

fMRI Activity Patterns in Human LOC Carry Information about Object Exemplars within Category

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Abstract

■ The lateral occipital complex (LOC) is a set of areas in the human occipito-temporal cortex responding to objects as opposed to low-level control stimuli. Conventional functional magnetic resonance imaging (fMRI) analysis methods based on regional averages could not detect signals discriminative of different types of objects in this region. Here, we examined fMRI signals using multivariate pattern recognition (support vector classification) to systematically explore the nature of object-related information available in fine-grained activity patterns in the LOC. Distributed fMRI signals from the LOC allowed for above-chance discrimination not only of the *category* but also of within-category *exemplars* of everyday man-made objects, and such exemplar-specific information generalized across changes in stimulus size and viewpoint, particularly in posterior subregions. Object identity could also be predicted from responses

of the early visual cortex, even significantly across the changes in size and viewpoint used here. However, a dissociation was observed between these two regions of interest in the degree of discrimination for objects relative to size: In the early visual cortex, two different sizes of the same object were even better discriminated than two different objects (in accordance with measures of pixelwise stimulus similarity), whereas the opposite was true in the LOC. These findings provide the first evidence that direct evoked fMRI activity patterns in the LOC can be different for individual object exemplars (within a single category). We propose that pattern recognition methods as used here may provide an alternative approach to study mechanisms of neuronal representation based on aspects of the fMRI response independent of those assessed in adaptation paradigms. ■

INTRODUCTION

Two photographs of the same object taken from different viewpoints, or under different lighting conditions, may show little similarity in their low-level physical properties. Despite this, our visual system can extract a representation of the object abstract enough to overcome such low-level differences, but specific enough to discriminate from a similar object of the same category. The computational mechanisms underlying this ability and their implementation in the human brain are still poorly understood. In humans, a complex of areas in the lateral occipital and inferior temporal cortex, termed the “lateral occipital complex” (LOC), is more active when viewing objects compared to textures or scrambled images (Grill-Spector, 2003; Malach et al., 1995). The LOC is considered a structure subserving general shape processing (common to all object types), but the precise nature of object-selective information within the LOC (i.e., in how far, and at what level of representation, LOC distinguishes individual objects) remains to be estab-

lished. Population measures of neural activity, such as functional magnetic resonance imaging (fMRI), are often considered unhelpful in resolving this type of question given the evidence that, at the level of single neurons, objects are likely to be represented in a distributed and spatially overlapping fashion (Hung, Kreiman, Poggio, & DiCarlo, 2005; Logothetis, Pauls, & Poggio, 1995; Rolls & Tovee, 1995; Gross, 1992; Young & Yamane, 1992) that is beyond the spatial resolution of conventional fMRI.

Indirect methods, such as repetition priming or fMRI adaptation paradigms, (e.g., Sawamura, Georgieva, Vogels, Vanduffel, & Orban, 2005; Avidan, Hasson, Hendler, Zohary, & Malach, 2002; James, Humphrey, Gati, Menon, & Goodale, 2002; Vuilleumier, Henson, Driver, & Dolan, 2002; Kourtzi & Kanwisher, 2000, 2001; Grill-Spector et al., 1999), have therefore been used to probe the nature of object representations in the LOC, but often with inconsistent findings. For example, studies differ in whether they suggest size and viewpoint-invariant representation of objects in different subparts of the LOC (Sawamura et al., 2005; James et al., 2002; Vuilleumier et al., 2002; Grill-Spector et al., 1999). Common to these studies is the reliance on a repetition-associated change

in activation (usually blood oxygenation level-dependent [BOLD] signal decrease) between consecutive presentations of the same (or a related) stimulus. Although these effects on the BOLD signal have been assumed to either reflect neural adaptation or some other change in the neural representation of the stimulus, the exact mechanisms are as yet unknown and probably complex (Grill-Spector, Henson, & Martin, 2006; Krekelberg, Boynton, & van Wezel, 2006). Because reliance on repetition-associated activity *changes* implies reliance on some form of mnemonic phenomenon, different mechanisms might be involved depending on the temporal lags between repetitions (Henson, 2003). These, in turn, may interact to a greater or lesser degree with task requirements (Henson, Shallice, Gorno-Tempini, & Dolan, 2002) or other factors, such as level of attention during repetition (Vuilleumier, Schwartz, Duhoux, Dolan, & Driver, 2005; Yi & Chun, 2005; Eger, Henson, Driver, & Dolan, 2004; Murray & Wojciulik, 2004).

In the light of these limitations in existing paradigms, here we sought to address the nature of LOC responses using an alternative approach, based on direct evoked fMRI activity (instead of changes of such activity due to repetition). Multivariate pattern classification has previously been used to show that object category information can be reflected in distributed activity patterns across extended areas of the inferotemporal cortex (O'Toole, Jiang, Abdi, & Haxby, 2005; Carlson, Schrater, & He, 2003; Cox & Savoy, 2003; Haxby et al., 2001). These studies were restricted to the discrimination of different object *categories*, not testing for any potential difference of response to exemplars within category, and thus, leaving open the extent to which effects reflect the representation of visual features per se (instead of, e.g., semantic differences associated with categories). More recently, pattern recognition techniques have been applied successfully to individual visual areas in the earlier visual cortex. For example, information sufficient to reconstruct the orientation of a stimulus can be decoded from human V1 (Haynes & Rees, 2005; Kamitani & Tong, 2005) even though the spatial layout of orientation-columns is below the spatial resolution of conventional fMRI.

We therefore hypothesized that such techniques might also provide more detailed insights into the nature of object representation within more circumscribed higher-level visual areas such as the LOC, even beyond discriminating responses to images of different categories. Conventional methods using average signals could not detect selective responses to different types of objects in this region, leading to the notion that this area may not be discriminative of different objects, and only involved in object detection (Grill-Spector, 2003; Malach et al., 1995). In a series of three experiments, we used multivariate pattern recognition to systematically explore whether distributed signals from this area carried information sufficient to discriminate object category, as well as the identity of individual exemplars of two everyday man-

made categories presented in different sizes or from different viewpoints. Furthermore, we compared discrimination results obtained in the LOC for different objects, sizes, and views, as well as generalization across changes in size and view, with those obtained in the early visual cortex (area 17/V1). Finally, we related our new fMRI findings to classification results and measures of low-level similarity based on the stimuli themselves.

METHODS

Participants and Data Acquisition

Eighteen healthy right-handed volunteers with normal or corrected-to-normal vision (7 men and 11 women, mean age = 27.3 ± 5.4 years) gave written informed consent to participate in the three separate experiments, which were approved by the local ethics committee. Functional images were acquired on a 3-T MR system with standard head coil (Siemens Allegra, Erlangen, Germany) as T2*-weighted echo-planar image (EPI) volumes with a TR of 1.4 sec (TE = 30 msec, 22 transverse slices, voxel size = $3 \times 3 \times 2$ mm, skip = 1 mm).

