representations of novel objects. Yet, its functional role is likely to differ from that of the medial FG. Moreover, a previous study using a sequential matching task with 3-D geometrical shapes (Gauthier et al. 2002) found that a lateral occipital/inferotemporal region (BA19) was sensitive to viewpoint manipulation but specifically during object recognition rather than during mental rotation. Here, we did not find any systematic viewpoint effects in LOC. However, there are a number of important methodological differences between our study and that of Gauthier et al. (2002), including stimulus type (meaningful categories vs. geometrical shapes), task characteristics (long-term priming vs. immediate matching), and experimental procedure, which preclude a systematic comparison between these studies.

We suggest that the LOC region identified here may code for elementary or intermediate parts of visual objects, which might be shared across different objects even from different categories (see Biederman 1987; Vogels et al. 2001; Ullman et al. 2002). Thus, neurons in LOC are probably not tuned to objects as a whole, but might instead represent complex fragments or shapes that are not unique to any specific object category (Baker et al. 2002; Lerner et al. 2002; Ullman et al. 2002) but can nonetheless be recovered across different views or different portions of an image (Kourtzi and Kanwisher 2001). Accordingly, LOC would not be selective to an object identity per se (requiring some abstract template) but tuned to more basic or intermediate parts or contours whose specific spatial arrangement can define more distinctive object types or

exemplars (Fujita et al. 1992; Wang et al. 1998; Baker et al. 2002). Such intermediate representation in LOC may allow a visual matching between 2 different views of the same exemplar but only if the angular rotation between 2 consecutive exposures of this object is not extreme. In keeping with this view, Fang et al. (2007) reported view-invariant decreases in LOC using a long-term adaptation procedure (i.e., 25 s exposure) for objects repeated with either no viewpoint change or a 30° angular rotation but not for objects repeated with 90° of angular rotation. The latter condition might impede the extraction of common parts or fragments across the 2 views and thus obviate stimulus-specific repetition-priming effects in LOC. In addition, Fang et al. (2007) reported that view-invariant effects were attenuated when using a short-term adaptation condition (i.e., 0.3 s exposure), demonstrating that the duration of stimulus exposure could influence the visual information extracted from individual stimuli and thus modulate the degree of item-specific (and view-independent) repetition effects in LOC. Taken together, these data suggest that some regions of LOC can form invariant representations of faces and objects only when it is possible to encode visual details or parts from object shapes and when the viewpoint transformation between study and test is not “extreme” (such that it does not completely prevent the overlap of fragment shapes between consecutive exposures). Consistent with this notion, Fang et al. (2007) suggested that their long-term adaptation paradigm could provide stronger evidence for viewer centered neural representations than short-term adaptation and that the neural mechanisms underlying short-term and long-term adaptation effects may be qualitatively different (see also Henson et al. 2004).

On the other hand, Eger et al. (2005) failed to observe reliable repetition-priming effects in bilateral LOC using famous and unfamiliar faces. These authors used a condition where the picture was changed between first and repeated presentations but mixed together various types of image transformations (including differences in facial expressions, lighting conditions, or hairstyles). As a result, the overlap between common parts or fragments (or even some combinations of visual features) between 2 views of the same face identity was probably more difficult to extract with these stimuli, as compared with the present stimuli (which were more uniform and underwent more regular viewpoint change, namely frontal to three-quarter and vice versa).

In sum, our fMRI results provide new support to the assumption that LOC may hold intermediate visual representations (fragments) or object parts (Ullman et al. 2002), which may underlie some aspect of view invariance for different object categories (including faces, chairs, and houses). However, further fMRI studies are still needed to identify more precisely the nature of the elementary or intermediate parts of visual objects (shared by several visual categories), which might be processed in bilateral LOC during visual object recognition.

