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Encoding the identity and location of objects in human LOC

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ABSTRACT

We are able to recognize objects independent of their location in the visual field. At the same time, we also keep track of the location of objects to orient ourselves and to interact with the environment. The lateral occipital complex (LOC) has been suggested as the prime cortical region for representation of object identity. However, the extent to which LOC also represents object location has remained debated. In this study we used high-resolution fMRI in combination with multivoxel pattern classification to investigate the cortical encoding of three object exemplars from four different categories presented in two different locations. This approach allowed us to study location-tolerant object information and object-tolerant location information in LOC, both at the level of categories and exemplars. We found evidence for both location-tolerant object information and object-tolerant location information in LOC at the level of categories and exemplars. Our results further highlight the mixing of identity and location information in the ventral visual pathway.

Introduction

When we see an object in one location of the visual scene, and at some other occasion in a different location, we can typically identify it without effort. This seemingly simple recognition involves two important computational problems: (1) we recognize the *identity* of the object independent of its location, and (2), simultaneously, in order to be able to interact with an object, we need information about its location. The lateral occipital complex (LOC) has been suggested to be the prime locus of object identity representation (Malach et al., 1995; Grill-Spector, 2003). LOC is a functionally defined set of regions in lateral occipital and inferior temporal cortex responding stronger to pictures of intact objects than to scrambled pictures (Malach et al., 1995). However, the way in which LOC represents objects (Op de Beeck et al., 2008b) and the extent of its location tolerance remain debated (Kravitz et al., 2008). In particular, three issues remain to be addressed.

Location-tolerant object representation

Location tolerance is a necessary requirement for a representation to underlie object recognition: only representations that are tolerant to changing viewing conditions can reliably signal the presence of an object (Riesenhuber and Poggio, 2002; DiCarlo and Cox, 2007). To which extent object representations in LOC are location-tolerant remains debated. Prior fMRI studies using BOLD activation and fMRI adaptation differed in their estimate of the degree of tolerance with which LOC responds to objects at different locations in the visual field (Grill-Spector et al., 1998, 1999; Niemeier et al., 2005; Hemond et al., 2007; MacEvoy and Epstein, 2007). Similarly, studies using multivoxel pattern classification differed in their estimate: While some studies found evidence for location-tolerant object representations (Schwarzlose et al., 2008; Sayres and Grill-Spector, 2008; Williams et al., 2008; Carlson et al., 2009), others did not (Kravitz et al., 2010).

Category-level vs. exemplar-level representation

In typical everyday situations we recognize and automatically *categorize* objects based on visual evidence at the level of *exemplars* within a category (Rosch et al., 1976; Mervis and Rosch, 1981). However, most fMRI studies investigated object representation at the level of categories by averaging over brain responses for single exemplars within a category (Haxby et al., 2001; Grill-Spector et al., 1998; O'Toole et al., 2005; Spiridon and Kanwisher, 2002). Only recently, fMRI and multivoxel pattern classification have been combined to explore object representation below the level of category (Op de Beeck et al., 2010.; Kriegeskorte et al., 2007, 2008; Eger et al., 2008a,b; Kravitz et al., 2010). Thus, in this study we investigated whether location-tolerance in LOC holds for the representation of exemplars as well as for the representation of categories.

Coding of location

Besides recognizing and categorizing objects, the visual system must also keep track of the *location* of objects to allow us to orient

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ourselves and to interact with the environment. An influential view of the visual system (Ungerleider and Mishkin, 1982) claims that location information is not contained in the ventral stream. However, later interpretations of the dorsal and ventral stream distinction claimed that there is location information in the ventral stream, though in a different format than in the dorsal stream (Milner and Goodale, 2006, 2008). Also, recent studies showed the encoding of location information in LOC (Schwarzlose et al., 2008; Sayres and Grill-Spector, 2008; Carlson et al., 2009; Kravitz et al., 2010). Furthermore, there is retinotopic information at least in parts of LOC (Brewer et al., 2005; Larsson and Heeger, 2006; Sayres and Grill-Spector, 2008), and LOC exhibits an eccentricity bias (Levy et al., 2001; Malach et al., 2002; Hasson et al., 2002). In consequence, the degree of location information in LOC remains under investigation. We therefore investigated whether LOC contains information about the location of objects independent of object identity.

In this study we used high-resolution fMRI and multivoxel pattern classification (Mika et al., 2001; Haxby et al., 2001; Spiridon and Kanwisher, 2002; Cox and Savoy, 2003; Carlson et al., 2003; Kamitani and Tong, 2005, 2006; Haynes and Rees, 2005, 2006; Norman et al., 2006; Haynes et al., 2007) to estimate two crucial types of information encoded in LOC. We assessed location-tolerant object information and object-tolerant location information using visual stimuli at the level of exemplars within a category.

Methods

Participants and experimental design

13 healthy subjects with normal or corrected-to-normal vision (4 female, mean age 27 years, SD ± 4.28) participated in the study. The study was approved by the local ethics committee of the Max-Planck Institute for Human Cognitive and Brain Sciences (Leipzig) and conducted according to the Declaration of Helsinki.

To identify object-selective cortical regions, participants completed a standard LOC localizer scan (Malach et al., 1995; Grill-Spector, 2003; Grill-Spector and Malach, 2004). Subjects viewed blocks of images (duration: 16 s) of common objects or images of scrambled objects in pseudo-random order. Blocks of images were interrupted by periods of a uniform black background (duration: 12 s). Each block consisted of 20 images (700 ms per image, 100 ms gap). In each block, randomly four of the images were repeated consecutively. Subjects were asked to maintain fixation on a central fixation dot. They performed a one-back task on image repetitions in order to sustain attention to the images, indicating the answer via a button press.