Stimuli and Design

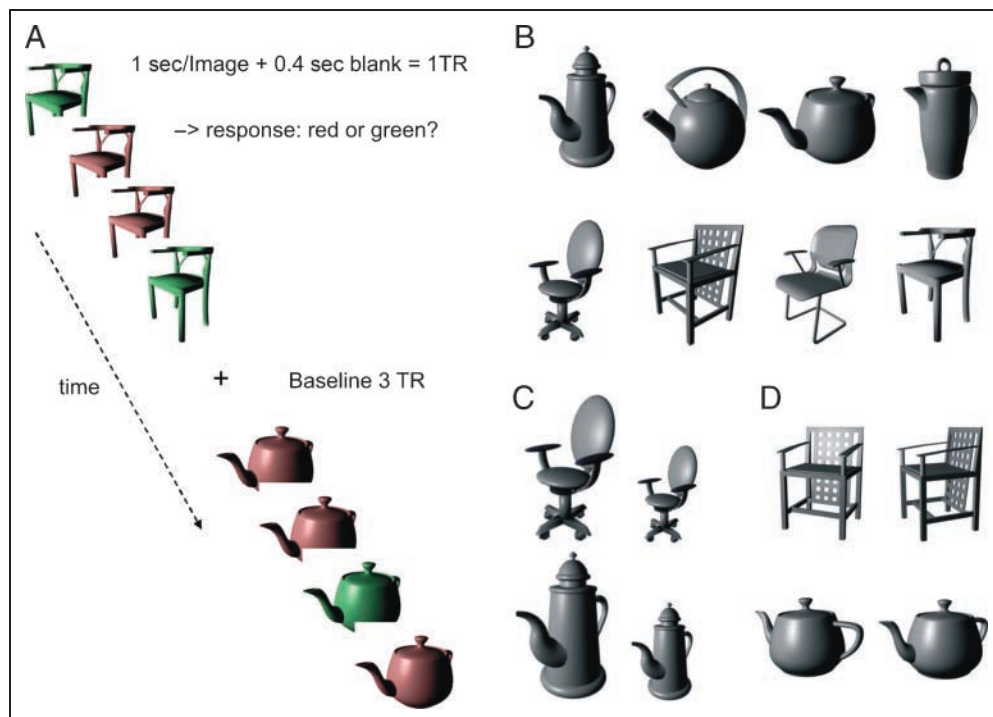
Stimuli (Figure 1) were created from 3-D models that were either freely available at various Internet sites, or created from scratch in Blender 2.3 (www.blender.org). All object models (4 chairs and 4 teapots) were equipped with the same surface texture of a uniform gray color, and illuminated with the same single light source. For the viewpoint experiment, two views were created separated by 60° rotation around the vertical axis, while avoiding strongly uncanonical views and occlusion of parts. In Experiments 1 and 3, rendered views subtended 200×200 pixels, whereas in Experiment 2 the small stimuli subtended 160×160 pixels, and the large stimuli subtended 240×240 pixels.

In Experiment 1, all participants were presented with pictures of chairs and teapots. In Experiments 2 and 3, half the participants were presented with the four teapots, and the other half were presented with the four chairs as stimuli (in two sizes, or two viewpoints each) to restrict the overall number of experimental conditions to eight.

Experimental Protocol and Task

Stimuli were back-projected onto a translucent screen located ~ 60 cm above the subject's head and viewed via a mirror on the head coil. The presented pictures subtended $\sim 5^\circ$ of visual angle. Objects were presented in short blocks of four pictures each (1 per TR, 1 sec stimulus, 0.4 sec blank), followed by a fixation baseline of 3 TR (Figure 1). The order of conditions was

Figure 1. Stimuli and experimental design. Across all three experiments, stimuli were presented in short blocks with four successive presentations of the same object, separated by short baseline periods (A). Participants were required to respond to each picture depending on the color of the object, which could randomly appear in a red or green hue. Two everyday man-made categories (teapots and chairs) with four different exemplars each served as stimuli (B). These were created from 3-D models with a unified surface texture and lighting. Objects were presented in two different sizes in Experiment 2 (C), and in two different views (D) in Experiment 3.



pseudorandomized. Within a given short block, each stimulus could randomly appear in a red or green hue, and participants were required to press one of two buttons on a keypad, depending on the color of the current stimulus. Five experimental sessions of 9.5 min length each were run for each participant with this task, encompassing 35 short blocks of each experimental condition.

In an additional scanning session of ~6 min in length, object-responsive areas were determined for all participants using a standard LOC localizer (Grill-Spector, 2003), comparing pictures of various common objects to scrambled versions of the same pictures in a blocked presentation with 500 msec per picture every 1 sec, and a block length of 12 sec (6 sec fixation baseline) during which participants performed a one-back repetition detection task. This functional localizer was used for definition of regions of interest (ROIs; see Figure 2) for the specific classification-based fMRI analysis performed, as described below.

Image Processing and Data Analysis

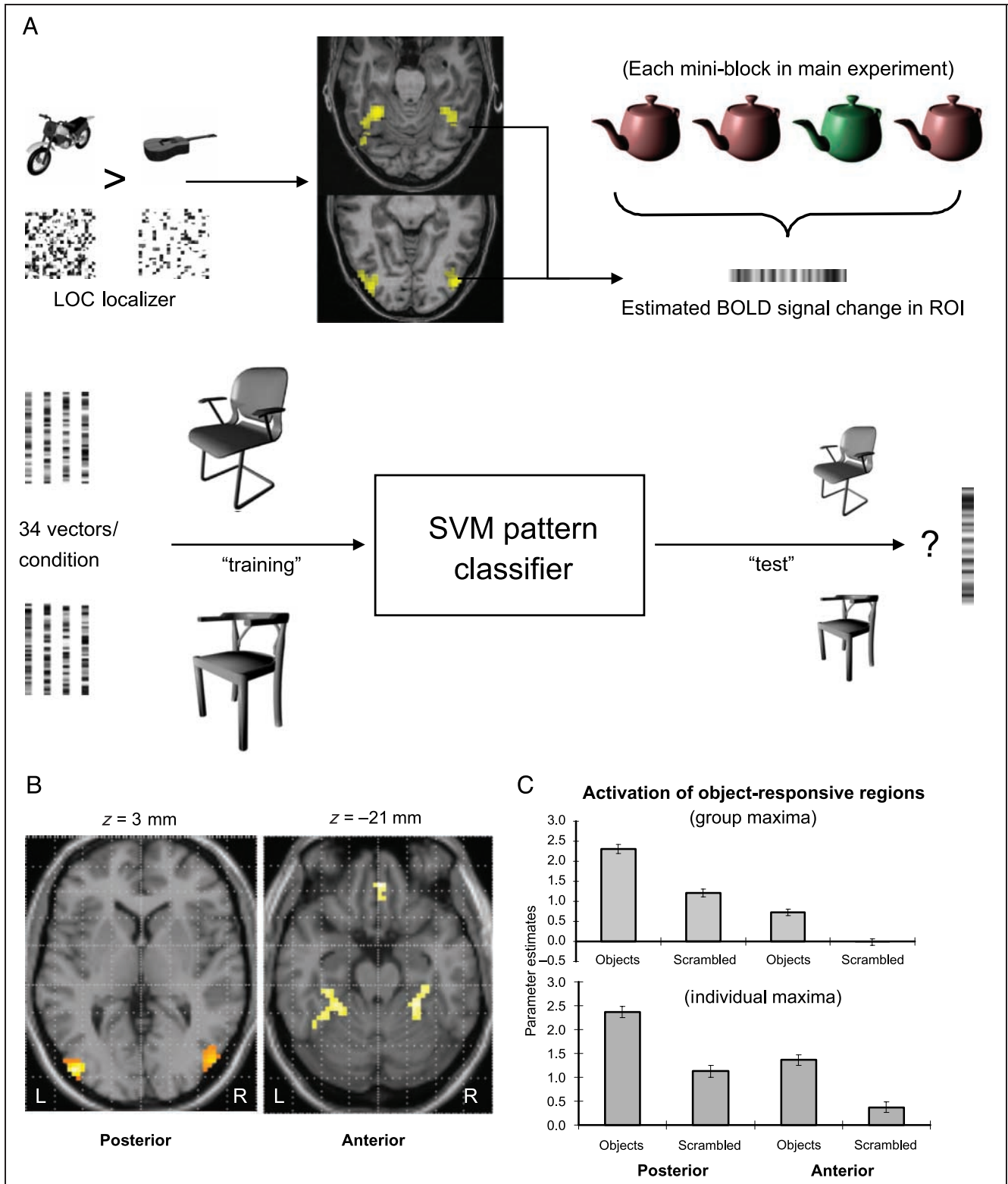
Initial analysis of the imaging data was performed in SPM2 (www.fil.ion.ucl.ac.uk/spm2.html). After motion correction, the unnormalized and unsmoothed EPI images were entered into a general linear model, modeling separately the effect of each short block (35/condition) convolved with a standard hemodynamic response function, while accounting for serial autocorrelation with an AR(1) model and removing low-frequency drift terms by a high-pass filter with cutoff 128 sec. This analysis yielded 35 independent estimates of BOLD signal change (images of regression coefficients) for each condition, which were subsequently entered into pattern recognition analysis.