View-Independent Processing in PPA

Lastly, we note that the repetition of house exemplars produced significant decreases in several brain regions, including the parahippocampal gyrus, which is typically involved in scene perception (Epstein et al. 1999, 2003; Grill-Spector 2003) and showed house-selective responses in our visual localizer scan. This result might seem to diverge

from earlier fMRI findings showing viewpoint-specific scene representations in human parahippocampal cortex (Epstein et al. 2003; Epstein et al. 2005; but see Ewbank et al. 2005). However, several differences between the 2 studies may contribute to an apparent discrepancy. Epstein et al. (2003) reported no adaptation effects in parahippocampal cortex for visual changes in scene geometry as compared with changes in a central object or no change, whereas in our study, changes in viewpoint were compared with conditions with no viewpoint change but a different size. The angular rotation in viewpoint (frontal vs. 3/4) of our house stimuli primarily induced a change in the observer’s perspective while preserving most of the intrinsic geometry of the scene. Moreover, unlike Epstein et al. (2003) who elegantly manipulated (scene) viewpoint by changing both the central object perspective and its concurrent background (layout), we used instead a uniform gray background in all pictures in order to selectively assess the processing of single objects. In addition, in the study of Epstein et al. (2003), changes in the central object of the scene (relative to changes in the position or viewpoint) produced significant fMRI decreases in parahippocampal cortex, suggesting that this region is not purely view dependent (given the substantial change in retinal image between the 2 visual scenes with a central object change). In any case, further studies may be needed to clarify the exact visual information encoded in parahippocampal cortex across different scene views.

Conclusions

Our new results extend our knowledge about the functional neuroanatomy of visual object recognition by showing that high-level, exemplar-specific information is represented across distributed regions of the human visual cortex and partly shared between multiple object categories (Ishai et al. 2000; Haxby et al. 2001; Ewbank et al. 2005; Schacter et al. 2007), including regions within LOC and medial FG. Although these 2 regions showed view-invariant repetition effects for object exemplars irrespective of category, different patterns of responses were found in each region and thus suggested distinct functional roles. View-invariant effects were similar for faces and other objects (houses and chairs) in LOC, suggesting a role for encoding visual information about elementary object parts across categories. By contrast, view-invariant effects in medial FG were stronger for faces than both houses and chairs, despite a lack of general category-selectivity in this region, suggesting a more complex sensitivity of this region to specific object attributes, such as the spatial arrangements of multiple parts or subordinate cues associated with unique exemplars. Finally, our data confirm a functional specialization of the right lateral FG that did not only show a high degree of category selectivity for faces but also high sensitivity to viewpoint transformation (Kanwisher and Yovel 2006; Fang et al. 2007). Taken together, these imaging findings highlight the complex functional architecture of human visual cortex and may help better understand the nature and diversity of visual recognition disorders following focal brain lesions in occipitotemporal regions.

Funding

Swiss National Science Foundation (to S.S. and P.V.).

Notes

We thank Reto Meuli as well as the radiologists and technicians at the Lemanic Bio-Medical Imaging Center and Centre Hospitalier Universitaire Vaudois for their help during data acquisition. *Conflict of Interest:* None declared.

Address correspondence to Gilles Pourtois, Department of Experimental clinical and health psychology, Ghent University, Henri Dunantlaan 2, 9000 Gent, Belgium. Email: gilles.pourtois@ugent.be.