For the main experiment, subjects viewed rendered 3D-meshes of 3 objects in 4 different categories (Fig. 1A), i.e. in total 12 different objects. The rendered images of objects were presented in mini-blocks (duration: 6 s). Mini-blocks were presented at a position either 4° right or left of fixation, subtending ~4.6° of visual angle (Fig. 1B). Each mini-block consisted of 6 images of an object (presented for 800 ms with 200 ms gap each). Each image displayed the object from a random viewpoint (with at least 30° difference in rotation in depth compared to the previous image) or it repeated the viewpoint of the previous image. During each mini-block a viewpoint was repeated once, twice or not at all. To ensure attention to the objects, subjects were asked to press a button when an object was shown from the same viewpoint consecutively (one-back task). Subjects were instructed to fixate a red dot in the middle of the screen. The number of repetitions of viewpoints was counterbalanced across objects. All objects had a uniform surface texture and were illuminated by the same 3-point lighting model. Illumination was kept identical for all objects under all conditions. In each run and for each object mini-blocks were repeated four times left and four times right of fixation. Subjects completed 5 runs of the main experiment.

fMRI acquisition

MRI data were acquired on a 3T Trio scanner (Siemens, Erlangen, Germany). Structural images were acquired using a T1-weighted sequence (192 sagittal slices, TR = 1900 ms, TE = 2.52 ms, flip angle = 9°, FOV = 256 mm). Functional images were acquired with a gradient-echo EPI sequence (TR = 2000 ms, TE = 30 ms, flip angle = 70°, FOV = 256 mm, matrix = 128 × 96, interleaved acquisition, no gap, 2 mm isotropic resolution, 24 slices). Slices were positioned along the slope of the temporal lobe and covered ventral visual cortex. The localizer comprised 226 volumes and each of the runs of the main experiment 412 volumes.

fMRI analysis

All functional data were first analyzed using SPM2 (www.fil.ion.ucl.ac.uk/spm). Images were slice-time corrected, realigned and normalized to the MNI template. Further analysis of the fMRI data will be described in two parts. First, we will explain the analysis of the LOC localizer run and the selection of regions-of-interest (ROIs). Then, we will proceed to the analysis of the main experiment.

LOC localizer and definition of regions of interest

First, functional data of the LOC localizer run were smoothed with a 4 mm FWHM Gaussian kernel. Then, we modeled the cortical response in the LOC localizer with a general linear model (GLM) for each subject. The effects of intact objects and scrambled objects were modeled as two separate conditions. Movement parameters were included in the GLM as regressors of no interest. Regressors were convolved with a hemodynamic response function (HRF). Next, we identified ROIs using a two-stage process. First, for each subject we generated a T-contrast "objects > scrambled objects" to identify object-sensitive voxels (Fig. 2A). Prior fMRI studies showed that sub-regions of LOC differ in the extent of tolerance (Grill-Spector et al., 2001; Eger et al., 2008b,a). Therefore, in a second step we subdivided LOC into a posterior (LO) and an anterior part (FUS) based on anatomical masks (WFU PickAtlas, http://fmri.wfubmc.edu/cms/software). Voxels located on inferior and medial occipital and temporal gyrus were allocated to LO, while voxels located on fusiform gyrus were allocated to FUS. The 500 most activated voxels for the contrast "objects > scrambled objects" in LO and FUS were identified in each hemisphere for each participant. Finally, to compare classification results in LO and FUS with results in early visual cortex we identified early visual areas (EV). Thus, we pre-selected voxels using a mask of BA17 (V1) from the WFU PickAtlas and then selected the 500 voxels most activated voxels (defined by the T-contrast ("objects & scrambled objects)> baseline"). ROIs (LO, FUS and EV) identified in this manner were used to select parameter estimates in the main experiment for further multivariate pattern classification. Note that the voxel selection is independent from the main experiment.

Analysis of main experiment

We modeled the cortical response to the experimental conditions in the main experiment for each subject. We treated each of the 12 objects (4 categories × 3 exemplars) presented either in the left or the right hemifield as single conditions, resulting in 24 conditions. Each of the five runs of the main experiment was modeled separately using a GLM. The onsets of the mini-blocks were entered into the GLM as regressors of interest and convolved with a HRF. This procedure yielded 24 parameter estimates per run, representing the responsiveness of each voxel to the 12 different objects presented in either the right or the left visual hemifield.