We used a two-stage procedure to define ROIs based on a standard independent “LOC localizer” scan (e.g., Grill-Spector, 2003). First, we identified voxels in the ventral occipito-temporal cortex in each participant that

Figure 2. Schematic illustration of analysis procedure (A). Based on a standard LOC localizer comparing pictures of different everyday objects to scrambled versions of the same stimuli, ROIs were defined in each participant, corresponding to the left and right posterior (lateral/inferior occipital) and anterior (ventral temporal) subparts of the LOC. Estimates of BOLD signal change were obtained for this ROI in the three main experiments, corresponding to regression coefficients for each of the short blocks with one given object, convolved with a standard hemodynamic response function. Thirty-five of such independent estimates were obtained for each experimental condition. These 35 multivoxel pattern vectors for each condition were entered into a classification procedure using SVM, corresponding to pairwise “leave-one-out” prediction with cross-validation (see Methods). (B) Group analysis ($n = 18$) of the LOC localizer (objects minus scrambled objects) thresholded at $p < .05$, corrected, for the whole brain, superimposed onto a standard brain in MNI space, displaying group activations for posterior (lateral occipital cortex) and anterior (fusiform/ventral temporal cortex) object responsive areas. MNI coordinates were 48 -84 -3 and -45 -84 0 for the posterior, and 39 -45 -24 and -24 -39 -21 for the anterior subregion. (C) Average responses to objects and scrambled objects (parameter estimates) derived from group maxima (upper panel) and individual maxima (lower panel), indicating stronger responses to objects than scrambled objects in both subregions, while the overall visual response is stronger in the posterior than in the anterior subregion.

showed significantly greater responses to visually presented objects versus scrambled objects (Figure 2). In line with previous findings, posterior and anterior sub-regions in the lateral occipital and fusiform cortex were apparent in this contrast (see Figure 2 for mean stereo-

tactic coordinates). We then identified the response maxima in these anterior and posterior regions on a per-participant basis and defined spherical ROIs of 10 mm radius around these maxima. A spherical restriction of ROIs was used as a means to obtain comparable



numbers of voxels across participant (as desirable for multivariate analysis) without the need for participant-specific thresholding. We further confirmed that ROIs in the anterior and posterior LOC were nonoverlapping, and that any regions of white matter included in the ROIs did not affect our findings. For the left and right ROIs together, these comprised, on average, 212 (± 37) voxels for the posterior and 275 (± 29) voxels for the anterior part across participants (the exact number of voxels differing slightly because not all voxels within the spheres contained data in each case, e.g., due to signal dropout or location outside of the brain mask). For the initial analyses, anterior and posterior ROIs were combined, whereas for subsequent analyses we compared anterior and posterior sampled subregions of the LOC.

For the analysis of the early visual cortex, ROIs were defined by a mask based on a probabilistic map of area 17/V1 in MNI space, derived from the Anatomy toolbox for SPM (www.fz-juelich.de/ime/spm_anatomy_toolbox). This mask was back-transformed onto the individual subjects' brains (Deformation toolbox for SPM) to create individual ROIs for each participant.

Pattern recognition analysis was used to predict from distributed response patterns in these ROIs which of two given stimuli was currently being presented. The BOLD signal change estimates of n voxels were extracted for each condition and for repeated blocks forming a set of pattern vectors \mathbf{x} , which can be considered as points in an n -dimensional Euclidean space. Pattern classification was performed using linear support vector machines (SVM; Christianini & Shawe-Taylor, 2000; Vapnik, 1995) in the implementation of Gunn (www.isis.ecs.soton.ac.uk/). A linear classifier finds a hyperplane

$$\mathbf{w}^T \mathbf{x} + b = 0$$

defined by weight vector \mathbf{w} and offset b separating the training points \mathbf{x} with two different given labels. The principle of SVM is to find the optimally separating hyperplane that maximizes the margin (given by $\frac{\|\mathbf{w}\|}{2}$) with respect to both training classes (see Christianini & Shawe-Taylor, 2000, for detailed algorithm). Under the presence of noise (as here), the response vectors of both stimuli might not be linearly separable and a so-called soft-margin classifier can be used, which allows for a certain proportion of misclassifications by minimizing

$$\frac{\|\mathbf{w}\|}{2} + C \sum \xi_i$$

subject to

$$y_i(\mathbf{w}\mathbf{x}_i + b) \geq 1 - \xi_i \quad i = 1, 2, \dots, N \quad \xi \geq 0$$

Where ξ_i is a slack variable representing misclassification error for the i th pattern \mathbf{x}_i with label $y_i \in \{1, -1\}$ and C a regularization parameter determining the tradeoff between largest margin and lowest number of misclassifications. In the analysis presented here, a linear soft-margin classifier with $C = 5$ was used throughout (value of C chosen based on literature and not tested for optimality with present data). The classifier was trained on all but one ($=34$) replications for two given experimental conditions, and subsequently, tested on the remaining data, with 35 possible assignments of independent training and test datasets (leave-one-out prediction with 35-fold cross-validation).

The number of training and test data in each pairwise comparison was identical in object, size, and view comparisons. Classification accuracies were computed across all different training and test data assignments as mean percent correct for the two objects in a given pair. This mean pairwise percent correct is independent of classifier bias, comparable to the signal detection measure d' in a choice reaction task as performed here by the classifier. Classification accuracies were subsequently averaged across all possible *pairwise* comparisons to yield mean classification performance (e.g., objects across categories, within category, size, or view). The theoretical chance level in this case corresponds to 50%, which was further confirmed by performing classification on data with randomized labels (see Figures 3–5 and 7). Significance of classification performance was assessed in two-tailed t tests (against chance = 50%) across the six subjects in each experiment. This, in addition to identical training and test conditions (see above), should ensure that the results are comparable across the different comparisons between objects, sizes, and views. Although comparisons across different brain regions are informative in showing *relative* differences between different types of comparisons (e.g., size discrimination and object discrimination), absolute effect sizes across regions may be less comparable because they are sensitive to different signal-to-noise ratios and other factors unrelated to the biological question under study.

For the analyses investigating prediction accuracies as a function of number of voxels included, voxels were rank-ordered based on their absolute pairwise t value for a given comparison of interest, derived from the training data only (identical for the conditions testing for discrimination of the same image, and generalization). Hereby, those voxels are selected that would be most informative using a mass-univariate framework. This analysis was conducted for 1, 5, 10, 20, 40, and further in steps of 40 up to 400 voxels. Due to the pairwise implementation of this selection, different voxels might be selected first in different pairwise comparisons between conditions (reflecting the working assumption that different voxels might be informative for discrimination of different pairs of objects, instead of the same voxels for all objects).

RESULTS

Discrimination between and within Categories

In the first experiment, we investigated whether signals from the LOC carried information sufficient to determine either object category or the identity of individual exemplars from that category. We presented participants with four successive pictures of the same view of a particular object, in short blocks interleaved with short baseline periods (Figure 1A), while brain activity was measured with fMRI (see Methods). Four different exemplars of everyday man-made objects from each of two different categories (teapots and chairs, one view for each object; see Figure 1B) were used, with different objects presented in different blocks. Participants' attention was engaged in a color judgment task for each object, which could randomly appear in a red or green hue.

BOLD contrast responses evoked by each object in the main experiment in the sampled subregions of the LOC were extracted separately for each block (see Methods). To determine whether distributed response patterns in the chosen ROIs could successfully discriminate between and within different object categories, we then applied a multivariate pattern recognition algorithm based on Support Vector Machines (see Methods). To compare the performance of our multivariate technique with more conventional analyses, we also determined whether successful prediction could be achieved based on the mean level of activation in the sampled LOC subregions, or on just a few maximally stimulus-selective voxels. Prediction accuracies tended to increase with larger numbers of voxels and plateau at around 200 voxels. Below we focus on reporting results for 1, 5, 10, 200, and all 400 voxels.