References

- Andrews TJ, Ewbank MP. 2004. Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *Neuroimage*. 23:905–913.
- Baker CI, Behrmann M, Olson CR. 2002. Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Nat Neurosci*. 5:1210–1216.
- Bar M, Tootell RB, Schacter DL, Greve DN, Fischl B, Mendola JD, Rosen BR, Dale AM. 2001. Cortical mechanisms specific to explicit visual object recognition. *Neuron*. 29:529–535.
- Biederman I. 1987. Recognition-by-components—a theory of human image understanding. *Psychol Rev*. 94:115–147.
- Biederman I, Bar M. 1999. One-shot viewpoint invariance in matching novel objects. *Vision Res*. 39:2885–2899.
- Biederman I, Kalocsai P. 1997. Neurocomputational bases of object and face recognition. *Philos Trans R Soc Lond B Biol Sci*. 352:1203–1219.
- Bruce V, Young A. 1986. Understanding face recognition. *Br J Psychol*. 77:305–327.
- Bulthoff HH, Edelman S. 1992. Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proc Natl Acad Sci USA*. 89:60–64.
- Bulthoff HH, Edelman SY, Tarr MJ. 1995. How are three-dimensional objects represented in the brain? *Cereb Cortex*. 5:247–260.
- Damasio AR, Tranel D, Damasio H. 1990. Face agnosia and the neural substrates of memory. *Annu Rev Neurosci*. 13:89–109.
- Desimone R. 1996. Neural mechanisms for visual memory and their role in attention. *Proc Natl Acad Sci USA*. 93:13494–13499.
- DiCarlo JJ, Maunsell JH. 2003. Anterior inferotemporal neurons of monkeys engaged in object recognition can be highly sensitive to object retinal position. *J Neurophysiol*. 89:3264–3278.
- Downing PE, Chan AW, Peelen MV, Dodds CM, Kanwisher N. 2006. Domain specificity in visual cortex. *Cereb Cortex*. 16:1453–1461.
- Eger E, Schweinberger SR, Dolan RJ, Henson RN. 2005. Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *Neuroimage*. 26:1128–1139.
- Epstein R, Graham KS, Downing PE. 2003. Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron*. 37:865–876.
- Epstein R, Harris A, Stanley D, Kanwisher N. 1999. The parahippocampal place area: recognition, navigation, or encoding? *Neuron*. 23:115–125.
- Epstein RA, Higgins JS, Thompson-Schill SL. 2005. Learning places from views: variation in scene processing as a function of experience and navigational ability. *J Cogn Neurosci*. 17:73–83.
- Epstein R, Kanwisher N. 1998. A cortical representation of the local visual environment. *Nature*. 392:598–601.
- Ewbank MP, Schluppeck D, Andrews TJ. 2005. fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. *Neuroimage*. 28:268–279.
- Fang F, Murray SO, He S. 2007. Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cereb Cortex*. 17:1402–1411.
- Friston KJ, Fletcher P, Josephs O, Holmes A, Rugg MD, Turner R. 1998. Event-related fMRI: characterizing differential responses. *Neuroimage*. 7:30–40.
- Friston KJ, Holmes AP, Price CJ, Buchel C, Worsley KJ. 1999. Multisubject fMRI studies and conjunction analyses. *Neuroimage*. 10:385–396.
- Fujita I, Tanaka K, Ito M, Cheng K. 1992. Columns for visual features of objects in monkey inferotemporal cortex. *Nature*. 360:343–346.
- Gauthier I, Hayward WG, Tarr MJ, Anderson AW, Skudlarski P, Gore JC. 2002. BOLD activity during mental rotation and viewpoint-dependent object recognition. *Neuron*. 34:161–171.
- Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW. 2000. The fusiform “face area” is part of a network that processes faces at the individual level. *J Cogn Neurosci*. 12:495–504.
- Genovese CR, Lazar NA, Nichols T. 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage*. 15:870–878.
- Gilaie-Dotan S, Malach R. 2007. Sub-exemplar shape tuning in human face-related areas. *Cereb Cortex*. 17:325–338.
- Grill-Spector K. 2003. The neural basis of object perception. *Curr Opin Neurobiol*. 13:159–166.
- Grill-Spector K, Henson R, Martin A. 2006. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn Sci*. 10:14–23.
- Grill-Spector K, Knouf N, Kanwisher N. 2004. The fusiform face area subserves face perception, not generic within-category identification. *Nat Neurosci*. 7:555–562.
- Grill-Spector K, Kourtzi Z, Kanwisher N. 2001. The lateral occipital complex and its role in object recognition. *Vision Res*. 41:1409–1422.
- Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzhak Y, Malach R. 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*. 24:187–203.
- Grill-Spector K, Malach R. 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol (Amst)*. 107:293–321.
- Grill-Spector K, Malach R. 2004. The human visual cortex. *Annu Rev Neurosci*. 27:649–677.
- Halgren E, Dale AM, Sereno MI, Tootell RB, Marinkovic K, Rosen BR. 1999. Location of human face-selective cortex with respect to retinotopic areas. *Hum Brain Mapp*. 7:29–37.
- Hasson U, Harel M, Levy I, Malach R. 2003. Large-scale mirror-symmetry organization of human occipito-temporal object areas. *Neuron*. 37:1027–1041.
- Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P. 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*. 293:2425–2430.
- Haxby JV, Hoffman EA, Gobbini MI. 2000. The distributed human neural system for face perception. *Trends Cogn Sci*. 4:223–233.
- Hayworth KJ, Biederman I. 2006. Neural evidence for intermediate representations in object recognition. *Vision Res*. 46:4024–4031.
- Henson RN, Goshen-Gottstein Y, Ganel T, Otten LJ, Quayle A, Rugg MD. 2003. Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cereb Cortex*. 13:793–805.
- Henson RN, Rugg MD. 2003. Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*. 41:263–270.
- Henson RN, Rylands A, Ross E, Vuillemeur P, Rugg MD. 2004. The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. *Neuroimage*. 21:1674–1689.
- Ishai A, Ungerleider LG, Martin A, Haxby JV. 2000. The representation of objects in the human occipital and temporal cortex. *J Cogn Neurosci*. 12(Suppl 2):35–51.
- Ishai A, Ungerleider LG, Martin A, Schouten JL, Haxby JV. 1999. Distributed representation of objects in the human ventral visual pathway. *Proc Natl Acad Sci USA*. 96:9379–9384.
- James TW, Humphrey GK, Gati JS, Menon RS, Goodale MA. 2002. Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron*. 35:793–801.
- Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*. 17:4302–4311.
- Kanwisher N, Yovel G. 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philos Trans R Soc Lond B Biol Sci*. 361:2109–2128.
- Kourtzi Z, Kanwisher N. 2000. Cortical regions involved in perceiving object shape. *J Neurosci*. 20:3310–3318.