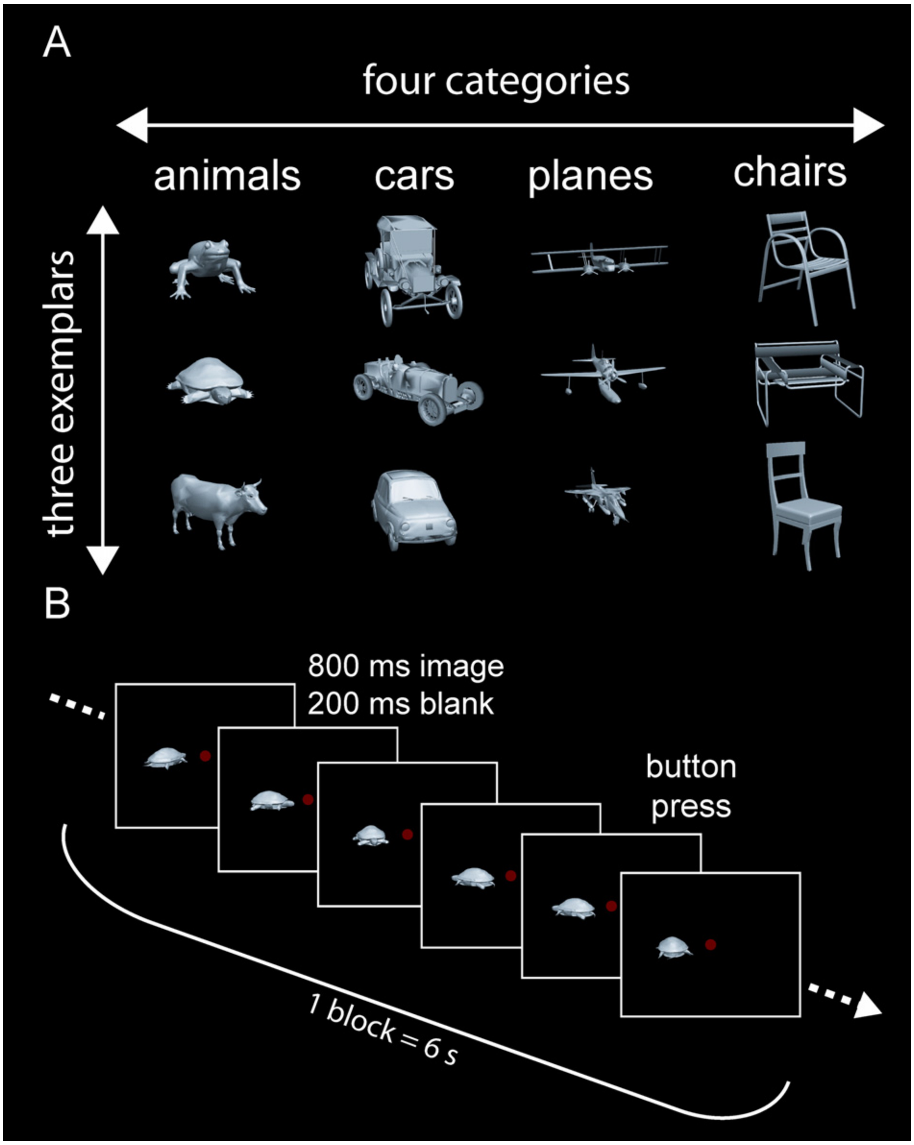


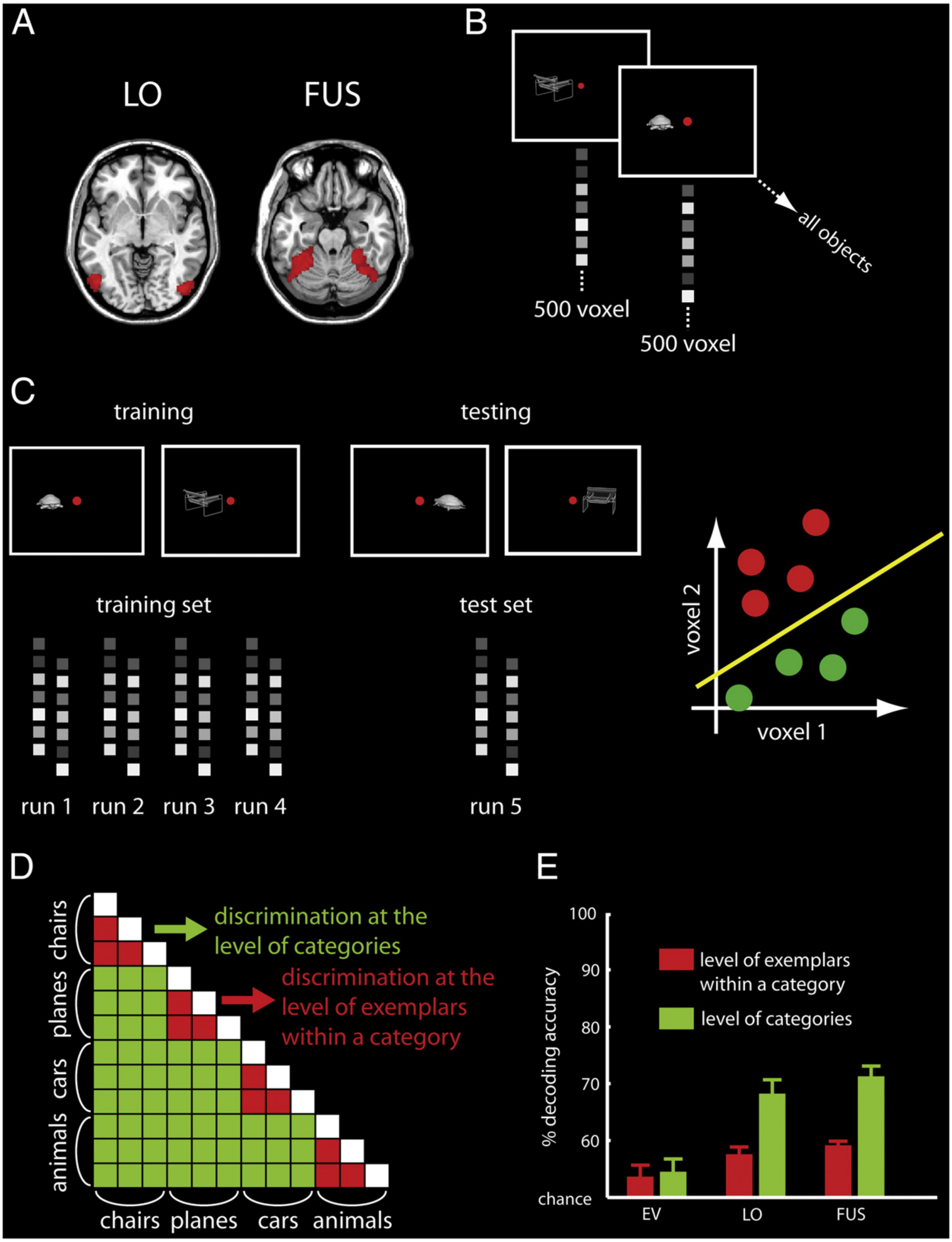
Fig. 1. Experimental stimuli and imaging paradigm of the main experiment. (A) The stimulus set comprised 3 objects in 4 categories each, i.e. in total 12 different objects. All objects were rendered 3D-meshes which had a uniform surface texture and were illuminated by the same 3-point lighting model. Illumination was kept identical for all objects under all conditions. (B) Subjects viewed images of objects in 6-s mini-blocks. Objects were presented either 4° right or left of fixation (here) and extended 4.6°. Each mini-block consisted of 6 random views of an object (presentation time 800 ms, 200 ms gap), rotated at least 30° in the depth plane with interspersed repetitions of a previous view. Subjects were instructed to maintain fixation and press a button whenever two consecutive views were identical in viewpoint (one-back task).

Pattern classification

Data from the main experiment were subjected to four multivoxel pattern classification analyses (Haxby et al., 2001; Kriegeskorte et al., 2006; Haynes and Rees, 2006; Norman et al., 2006; Williams et al., 2008) using a linear support vector classifier (SVC). Each analysis shared a basic framework that was adapted. All analyses were conducted independently for each ROI. For each subject and for each run we extracted parameter estimates evoked by the experimental conditions under investigation (further details below). These parameter estimates were transformed into pattern vectors representing the average spatial response patterns. Pattern vectors from 4 out of 5 runs were assigned to a *training data set* which was used to train a linear SVC with a fixed regularization parameter C = 1 in the LibSVM implementation (www.csie.ntu.edu.tw/~cjlin/libsvm). The trained SVC was used to classify pattern vectors from the independent test data set consisting of the 5th run. Five-fold cross-validation was carried out by repeating this procedure, each time with pattern vectors from a different run assigned to the independent *test data set*. Decoding accuracy was averaged over these 5 iterations. An exemplification of the basic framework for object classification across locations can be found in Fig. 2A–E. We conducted second-level analyses across all subjects on decoding accuracies by means of repeated-measures analyses of variance (ANOVA), paired *t*-tests and one-sample *t*-tests against classification chance level (for pair-wise classification always 50% decoding accuracy). All post-hoc *t*-tests were Bonferroni-corrected.