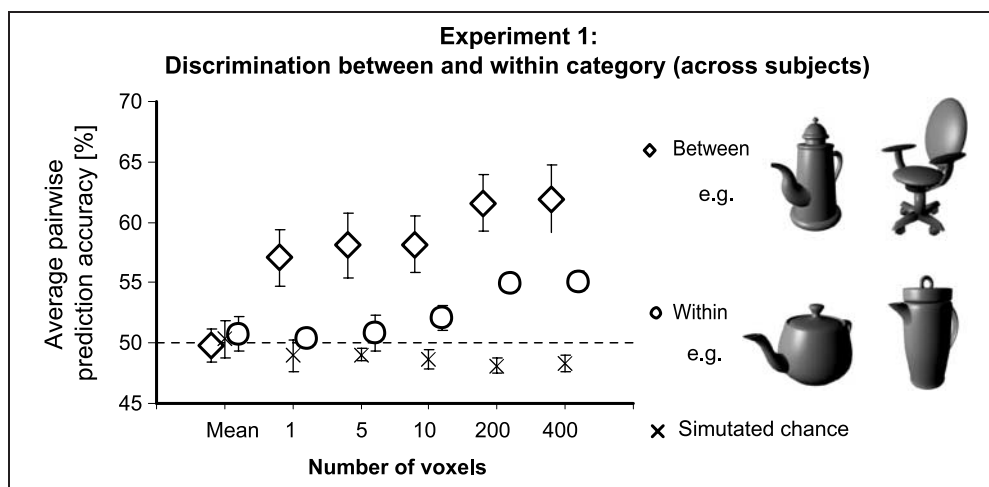
Classification accuracy was significantly above chance for both *between* and *within* category comparisons when

using 200 [between: $t(5) = 4.84, p < .01$; within: $t(5) = 9.65, p < .001$] or the maximum of 400 [between: $t(5) = 4.31, p < .01$; within: $t(5) = 6.19, p < .01$] voxels. In contrast, pairwise classification accuracy was at chance when based on mean activity for both comparisons. Accuracy was also not significantly different from chance (across subjects) for within-category comparisons when using the 1 to 10 most discriminative voxels, indicating that the fMRI pattern signal upon which successful classification was based encompassed relatively large areas of the LOC. Thus, although the mean signal in the LOC (as for conventional fMRI analyses) did not discriminate between and within object categories, the multivariate pattern signal now allowed successful classification performance. This indicates that neural population responses within the human LOC, in addition to discriminating between categories, also carry information sufficient to discriminate finer detail between individual object exemplars. Finally, although both comparisons were significant, between-category prediction accuracies were better (average 62% at 200 voxels) than within-category prediction accuracies (average 55% at 200 voxels), $t(5) = 3.14, p < .05$, and between-category comparisons were already above chance for up to 10 most discriminative voxels (see Figure 3).

Discrimination within Category and Effects of Size

In the second experiment, we determined whether the signals used for successful discrimination *within* a single category were invariant to stimulus size. A further six participants were now presented with four exemplars from just one of the two categories. However, the individual exemplars were presented in two different sizes (50% increase from small to large; see Figure 1C). This experiment thus focused on within-category comparisons

Figure 3. Discrimination performance for Experiment 1 (object discrimination between and within category), displaying means and *SEM* across six subjects for pairwise prediction accuracies (averaged across all possible pairwise between-category and within-category comparisons, also shown is the simulated “chance” performance obtained with randomized labels of conditions). Accuracies are plotted for prediction based on mean activity across the ROI, and for 1, 5, 10, 200, or 400 voxels, for which voxels were rank-ordered depending on their *t* value for a given pairwise comparison in the training data.



alone. Pattern classification proceeded in the same way as in Experiment 1, but we now, in addition, (1) changed object size between training and test to determine whether information from LOC signals used by our classifier was sufficient to generalize across size, and (2) attempted to directly discriminate the two sizes of each object, to test whether the LOC contains information about size in addition to object shape.

When training and test were carried out with data corresponding to the same object in a different size, significant above-chance accuracies were obtained for object classification based on higher voxel numbers within the LOC [200 voxels: $t(5) = 3.50, p < .05$; 400 voxels: $t(5) = 3.79, p < .05$]. Thus, pattern signals within the human LOC represent information sufficient to identify individual objects across changes in their size. For training and test using the same size objects, we replicated the within-category findings from Experiment 1. Significant above-chance classification performance for within-category discrimination was found when using either 200 [$t(5) = 3.53, p < .05$] or 400 [$t(5) = 2.51, p = .05$] voxels, testing with data corresponding to the same size. As before, classification based on the mean signal or the most discriminate voxels was not significantly different from chance (Figure 4). Prediction of object size resulted in, on average, lower discrimination performance than prediction of object exemplar (see Figure 4), which failed to reach significance for 200 [$t(5) = 1.4, p = .22$] and 400 [$t(5) = 2.0, p = .10$] voxels.

Discrimination within Category and Effects of View

Having established generalization of distributed LOC response patterns across changes in stimulus size, in a third experiment, we investigated whether signals sam-

pled from the LOC showed generalization across views within a single object category. A further six participants were presented with four exemplars of just one of the two categories. However, each exemplar could be presented from two viewing angles that differed by a 60° rotation around the vertical axis (Figure 1D). Analogous to the size experiment, in the different view condition, the classifier was trained on one view, and then subsequently tested on the different view of the object, in addition to directly comparing the two views of each object.

Significant above-chance discrimination performance was once again obtained when based on the higher voxel numbers [same view: 200 voxels, $t(5) = 4.63, p < .01$; 400 voxels, $t(5) = 5.55, p < .01$; different view: 200 voxels, $t(5) = 3.37, p < .05$; 400 voxels, $t(5) = 3.84, p < .05$; see Figure 5]. In this experiment, prediction based on mean activity derived from the five most predictive voxels reached significance for same views. However, because combining the data for the same image condition across all three experiments did not yield a significant effect [e.g., prediction for identical images based on mean activity across all three experiments, $t(17) = .07, p = .94$], we do not place much emphasis on these tendencies observed in Experiment 3 alone. As for object size in Experiment 2, prediction of object view resulted in, on average, lower discrimination performance than prediction of the object exemplar (Figure 5). For samples of 200 voxels, view discrimination showed a trend for significance [$t(5) = 2.2, p = .08$] and was nonsignificant [$t(5) = 1.9, p = .12$] for 400 voxels.

Comparison of Posterior and Anterior Subregions of the LOC

The results reported above show that BOLD pattern signals sampled from the LOC contained distributed

Figure 4. Discrimination performance for Experiment 2 (object discrimination within category, generalization across size, and size discrimination), displaying means and SEM across six subjects for pairwise prediction accuracies (averaged across all possible pairwise comparisons, also shown is the simulated “chance” performance obtained with randomized labels of conditions). Accuracies are plotted for prediction based on mean activity across the ROI, and for 1, 5, 10, 200, or 400 voxels, for which voxels were rank-ordered depending on their t value for a given pairwise comparison in the training data.