- Kourtzi Z, Kanwisher N. 2001. Representation of perceived object shape by the human lateral occipital complex. *Science*. 293:1506-1509.
- Koutstaal W, Wagner AD, Rotte M, Maril A, Buckner RL, Schacter DL. 2001. Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*. 39:184-199.
- Krekelberg B, Boynton GM, van Wezel RJ. 2006. Adaptation: from single cells to BOLD signals. *Trends Neurosci*. 29:250-256.
- Laeng B, Caviness VS. 2001. Prosopagnosia as a deficit in encoding curved surface. *J Cogn Neurosci*. 13:556-576.
- Lerner Y, Hendler T, Malach R. 2002. Object-completion effects in the human lateral occipital complex. *Cereb Cortex*. 12:163-177.
- Logothetis NK. 2000. Object recognition: holistic representations in the monkey brain. *Spat Vis*. 13:165-178.
- Logothetis NK, Pauls J. 1995. Psychophysical and physiological evidence for viewer-centered object representations in the primate. *Cereb Cortex*. 5:270-288.
- Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB. 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci USA*. 92:8135-8139.
- Marr D. 1982. *Vision*. San Francisco: W.H. Freeman.
- Maurer D, Grand RL, Mondloch CJ. 2002. The many faces of configural processing. *Trends Cogn Sci*. 6:255-260.
- Murray SO, He S. 2006. Contrast invariance in the human lateral occipital complex depends on attention. *Curr Biol*. 16:606-611.
- Naccache L, Dehaene S. 2001. The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cereb Cortex*. 11:966-974.
- Nakamura K, Kawashima R, Sato N, Nakamura A, Sugiura M, Kato T, Hatano K, Ito K, Fukuda H, Schormann T, et al. 2000. Functional delineation of the human occipito-temporal areas related to face and scene processing. A PET study. *Brain*. 123(Pt 9):1903-1912.
- Nichols T, Brett M, Andersson J, Wager T, Poline JB. 2005. Valid conjunction inference with the minimum statistic. *Neuroimage*. 25:653-660.
- Perrett DI, Oram MW, Ashbridge E. 1998. Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations. *Cognition*. 67:111-145.
- Pourtois G, Schwartz S, Seghier ML, Lazeyras F, Vuilleumier P. 2005a. Portraits or people? Distinct representations of face identity in the human visual cortex. *J Cogn Neurosci*. 17:1043-1057.
- Pourtois G, Schwartz S, Seghier ML, Lazeyras F, Vuilleumier P. 2005b. View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: an event-related fMRI study. *Neuroimage*. 24:1214-1224.
- Rhodes G. 1985. Lateralized processes in face recognition. *Br J Psychol*. 76:249-271.
- Riesenhuber M, Poggio T. 2002. Neural mechanisms of object recognition. *Curr Opin Neurobiol*. 12:162-168.
- Rolls ET. 2000. Functions of the primate temporal lobe cortical visual areas in invariant visual object and face recognition. *Neuron*. 27:205-218.
- Rotshtein P, Henson RN, Treves A, Driver J, Dolan RJ. 2005. Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nat Neurosci*. 8:107-113.
- Sawamura H, Georgieva S, Vogels R, Vanduffel W, Orban GA. 2005. Using functional magnetic resonance imaging to assess adaptation and size invariance of shape processing by humans and monkeys. *J Neurosci*. 25:4294-4306.
- Sayres R, Grill-Spector K. 2006. Object-selective cortex exhibits performance-independent repetition suppression. *J Neurophysiol*. 95:995-1007.
- Schacter DL, Buckner RL. 1998. Priming and the brain. *Neuron*. 20:185-195.
- Schacter DL, Wig GS, Stevens WD. 2007. Reductions in cortical activity during priming. *Curr Opin Neurobiol*. 17:171-176.
- Shepard RN, Metzler J. 1971. Mental rotation of three-dimensional objects. *Science*. 171:701-703.
- Simons JS, Koutstaal W, Prince S, Wagner AD, Schacter DL. 2003. Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex. *Neuroimage*. 19:613-626.
- Spiridon M, Fischl B, Kanwisher N. 2006. Location and spatial profile of category-specific regions in human extrastriate cortex. *Hum Brain Mapp*. 27:77-89.
- Spiridon M, Kanwisher N. 2002. How distributed is visual category information in human occipito-temporal cortex? An fMRI study. *Neuron*. 35:1157-1165.
- Tulving E, Schacter DL. 1990. Priming and human memory systems. *Science*. 247:301-306.
- Ullman S. 1998. Three-dimensional object recognition based on the combination of views. In: Tarr M, Bulthoff H, editors. *Object recognition in man, monkey, and machine*. Cambridge, MA: The MIT Press.
- Ullman S, Vidal-Naquet M, Sali E. 2002. Visual features of intermediate complexity and their use in classification. *Nat Neurosci*. 5:682-687.
- Vogels R, Biederman I, Bar M, Lorincz A. 2001. Inferior temporal neurons show greater sensitivity to nonaccidental than to metric shape differences. *J Cogn Neurosci*. 13:444-453.
- Vuilleumier P. 2007. Neural representation of faces in human visual cortex: the roles of attention, emotion, and viewpoint. In: Osaka N, Rentschler I, Biederman I, editors. *Object recognition, attention, and action*. Tokyo: Springer. p. 109-128.
- Vuilleumier P, Henson RN, Driver J, Dolan RJ. 2002. Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nat Neurosci*. 5:491-499.
- Wang G, Tanaka K, Tanifuji M. 1996. Optical imaging of functional organization in the monkey inferotemporal cortex. *Science*. 272:1665-1668.
- Wang G, Tanifuji M, Tanaka K. 1998. Functional architecture in monkey inferotemporal cortex revealed by in vivo optical imaging. *Neurosci Res*. 32:33-46.
- Worsley KJ, Marrett S, Neelin P, Vandal AC, Friston KJ, Evans AC. 1996. A unified statistical approach for determining significant signals in images of cerebral activation. *Hum Brain Mapp*. 4:58-73.
- Zago L, Fenske MJ, Aminoff E, Bar M. 2005. The rise and fall of priming: how visual exposure shapes cortical representations of objects. *Cereb Cortex*. 15:1655-1665.