Classification of categories and exemplars across locations

In the first multivoxel pattern classification analysis we determined whether activity patterns allow the read-out of object information about the 12 individual objects (Fig. 2C) across locations. That is, we tested whether LO and FUS contain location-*tolerant* object information. For this aim, we trained a pair-wise classifier to differentiate between activity patterns evoked by these objects presented in one hemifield. Then we tested the classifier on activity patterns evoked by objects presented in the other hemifield. The classification was conducted for all possible object pairs and for both possible location assignments to the training and test set. Next, we separately compiled the category- and the exemplar-related decoding results (Fig. 2D). In detail, discriminations between object exemplars belonging to the same category (e.g., 2 different cars) were grouped as reflecting information at the level of exemplars within a category. In contrast, discriminations between object exemplars belonging to different categories (e.g., a car and a plane) were grouped as reflecting information at the level of categories.



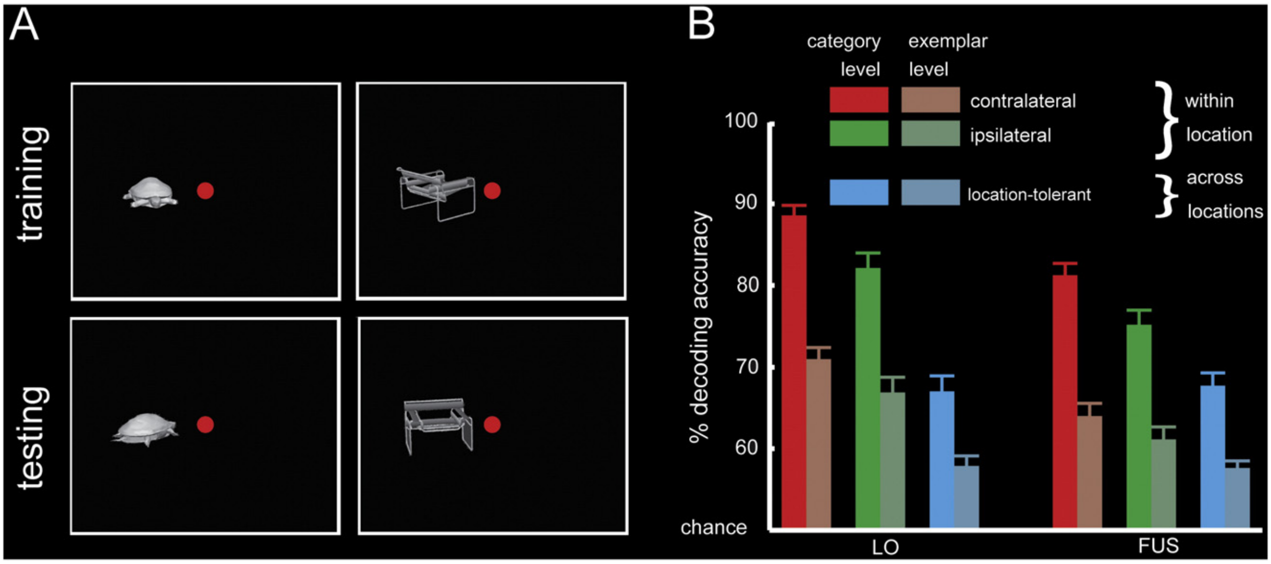


Fig. 3. Classification of objects within location. (A) Example of data entered into the classifier. A classifier was trained to distinguish between two objects (shown here for turtle and bureau chair) presented in the same location (here: left hemifield). Decoding results based on activity patterns in a ROI contralateral to the hemifield of object presentation were grouped together, as were decoding results based on activity patterns in a ROI ipsilateral to the hemifield of object presentation. (B) Results. Decoding accuracy for object classification within location was significantly above chance. This indicates that LO and FUS contain location-dependent object representations at the level of exemplars within a category and at the level of categories. Further, in most cases there was significantly more location-dependent object information ipsilateral to visual stimulation than location-tolerant information. Moreover, there was more object information in a ROI when stimuli were presented in the contralateral hemifield than in the ipsilateral hemifield at the level of categories. This corroborates the known contralateral hemifield preference in LO and FUS. Finally, there was more location-dependent object information at the level of categories than at the level of exemplars within a category, as was also the case for location-tolerant object information. Summary graphs depict mean decoding accuracies across 13 subjects ± SEM. Darker bars indicate decoding accuracies at the level of categories, and lighter bars indicate decoding accuracies at the level of exemplars within a category.

Classification of categories and exemplars within location

In the second analysis we determined whether activity patterns in LOC allow the read-out of information about the 12 individual objects (Fig. 2C) within location. That is, we tested whether LO and FUS contain location-*dependent* object information. For each ROI in each hemisphere separately, a classifier was trained and tested on activity patterns evoked by the same objects presented at the same location in the visual field (Fig. 3A). The analysis was repeated for both object locations. Whether activity patterns in ROIs contra- or ipsilateral to the hemifield of object presentation are classified is important for this analysis. Activity patterns in contralateral ROIs do not require transcallosal connections, whereas activity patterns in ipsilateral ROIs depend on them crucially (Kravitz et al., 2008). Therefore decoding results were grouped dependent on whether classification was conducted on activity patterns in ipsi- or contralateral ROIs. Finally, decoding accuracies were grouped depending on whether the classifier discriminated between objects at the level of categories or at the level of exemplars within a category.

Generalization across exemplars

In a third analysis we determined whether activity patterns for *specific* exemplars generalize sufficiently to allow correct classification of *other* object exemplars (Fig. 4A). For this, we trained a classifier to distinguish between activity patterns evoked by two object exemplars from two different categories. Then we tested the classifier on activity patterns evoked by two *different exemplars* from the *same categories* as used for training. In order to additionally avoid any influence of low-level similarity at the retinotopic level we always used opposite hemifields for training and testing data sets. This was repeated for every possible combination of exemplars for each category.