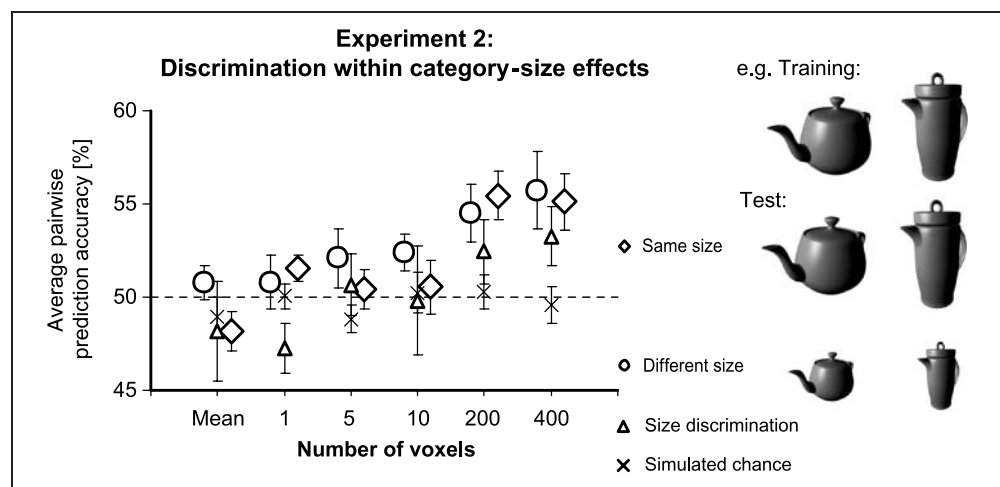
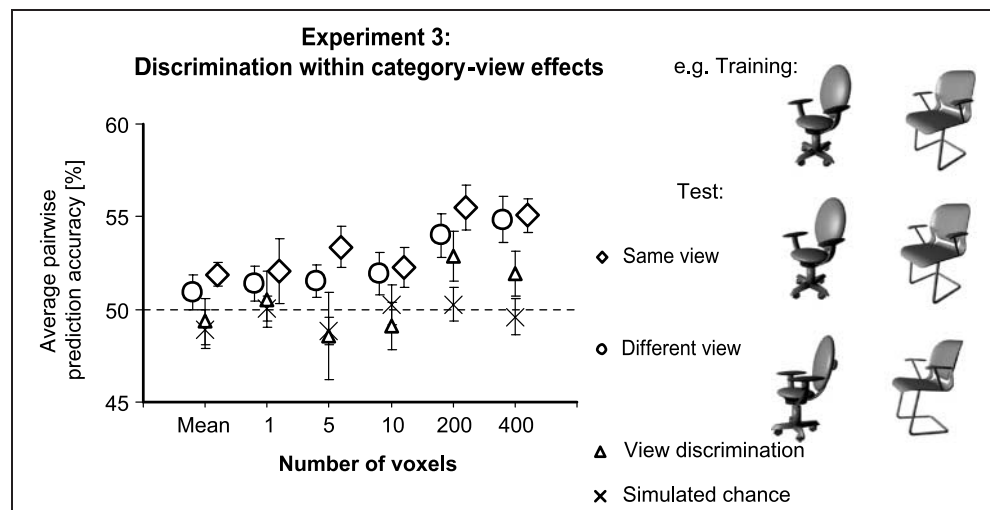


Figure 5. Discrimination performance for Experiment 3 (object discrimination within category, generalization across views, and view discrimination), displaying means and *SEM* across six subjects for pairwise prediction accuracies (averaged across all possible pairwise comparisons, also shown is the simulated “chance” performance obtained with randomized labels of conditions). Accuracies are plotted for prediction based on mean activity across the ROI, and for 1, 5, 10, 200, or 400 voxels, for which voxels were rank-ordered depending on their *t* value for a given pairwise comparison in the training data.



information sufficient to discriminate between objects of different categories as well as of the same category, whereas average discrimination performance for sizes and views of the same object was lower. Furthermore, for individual objects, object discrimination generalized across moderate changes in stimulus size and viewpoint. As previous reports have suggested a functional distinction between anterior and posterior subparts of the LOC (e.g., Sawamura et al., 2005; Grill-Spector et al., 1999), we next performed *separate* analyses for the sampled posterior and anterior portions of the LOC (Figure 6). These analyses included all voxels in the posterior (located in the lateral/inferior occipital cortex; see above and Methods for full details of sampling) or anterior (located in the ventral temporal cortex) ROIs without further preselection.

In Experiment 1, an analysis of variance (ANOVA) with the factors region (posterior/anterior) and object condition (between category/within category) revealed significant main effects of region [$F(1, 5) = 6.72, p < .05$] and object condition [$F(1, 5) = 17.4, p < .01$], without a significant interaction [$F(1, 5) = 0.96, p = .37$]. As Figure 6A indicates, these results reflected higher classification accuracies for the posterior LOC (compared to anterior), and also better accuracies for between-category comparisons. A similar ANOVA on the data from Experiment 2 revealed a trend for an effect of region [$F(1, 5) = 4.7, p = .08$], but no effect of object condition (same size/different size) [$F(1, 5) = 0.17, p = .69$], and no interaction [$F(1, 5) = 0.71, p = .44$]. Again, the observed tendency for significance reflected better discrimination performance in the posterior LOC (Figure 6B). Finally, an ANOVA for Experiment 3 showed a significant main effect of region [$F(1, 5) = 20.6, p < .01$], without a significant effect of object condition (same view/different view) [$F(1, 5) = 1.65, p = .25$], or interaction [$F(1, 5) = 3.56, p = .12$],

once again indicating better classification performance for the posterior than anterior LOC (Figure 6C).

Separate ANOVAs were conducted to assess effects of discrimination type (object vs. size/view) across regions. In Experiment 2, this ANOVA revealed a significant main effect of discrimination type [$F(1, 5) = 59.0, p < .001$], indicating better discrimination for different objects in the same size than for different sizes, without neither a significant effect of region [$F(1, 5) = 13.7, p = .16$], nor interaction [$F(1, 5) = 7.4, p = .34$]. In Experiment 3, there was a trend for a main effect of region [$F(1, 5) = 5.0, p = .08$], whereas the main effect of discrimination type [$F(1, 5) = .49, p = .50$] and the interaction [$F(1, 5) = 1.4, p = .30$] remained nonsignificant.

Taken together, the results of our comparisons between sampling the anterior and posterior LOC reveal consistently better prediction accuracies for sampled data from the posterior LOC. Although collapsed across all three experiments, prediction accuracies for identical images within categories reached significance for the anterior LOC [$t(17) = 3.14, p < .01$], whereas mean classification accuracy was only marginally above chance (52%).¹ This analysis further confirmed higher discrimination performance for different objects than different sizes of the same object, although this did not reach significance for the comparison object versus view.

Occipito-temporal Regions of Interest Defined in Main Experiments

The use of independent functional localizer sessions (as here for the LOC) has recently been debated controversially (Friston, Rotshtein, Geng, Sterzer, & Henson, 2006; Saxe, Brett, & Kanwisher, 2006). For this reason, we also conducted an alternative analysis where ROIs were defined on the basis of lateral occipital and fusiform