Location classification across objects

In a fourth analysis we investigated location information independent of object identity. We asked whether activity patterns contain information about object location tolerant to the object presented. For this aim a classifier was trained to distinguish between

Fig. 2. Schema of the analysis procedure for location-tolerant object information (A) Result of the LOC localizer for a representative subject. Results (T-contrast "objects > scrambled") are thresholded at $p<0.05$, FWE-corrected, and superimposed on a standard brain in MNI space. The sub-regions of LOC, i.e. LO in lateral-occipital cortex and FUS in fusiform gyrus are clearly discernable. For further analysis, in anatomically masked LO and FUS, we selected the 500 most activated voxels each. These voxels were used to select parameter estimates from the main experiment for multivariate pattern classification. Please note that voxel selection was conducted *independently* of the main experiment. (B) Extraction of parameter estimates for classification. In each ROI, parameter estimates from the selected voxels were extracted for each experimental condition, i.e. for each object presented either in the left or in the right visual hemifield (here left). Then the parameter estimates were ordered into pattern vectors. (C) Classification of objects across locations. We assessed whether location-tolerant information about object exemplars, i.e. information tolerant to changes in location was encoded in the spatial response patterns. Pattern vectors evoked by the presentation of two objects (here: chair and turtle) in one visual hemifield (here: left) from 4 out of 5 runs were assigned to a *training data set. The training data set* was used to train a linear support vector classifier (here illustrated by a 2-dimensional feature space as a simplification of the 500-dimensional feature space actually used). Then we tested the classifier on activity patterns evoked by the same objects presented in the other visual hemifield (here: right) from the remaining 5th run (*test data set*). Five-fold cross-validation was conducted by repeating this procedure, each time with pattern vectors from a different run assigned to the independent test data set. Decoding accuracy was averaged over these 5 iterations. (D) Scheme of possible discriminations between objects. Decoding results were grouped and averaged depending on whether the classifier discriminated between objects at the level of categories (green color) or at the level of exemplars within a category (red color). In detail, discriminations between object exemplars belonging to the same category (e.g., 2 different cars) were grouped as reflecting information at the level of exemplars within a category. Conversely, discriminations between object exemplars belonging to different categories (e.g., a car and a plane), were grouped as reflecting information at the level of categories. (E) Results. LO and FUS contained location-tolerant information about objects at the level of categories as well as at the level of exemplars within a category. In contrast, early visual cortex (EV) did not contain information about objects independent of location. Summary graphs depict mean decoding accuracies across 13 subjects ± SEM.

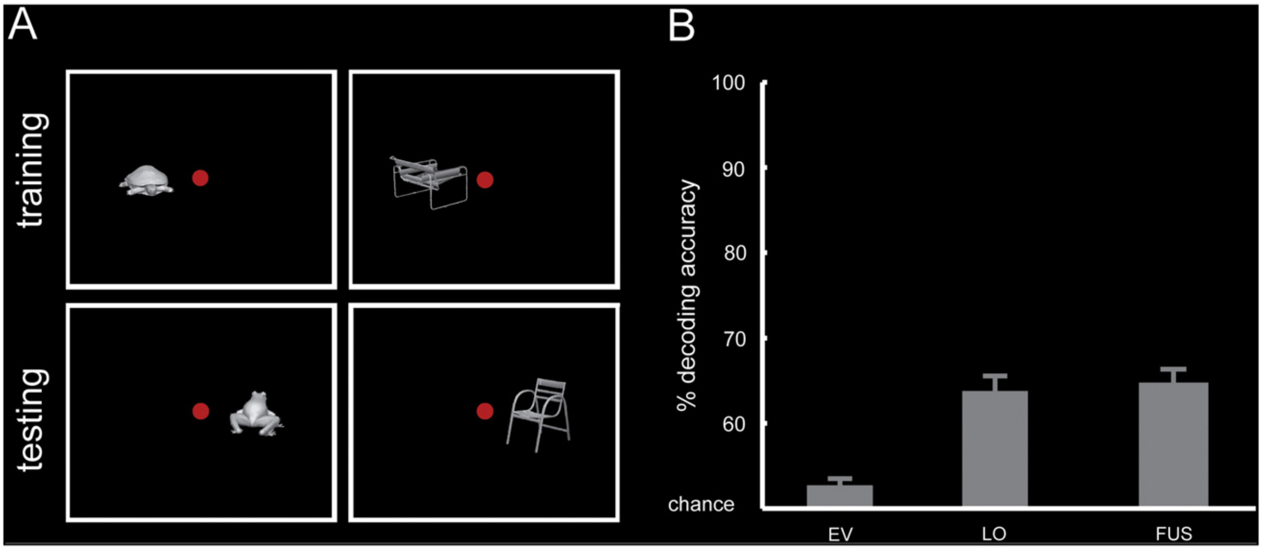


Fig. 4. Object identity representations in LOC generalize across different exemplars. (A) Example of data entered into the classifier. The classifier was trained on two objects (here: turtle and bureau chair) from two different categories presented in one hemifield (here: left) and tested on two other objects from the same categories (animals and chairs, so here: frog and wooden chair) presented in the opposite visual hemifield (here: right). (B) Results. We found that LO and FUS contained exemplar- and location-tolerant category information, whereas EV did not. This indicates that object representations at the exemplars within a category level generalize sufficiently to allow for object classification. Summary graphs depict mean decoding accuracies across 13 subjects ± SEM.

the two locations of a specific object. We then tested the classifier on the two locations of a *different* object from a different category (Fig. 5A). This analysis was repeated for all possible object pairs and decoding accuracies were averaged.

Results

Classification of categories and exemplars across locations

We investigated whether spatial patterns of brain activity in LO and FUS were predictive of objects presented in different visual hemifields (Fig. 2C and D). That is, we determined whether LO and FUS contain location-tolerant information about objects at the level of categories and exemplars within a category. We conducted one-sample t-tests against chance on decoding accuracy for object information at the level of categories as well as exemplars within a category. We found significant above-chance decoding accuracy for object discriminations at both the level of categories and exemplars within a category in LO and FUS (all $p<0.0001$, Fig. 2E, Supplementary Table 1). This indicates that location-tolerance in LO and FUS holds for information about exemplars as well as for information about categories. In contrast, we found no significant above-chance decoding accuracy for location-tolerant object discrimination at the level of categories ass well as exemplars within a category in early visual areas (all $p>0.05$, Fig. 2E, Supplementary Table 1). Concurrent with the assumption of a retinotopic structure, this indicates that for our stimulus set early visual cortex does not contain location-tolerant object information.

Next, we asked whether LO and FUS contain more information about objects at the level of categories than at the level of exemplars within a category. Thus, we conducted paired t-tests comparing decoding accuracy for object classification at the level of categories vs. the level of exemplars within a category. The analysis revealed that decoding

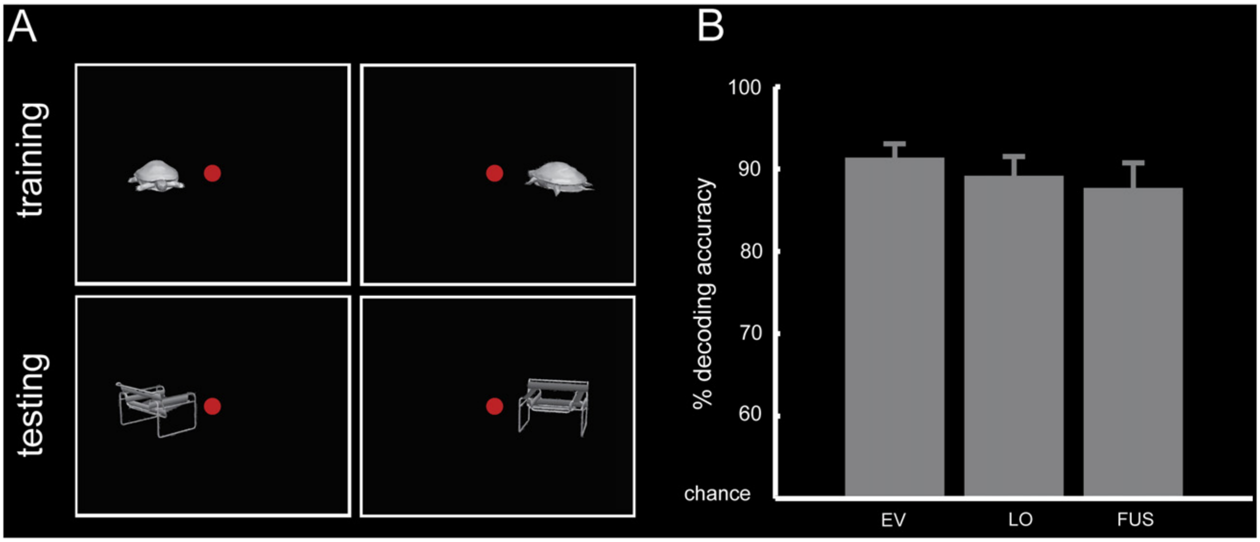


Fig. 5. Object-tolerant location information. (A) Example of data entered into the classifier. A classifier was trained to discriminate between the location of stimuli presentations of one object (here: turtle left and right) and tested on two locations of another object (here: bureau chair left and right). (B) Results. As expected, early visual cortex (EV) contained object-tolerant location information. Importantly, also LO and FUS contained object-tolerant location information. Summary graphs depict mean decoding accuracies across 13 subjects ± SEM.

accuracy was higher for classifications at the level of categories than at the level of exemplars within a category in both LO and FUS ($p<0.001$, Supplementary Table 2). This indicates that LO and FUS contain more information differentiating between objects at the level of categories than at the level of exemplars within a category.

Classification of categories and exemplars within location

We investigated to which extent spatial patterns of brain activity in LO and FUS were predictive of objects presented at the same location (Fig. 3A). Thus, we determined how much *location-dependent* object information is contained in LO and FUS ipsi- and contralateral to the hemifield of object presentation. The results are portrayed and compared with location-tolerant information in Fig. 3B. We found that LO and FUS contained location-dependent information about objects at the level of categories and the level of exemplars within a category (one-sample *t*-tests against chance, all $p<0.001$, Fig. 3B, Supplementary Table 3). Hence, in conjunction with the prior analysis, this indicates that both kinds of object information, location-dependent and location-tolerant, can be read out from LOC.

Next, we asked whether LO and FUS differ in the amount of object information dependent on whether it is location-dependent or location-tolerant. In addition, we investigated whether LO and FUS exhibit a preference for the contralateral hemifield as indicated by prior studies using BOLD activation levels (Niemeier et al., 2005; Hemond et al., 2007; MacEvoy and Epstein, 2007; Sayres and Grill-Spector, 2008) and pattern classification methods (Kravitz et al., 2010). That is, we asked whether LO and FUS contralateral to the hemifield of object presentation contain more information than ipsilateral to the hemifield of object presentation. Thus, we compared decoding accuracy of location-dependent and location-tolerant object classification. For this aim we carried out a 2×2 repeated-measures ANOVAs with factors *source-of-object-information* (ipsilateral vs. contralateral vs. location-tolerant) and *representational level* (level of categories vs. level of exemplars within a category) for LO and FUS separately. In LO and FUS both main effects and the interaction effect were significant (all $p<0.001$, Supplementary Table 4). We conducted post-hoc *t*-tests to investigate these effects in detail. We compared decoding accuracies of location-tolerant object classification with location-dependent object classification in LO and FUS *contralateral*, then *ipsilateral* to the hemifield of object presentation. Decoding accuracies were found to be higher for location-dependent classification than for location-tolerant classification in *contralateral* LO and FUS at both representational levels ($p<0.001$, Supplementary Table 5). The same was the case in *ipsilateral* LO at both representational levels ($p<0.001$, Supplementary Table 6), and in *ipsilateral* FUS at the level of categories ($p<0.001$), with a trend at the level of exemplars (*n.s.*, Supplementary Table 6). Taken together, in most cases there was more location-dependent than location-tolerant object information in LOC.

Next, we compared decoding accuracy of location-dependent classification dependent on the hemifield of object presentation (ipsi- vs. contralateral). In both LO and FUS decoding accuracy was significantly higher contralateral than ipsilateral at the level of categories ($p<0.01$), but not at the level of exemplars (*n.s.*, Supplementary Table 7). This indicates that our analysis was sensitive enough to detect the contralateral preference in LOC at the level of categories, but not at the level of exemplars.