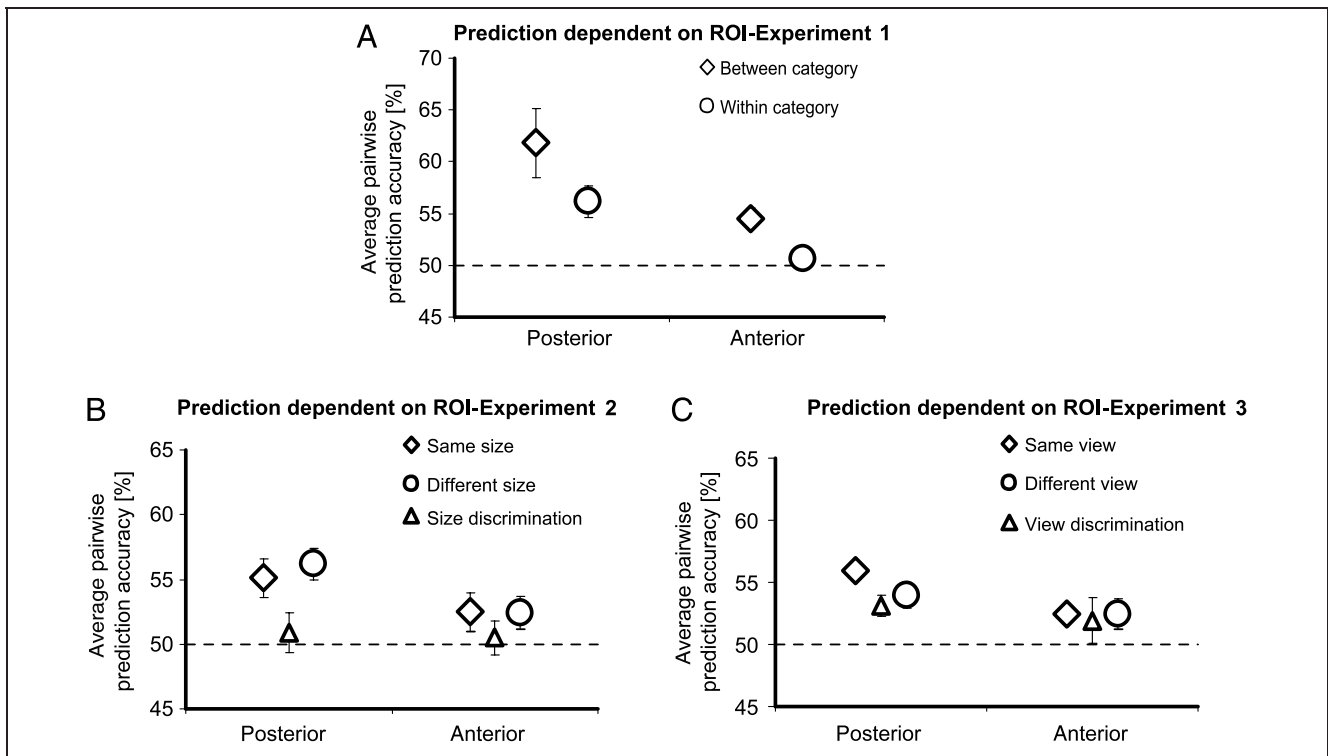


Figure 6. Prediction accuracies when separately testing posterior (lateral occipital) and anterior (fusiform) parts of the LOC. Consistently better discrimination (across the three experiments A–C) was possible based on MR signal in posterior compared to anterior parts (see text for details and statistics). In these analyses, all voxels were included without preselection. Means and *SEM* across six subjects are shown in all graphs.

clusters activated in the main experiment (for Experiment 1). Because objects were presented here against a baseline of fixation, this contrast is likely to include voxels that respond to any visual stimulus and not necessarily more strongly to objects as opposed to scrambled objects. For pattern recognition analysis, individual clusters activated for objects > baseline were identified in lateral occipital and fusiform regions, after which data were sampled and analyzed from these regions in a way analogous to the analysis based on the LOC localizer. The regions of interest defined on the basis of the main experiment were on average located somewhat more posterior than those defined by the LOC localizer, in particular for the anterior subregion (mean difference in *y* coordinates 4 mm for the posterior, and 10 mm for the anterior ROIs).

Analysis of occipito-temporal ROIs defined in this way yielded similar results with, on average, only slightly higher prediction accuracies (~64% correct for discrimination between categories, ~58% correct for discrimination within categories when selecting from all voxels, and for the same comparisons ~63 vs ~57% correct for the posterior ROI, and ~59 vs ~53% correct for the anterior ROI).

Quantification of Image Changes

Generalization of classification performance across image transformations, as shown here, could arise through

abstract representation by the neuronal populations, but could also, to some degree, reflect overlap in low-level visual features. To better understand the implications of our findings from the LOC, we quantified the degree to which our images of objects differed in their physical (low-level) image properties. We calculated a pixelwise dissimilarity measure (Euclidean distance) as performed previously (e.g., Vuilleumier et al., 2002; Grill-Spector et al., 1999) for all relevant stimulus comparisons. The mean (across pairwise comparisons) and *SD* pixelwise change was 78.4 ± 6.6 between category, 70.6 ± 9.2 within category, 78.1 ± 11.8 between same objects in different sizes, and 52.7 ± 13.1 between same objects in different views. The pixelwise change induced by different sizes was thus larger than that induced by exemplar change (and even comparable to that induced by different categories), but the difference due to view changes was smaller than that due to different exemplars. The pattern of discrimination performance obtained in the LOC for objects, sizes, and views is therefore not completely explained by the pixelwise similarity of the stimuli, because in the size experiment, the pattern of results for discrimination of objects versus sizes is opposite to one expected on the basis of this similarity measure.

In addition, we simulated generalization performance by entering the stimulus images themselves into an SVM and testing whether object images could be correctly

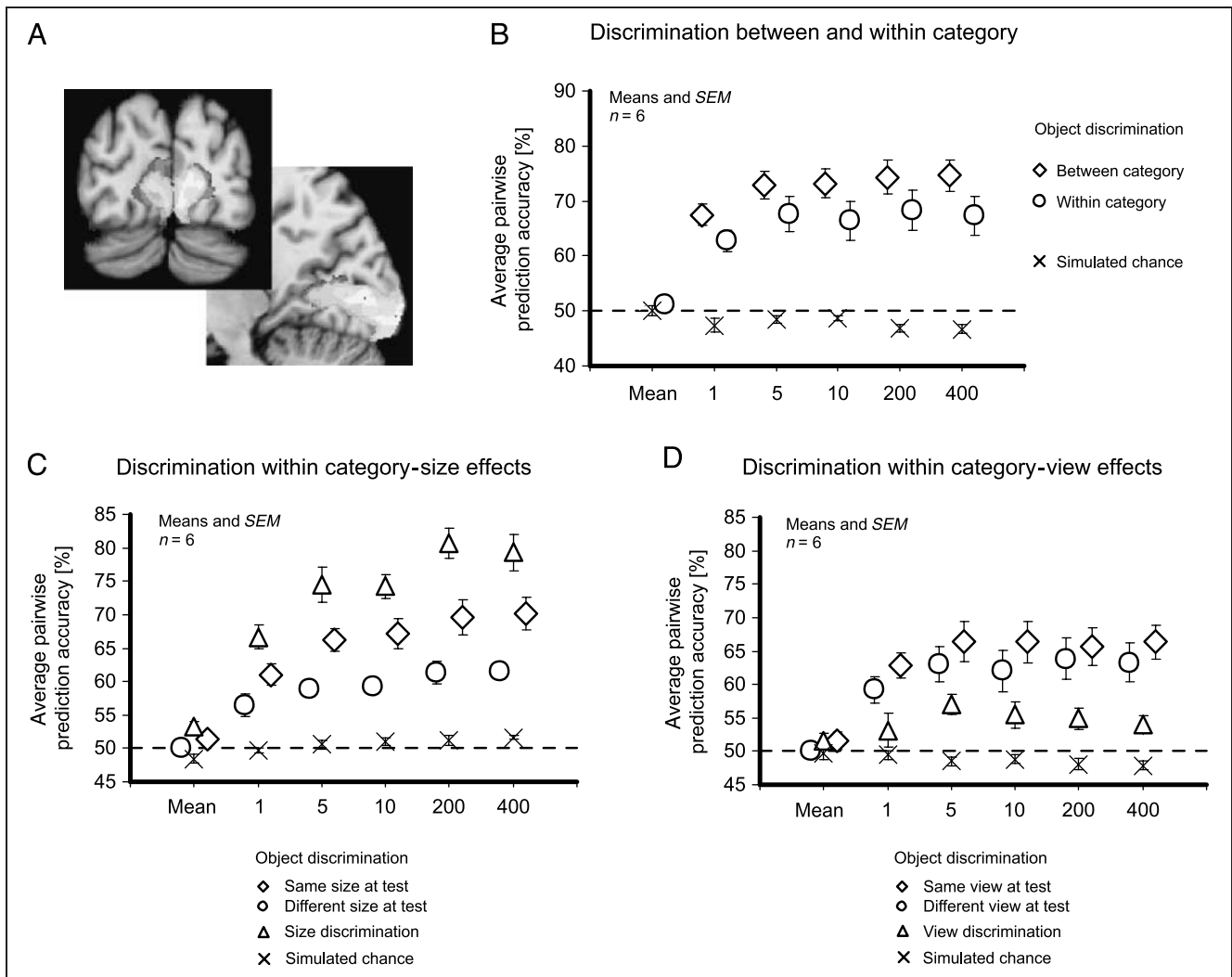


Figure 7. Prediction accuracies for the early visual cortex. (A) ROIs in MNI space (derived from a probabilistic map of area 17/V1 using the anatomy toolbox for SPM) that was transformed back onto individual subjects' brains. (B) Prediction accuracies for object discrimination across and within category (Experiment 1), means across six subjects and *SEM*. (C) Prediction accuracies for object discrimination within category, generalization across size, and size discrimination (Experiment 2), means across six subjects and *SEM*. (D) Prediction accuracies for object discrimination within category, generalization across size, and size discrimination (Experiment 2), means across six subjects and *SEM*. In all cases, results are plotted for mean activity and the same numbers of voxels (rank-ordered based on pairwise *t* test in training data) as used for the LOC. Also shown is the simulated "chance" performance obtained with randomized labels of the conditions. Inclusion of further voxels did not increase prediction accuracies for early visual areas.

classified on the basis of their pixelwise physical characteristics alone (see O'Toole et al., 2005, for a similar classification analysis of stimulus images). Across changes in size, object stimuli could be identified in 32 of 48 cases (67%) and across changes in view in 47 of 48 cases (98%). The reference value for identical images in these cases is 100% correct. These findings demonstrate that generalization in SVM classification can occur based on a low-level pixelwise representation of the stimuli (despite the pixel-wise change, on average, across all size comparisons being bigger than across all object comparisons; see above). However, these results also indicate that generalization based on such a representation does not reach the same level of discrimination accuracy as for identical images for the size changes used here.

Object Discrimination in the Early Visual Cortex

Finally, we also analyzed responses of the early visual cortex to determine whether the pattern of discrimination performance there was different from the one obtained in the LOC. Patterns of activation in the early visual cortex discriminate between physically different simple stimuli (e.g., Haynes & Rees, 2005; Kamitani & Tong, 2005), so we anticipated that these regions would also discriminate between the different objects used here (because different shapes are invariably associated with different local properties, which may be efficiently discriminated by the small receptive fields of early visual cortical regions). However, the extent to which early visual responses would also generalize across the

size and view changes in Experiments 2 and 3 was less clear, and therefore, of more general interest.

We assessed brain responses within a new ROI defined by a mask derived from a probabilistic map of Brodmann's area 17 that therefore identified regions of the cortex consistent with the primary visual cortex (see Methods for details). Results are summarized in Figure 7 (reported here for identical numbers of voxels as also used in the analysis of the LOC, although inclusion of more voxels did not further improve classification accuracies). In Experiment 1, reliable above-chance discrimination performance was observed for both comparisons across [e.g., for 400 voxels, $t(5) = 8.5$, $p < .001$] and within [e.g., for 400 voxels, $t(5) = 5.0$, $p < .01$] categories, accuracies being higher for comparisons across than within category [for 400 voxels, $t(5) = 8.4$, $p < .001$]. In Experiment 2, both discrimination of same images [for 400 voxels, $t(5) = 8.3$, $p < .001$] and generalization across size [for 400 voxels, $t(5) = 8.4$, $p < .001$] were above chance, however, with a marked difference in accuracy level [higher for test on data from identical than different image, at 400 voxels, $t(5) = 6.5$, $p < .01$].

Importantly, size discrimination yielded *even higher* prediction accuracies than object discrimination [see Figure 7; difference between size and object discrimination at 400 voxels, $t(5) = 4.1$, $p < .01$]. These results fit well with our quantification of pixelwise stimulus similarity as presented above, and show that the simple measure of image dissimilarity used here may account for much of the discrimination performance obtained in this region. Finally, in Experiment 3, above-chance discrimination performance was observed for discrimination of object exemplars in same [for 400 voxels, $t(5) 6.4$, $p < .01$] and different [for 400 voxels, $t(5) 4.6$, $p < .01$] views, at a comparable level of accuracy. Discrimination of view, although also above chance [for 400 voxels, $t(5) 2.8$, $p < .05$], was lower than object discrimination [difference between view and object discrimination for 400 voxels, $t(5) 4.6$, $p < .01$].

These results indicate that not only object discrimination based on identical images but also object discrimination across changes in size and view (although not always at comparable levels of accuracy as for identical images, see size experiment) was possible based on activity patterns of the early visual cortex. However, the pattern of findings in the early visual cortex was partially distinct from that in the LOC. Although early visual responses allowed better discrimination of *different sizes* of the same object than *different objects* in the same size, the opposite pattern was found in the LOC, as confirmed by a highly significant interaction between region and type of discrimination [object vs. size: $F(1, 5) = 43.1$, $p < .001$]. The fact that the same pattern was not observed for comparison of object versus view discrimination may be related to the greater pixelwise similarity of the different views used here.

DISCUSSION

In three independent experiments, we tested whether distributed fMRI signals sampled from the functionally defined human LOC represented information that supported discrimination between individual objects within a category, in addition to discrimination between categories. Using pattern-based multivariate analysis on fMRI signals, we could successfully use signals sampled from the LOC not only to predict the category of a given object, as done previously, but also discriminate between exemplars within the same category. Moreover, successful discrimination of individual category exemplars was possible when different stimulus sizes and viewing angles were used for training and test. Discrimination of objects, as well as generalization across the size and view changes, was also possible based on early visual cortex activity with high accuracy, but differences between the LOC and early visual regions were found in the detailed pattern of results for discrimination of different properties (notably objects vs. size).

Our results provide further support of the idea that distributed information about object categories is represented in the ventral occipito-temporal cortex (O'Toole et al., 2005; Carlson et al., 2003; Cox & Savoy, 2003; Haxby et al., 2001). Beyond this, we show that such distributed discriminatory information is not limited to the relatively coarse shape differences between different categories (which are accompanied by additional semantic differences), but is also found within a single category. Our results are obtained with a limited number of categories and exemplars due to the constraints imposed by the current level of sensitivity of fMRI that restricts the number of experimental conditions, and further work will be needed to show how far these results generalize to further object categories and exemplars. Overall prediction accuracies in our study were somewhat lower than those found in previous studies using the multivariate approach in relation to object categories (O'Toole et al., 2005; Carlson et al., 2003; Cox & Savoy, 2003; Haxby et al., 2001). This may be related to the specific categories used, differences in experimental design (short mini-blocks of only four objects here), or perhaps most importantly, due to our use of an orthogonal task (color judgment). We chose this task to avoid task-by-condition confounds, but the reduced attention to object shape might have weakened object-related activity. The effects described here are therefore most likely a conservative estimate of discriminability of single-object response patterns.

Our findings are also informative as to why investigations that based their analyses on the mean level of activity within an ROI (see e.g., Grill-Spector, 2003; Malach et al., 1995) failed to detect selectivity for different types of objects in the same cortical areas. Our analyses indicate that discrimination of categories (and exemplars) is possible when using patterns of activity across *multiple* voxels, but not for predictions based upon mean

activity or the few most selective voxels in the case of exemplar discrimination (Experiment 1). Prediction accuracies increased with the number of voxels included, compatible with the notion that also within the same category, representation of object shape is not restricted to the most discriminative voxels (as proposed in the distributed representation model for object categories; Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999).

A more detailed analysis of our data investigated activity sampled from posterior (lateral occipital) and anterior (fusiform) subregions of the LOC. Across the three experiments, the overall level of prediction accuracy was higher for the posterior compared to anterior LOC. In the first experiment, prediction accuracies were also higher for between-category than within-category comparisons, resulting in within-category comparisons being close to chance in the anterior LOC. These data are somewhat inconsistent with the notion of a simple object processing hierarchy according to which more posterior subregions would just be responsive to any object, potentially subserving “object detection,” whereas more anterior regions in the ventral temporal cortex (as also our anterior ROI) contain subregions discriminative between objects (see Grill-Spector, 2003; Malach et al., 1995). Our results show that the posterior object responsive regions located in the lateral/inferior occipital cortex alone can discriminate not only between categories but also exemplars at the level of distributed responses, whereas some previous work (see Ishai, Ungerleider, Martin, & Haxby, 2000) already suggested differential responses to categories such as faces, houses, and chairs in similar locations in the ventral occipito-temporal cortex.