Finally, we found that LO and FUS contained more information about objects at the category-level than at the exemplar level both ipsi- and contralateral to the hemifield of object presentation ($p<0.001$, Supplementary Table 8).

Generalization across exemplars

If LOC contains category representations, one would expect that these representations should generalize across different exemplars from the same category. To explicitly test this, we trained a classifier to differentiate between two exemplars from two different categories and tested the classifier on two different exemplars from the same two categories (Fig. 4A). We conducted one-sample *t*-tests of the resulting decoding accuracy against chance. We found that LO ($T(12)=7.03$, $p<0.001$) and FUS ($T(12)=8.38$, $p<0.001$) contained exemplar- and location-tolerant category information, whereas EV did not ($T(12)=2.58$, *n.s.*) (Fig. 4B). These findings indicate that activity patterns in LOC at the level of exemplars within a category are general enough to predict the category of other exemplars.

Location classification across objects

Finally, we tested whether spatial patterns of brain activity were predictive of object location independent of the object seen (Fig. 5A). We conducted one-sample *t*-tests of the resulting decoding accuracy against chance. As expected from its retinotopic structure, early visual cortex contained object-tolerant location information ($T(12)=38.09$, $p<0.001$). Importantly, we also found that LO ($T(12)=25.22$, $p<0.001$) and FUS ($T(12)=15.57$, $p<0.001$ contained object-tolerant location information (Fig. 5B).

Discussion

Using high-resolution fMRI and multivariate pattern classification we demonstrated that LOC contained location-tolerant object information both at the level of categories and at the level of exemplars within a category. Moreover, location-tolerant information of objects at the level of exemplars within a category was general enough for categorization of other exemplars. LOC also contained location-dependent object information. Interestingly, there was more location-dependent than location-tolerant object information in LOC. Finally, we found that LOC also contained object-tolerant location information. These findings extend our knowledge of the link between object representation and LOC in several important ways.

LOC contains location-tolerant object information at the levels of exemplars within a category

Most prior fMRI studies investigating whether LOC contains location-tolerant object information used object categories as conditions (Grill-Spector et al., 1998; Hemond et al., 2007; MacEvoy and Epstein, 2007; Sayres and Grill-Spector, 2008; Williams et al., 2008; Carlson et al., 2009). However, category membership is correlated with semantic information, evolutionary significance, familiarity, meaning, type of processing and retinotopic bias. Thus, prior results might not only reflect object shape representations in LOC, but possibly also other attributes associated with category membership. Here we showed that LOC contained location-tolerant information about object identity, i.e. at the level of *exemplars within a category*, reducing an influence of category membership.

However, the reduction in the influence of category membership in our study may be limited by two factors. First, “category,” as we use it here, is an inherently relative and vague concept. This also holds for the sub-ordinate distinction “exemplars within a category.” Thus, neuroimaging studies have investigated object category representations at very different levels, e.g. distinguishing between living and non-living things or animals and tools (Martin et al., 1996; Chao et al., 1999; Panis et al., 2008; Mahon et al., 2009), introducing artificial categories (Op de Beeck et al., 2006; Williams et al., 2007), or most commonly, distinguishing objects at the level of everyday categories (Haxby et al., 2001; Spiridon and Kanwisher, 2002; Cox and Savoy, 2003; O'Toole et al., 2005).

A second limiting factor is that to increase the chance of finding discriminating information at the level of exemplars within a category, we aimed to maximize the differences between exemplars. We deemed this necessary, as prior evidence for object representation in LOC at a level subordinate to the level of category is sparse. A recent study found information barely above chance about different teapots and chairs in LOC (Eger et al., 2008a). Op de Beeck et al. (2010) found evidence for subordinate object distinctions for categories processed in a focal, modular manner, leaving open the question whether the result would transfer to other object categories. Finally, a recent study found no location-tolerant object information in LOC at a level subordinate to category (Kravitz et al., 2010).

The two limiting factors together, i.e. the relativity of the concept "exemplar" combined with strong differences between the stimuli, suggest that each of the exemplars in our study might be a category itself. However, as we used stimuli at a level subordinate to the level usually used in fMRI studies of object recognition, the influence of semantic associations should be smaller than in most previous studies, and comparable to recent studies which studied object representations at a level subordinate to the level of categories (Op de Beeck et al., 2010; Kriegeskorte et al., 2008; Kravitz et al., 2010).

Further, not all stimuli of our data set might be at the same level of abstraction. That is, the distinction between different animals might be at a different level than the distinction between different chairs. To exclude this possibility, we compared classification results at the level of exemplars within category across categories and found no significant difference (Supplementary Fig. 2). Especially we found no advantage by more heterogeneous categories (animals) than for less heterogeneous categories (e.g. planes). Furthermore, this excludes the possibility that our results were only driven by one, particularly heterogeneous category. However, future research that objectively measures the level of abstractness, similarity and semantic association of natural visual objects and their relation to neural representation is necessary (Op de Beeck et al., 2010; Haushofer et al., 2008; Op de Beeck et al., 2008b; Panis et al., 2008).

As to the origin of location-tolerant object information in LOC, two different explanations are possible. First, the presence of location-tolerant object information in LOC can be explained by neurons with large receptive fields (RFs). Electrophysiological studies in monkey have reported varying sizes for RFs in inferior temporal cortex (IT), the monkey homologue to human LOC. Whereas older studies reported very large receptive fields, i.e. 30° and larger (Boussaoud et al., 1991; Desimone et al., 1984; Gross et al., 1969, 1972; Kobatake and Tanaka, 1994; Richmond et al., 1983, Tovee et al., 1994), more recent studies reported that IT also contains cells which have smaller RFs are more sensitive to position (Op de Beeck and Vogels, 2000; DiCarlo and Maunsell, 2003; Li et al., 2009). However, even in most recent studies mean RF sizes were about 5–10°. In our study, the centers of the stimuli were about 8° apart, i.e. many neurons in LOC might have RFs that are sufficiently big to at least partly encompass our stimuli. This explanation suggests that feed-forward processing might be sufficient to allow the read-out of location-tolerant information from population responses in LOC (Hung et al., 2005). Please note, however, that especially for linear classifiers the read-out of location-tolerant information from fMRI activity patterns might depend partly on the degree to which individual voxels are tolerant (Goris and Op de Beeck, 2009).