Whether the anterior–posterior difference observed here reflects a physiological difference in encoding (of processing converging more onto category prototypes than individual exemplars in anterior regions) cannot be determined on the basis of our data alone. We did not observe any interaction between region and stimulus condition in between- versus within-category performance, however, because discrimination of exemplars was close to chance in the anterior LOC, this could reflect a floor effect. Thus, our results need not imply that identity information (and potential invariance to size and view) is not represented in the anterior regions; rather, that it was merely not detectable with the methods used here. Differences could exist in the BOLD signal-to-noise characteristics between the two regions (also see Figure 2 for differences in the overall visual response between the occipital and ventral temporal subparts; and note that the overall difference in level of prediction accuracies between the early visual cortex and the LOC is likely to result from differences in signal-to-noise). An additional analysis performed on occipital and fusiform activation foci from the main experiment yielded slightly higher average classification performance, however, the

anterior ROIs defined on the basis of the main effect were also located slightly more posterior. This suggests that the more anterior regions defined by the LOC localizer showed no very strong activation compared to baseline in our main experiment, potentially due to the use of an unrelated task (color judgment).

Other contributing factors to any differences in classification performance may include adaptation across repetitions of the same stimuli (potentially more pronounced in the anterior region), or differences in the spatial scale of the underlying object selectivities. Any variation in this spatial layout would be sampled in a more or less efficient way at a particular MRI resolution, leading to differences in performance of the multivariate classification algorithm (Haynes & Rees, 2005). Future studies using higher scanning resolution and/or different paradigms may disambiguate between these potential explanations. Little is currently known about the spatial scale of object selectivities in the human cortex, whereas monkey neurophysiology suggests that a column-like selectivity for object features might exist in the order of 500 μm (Fujita, Tanaka, Ito, & Cheng, 1992). In this case (assuming no limitations in the spatial resolution of the BOLD effect itself), higher spatial resolution should improve classification performance, but even 1 mm sampling resolution would still not resolve the true underlying pattern of object selectivities, but rely on partial volume effects.

The finding that the early visual cortex could also discriminate between the different object images used here was expected and is in line with previous studies using object categories (Cox & Savoy, 2003) which reported the highest classification accuracies for discrimination of categories when the classifier was allowed to select voxels from multiple areas including the low-level visual cortex, as opposed to an analysis on high-level object responsive areas only. Finding above-chance discrimination of activity patterns for objects in a given brain region thus need not necessarily reflect processing at the level of objects (instead of low-level local properties of the images). Beyond using pattern recognition to only quantify separability of responses to different conditions in this way, our experiments constitute a first step into the direction of using these techniques for the more challenging task of understanding mechanisms of representation of visual information at different stages of the processing pathway. The fact that we observed above-chance generalization of classification across sizes and views in the LOC, but also, less expected, in the early visual cortex, suggests that generalization of the classifier, although necessary, is not alone sufficient to conclude invariant representation by the neuronal population. Generalization further need not imply that the patterns for both conditions are identical, but may arise based on just a few voxels that show overlapping activation, for example, in foveal areas. Important additional information is therefore derived from the joint

consideration of generalization across, and the discrimination of a given feature. This revealed a dissociation between the LOC and the early visual cortex in the size experiment, where the relative pattern of accuracies (for discrimination of objects in same or different size, and discrimination of size for the same object) was less well predicted by our quantification of pixelwise stimulus similarity in the LOC than in the early visual cortex. Our data therefore support some degree of size-invariant coding of object shape in the LOC, but do not allow us to determine whether the representation is any more abstract than this, because given the pixelwise similarity results in the view experiment, an interpretation of the LOC results in terms of low-level overlap cannot be excluded.

The finding regarding size invariance in the LOC may appear to contrast with reports that only a small percentage of single neurons in the monkey IT cortex generalize across size or viewpoint (Booth & Rolls, 1998; Ito, Tawamura, Fujita, & Tanaka, 1995; Logothetis et al., 1995; Lueschow, Miller, & Desimone, 1994). However, these studies measured invariance of stimulus selectivity at the single-neuron level, which does not exclude invariance expressed at the population level that may be measurable with fMRI. Although in the data shown here, the different sizes of objects (despite their higher pixelwise dissimilarity) were not discriminated in the LOC, the possibility remains that higher spatial sampling (or using even larger changes in stimulus size) would reveal independent information about object shape and size also in the LOC. Indeed, such independent coding is suggested by recent findings that employed pattern recognition methods on populations of single neurons in the monkey IT cortex (Hung et al., 2005), and this would also be compatible with fMRI results that show some retinotopic organization in area LO, albeit weaker than in earlier areas (Larsson & Heeger, 2006).

Previous imaging studies investigating size and/or viewpoint invariance of object representation, using paradigms based on adaptation/priming, provided findings that range from size invariance being more pronounced in (or restricted to) anterior parts of the LOC (Sawamura et al., 2005; Grill-Spector et al., 1999), through size invariance in the occipito-temporal cortex and view invariance only in more anterior regions of the left fusiform gyrus (Vuilleumier et al., 2002) to view invariance in bilateral fusiform (but not posterior LO) regions (James et al., 2002). Here, we relied on aspects of BOLD activity that were constant across multiple replications of the same stimulus condition, rather than repetition-associated changes. Our results provide converging evidence for size invariance in the LOC, however, using this alternative approach, we found evidence for generalization across size, and inferior discrimination for sizes as compared to objects, already in the posterior subpart of the LOC. One possibility is that an overall weaker adaptability in the posterior as compared to anterior LOC (Sawamura et al., 2005) might account for the fact that some pre-

vious studies using repetition paradigms did not detect generalization of adaptation across size changes in that region.

Beyond differences associated with paradigms, it is likely that object discrimination and generalization of neuronal responses across stimulus attributes as size and view are not absolute, but depend on stimulus change in a gradual manner not only in earlier but also in higher areas as indicated by behavioral research (Lawson, 1999; Ashbridge & Perrett, 1998; Tarr & Bulthoff, 1998). We employed moderate changes in our first experiments presented here, which are, however, within the range used in previous studies (James et al., 2002; Vuilleumier et al., 2002; Grill-Spector et al., 1999), to ensure that the chosen manipulation did not result in, for example, strongly unusual views, or occlusion of parts. More studies will be required to reveal the extent of generalization (“tuning”) of fMRI response patterns across a wider range of changes, and across a broader range of (potentially parameterized) changes in object shape. Increasing the spatial resolution of the MRI acquisition, together with further development of methodological aspects, should provide additional sensitivity to investigate more subtle aspects of shape representation across a higher number of experimental conditions. Therefore, the pattern recognition approach as used here could, in the future, prove fruitful to approach the most interesting question of the nature of structural primitives (e.g., image-like “views,” or more structured part-based elements; see Riesenhuber & Poggio, 1999; Biederman & Kalocsai, 1997; Bulthoff, Edelman, & Tarr, 1995) underlying the representation of the visual input at different levels of the cortical hierarchy.

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Note

1. Because ROIs were based on spheres around the activation maxima, one potential factor contributing to inferior classification performance in anterior subregions could be that this region is situated close to areas of MR susceptibility artifact, and thus, classification could have included voxels where signal is very low. To rule out this possibility, analysis was repeated using only voxels within the chosen spheres that showed a significant difference between object and scrambled pictures in the localizer scan, which yielded qualitatively unchanged results. Likewise, restriction of the analysis to gray matter voxels using a gray matter mask derived from SPM segmentation did not change results, indicating that any inclusion of white matter voxels in our ROIs did not affect the findings.

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