An alternative explanation for the read-out of location-tolerant object information in LOC might be feedback from up-stream areas. Previous research has indicated that feedback during imagery can activate object-selective regions in a content-specific manner which might be location-tolerant (O'Craven and Kanwisher, 2000; Stokes et al., 2009; Reddy et al., 2010). Moreover, as our task required attention to the stimulus, the location-tolerant object information in LOC might reflect effects of feature-based attention. The effect of feature-based attention has been shown to spread across the whole visual field outside the focus of spatial attention in humans (Saenz et al., 2002; Serences and Boynton, 2007; Peelen et al., 2009) and in monkey (Treue and Trujillo, 1999; Bichot et al., 2005). Such an explanation would suggest that feedback processing is necessary to induce location-tolerant responses in LOC.

The latter explanation might also elucidate the contrast between our finding and a study by (Kravitz et al., 2010), who did not find location-tolerant object information in LOC. Whereas in our study participants carried out a one-back task on the orientation of the presented object, participants in the study of Kravitz et al. (2010) performed a combined color detection task on the object and on fixation. Thus, in our experiment the shape of the object was important and subjects attended to it. Interestingly, previous research has indicated that contrast invariance in LOC depends on attention (Murray and He, 2006), and that tolerance to clutter is enhanced by attention (Reddy and Kanwisher, 2007). Thus, attention might be necessary for location-tolerant responses in LOC to emerge. It remains an intriguing task for further research to investigate the influence of attention on location-tolerance of object information in the brain by parametrically modulating the state of attention.

Several other explanations are possible for the apparent contrast between our study and Kravitz et al. (2010). First, attention has been reported to sharpen the selectivity of responses in LOC (Murray and Wojciulik, 2004). Thus, our task might have induced sharpening of the selectivity of responses in LOC which might have led to better separability of response patterns in the classification analysis. Second, Kravitz et al. (2010) used a larger data set (24 objects) and tested four locations (i.e. 96 conditions) in an event-related design with line drawings of objects as stimuli, whereas we used a smaller data set (12 objects) of 3D-rendered shapes and tested only 2 locations (i.e. 24 conditions) in a mini-block design. Thus, as we used less conditions and perceptually richer stimuli, the fMRI signal acquired for each condition in the study of Kravitz et al. (2010) might be weaker than in our study.

Our finding of location-tolerant object information at the level of exemplars has several interesting implications. First, it suggests that object representations in LOC may underlie human everyday behaviour: it is exemplars that we recognize across the visual field, not the category. Thus, our results suggest a neural basis for behavioural studies which argued for location tolerance of visual object representations (Biederman and Cooper, 1991; Fiser and Biederman, 2001).

Moreover, the presence of location-tolerant object representations at the level of exemplars within a category offers an opportunity to further characterize the coding scheme in LOC (Grill-Spector, 2003; Reddy and Kanwisher, 2006; Op de Beeck et al., 2008a; Hoffman and Logothetis, 2009). We found that location-tolerant object representations in LOC were distributed and overlapping both at the level of categories and at the level of exemplars within a category (Supplementary Analysis 1). This extends the concept of distributed and overlapping representation from the level of object categories to the level of object exemplars within a category (Haxby et al., 2001).

Last, by showing activity patterns in LOC are fine-grained enough to distinguish between visual stimuli at the level of exemplars, we corroborate previous studies in narrowing the gap between stimulus material used in human fMRI and monkey electrophysiology (Op de Beeck et al., 2010; Kriegeskorte et al., 2007, 2008; Eger et al., 2008a). Thus, our results encourage further research comparing object representations in humans and monkeys using the same stimulus sets.

LOC contains more location-dependent than location-tolerant object information within than across locations

We found more location-dependent than location-tolerant object information in LOC (Fig. 3). One potential explanation of this difference is a population of neurons with various RF sizes. During location-dependent read-out neurons with small and large RFs would provide information about the stimulus, whereas during location-tolerant read-out the stimuli only neurons with large RFs would. In effect, the location-dependent read-out benefits from patterns created by neurons with small and large RFs, whereas location-tolerant read-out will only benefit from patterns created by neurons with large RFs.

The interpretation of the drop in object information for location-dependent compared with location-tolerant read-out depends on a priori assumptions about the function of LOC. For one, one may assume that the function of LOC is to signal the presence of objects independent of changes in location. Thus, the plus in location-dependent over location-tolerant object information in LOC might be interpreted as reflecting engagement of LOC by low-level visual features at the retinotopic level irrelevant to LOC's function. In contrast, under the assumption that the function of LOC includes signalling the presence of an object dependent on location, it could be concluded that object representations in LOC are strongly constrained by location (Kravitz et al., 2010). On this view the comparatively low location-tolerant read-out of object information would suggest that this type of information does not play a major role in LOC.

One might distinguish between these interpretations in two ways. First, one could test whether location-dependent, or only location-tolerant object information in LOC is behaviorally relevant. Along these lines Kravitz et al. (2010) suggested that location-dependent object information in LOC is behaviourally relevant, as they found object priming to be abolished when the location of the object was changed. Future studies might further test whether the location-dependent or location-tolerant patterns are read out during object recognition (Williams et al., 2007). Moreover, the two different interpretations make strong and diverging predictions for the effect of one-sided lesions in LOC on behaviour. If only location-tolerant information plays a functional role, object recognition should be impaired equally strongly in both visual hemifields. If however, location-dependent information is also causally efficacious, object recognition should be more impaired in the contralateral than in the ipsilateral hemisphere.

Activity patterns in LOC generalize across different exemplars

The presence of location-tolerant category information in LOC implies that the underlying activity patterns should generalize across different exemplars from the same category. We explicitly tested this and found that activity patterns evoked by object exemplars in LOC generalize sufficiently to allow for categorization of objects independent of exemplar (Spiridon and Kanwisher, 2002; Cox and Savoy, 2003). This finding lends plausibility to the functional role of object identity information in LOC: The brain could easily read out the category of the perceived objects from activity patterns evoked by single object exemplars in LOC. Thus, it suggests that object information in LOC may underlie automatic classification of object exemplars into categories (Rosch et al., 1976; Mervis and Rosch, 1981). Also, it demonstrates that it could underlie the capacity of the visual system to apply what has been learned from limited experience to novel situations (Poggio and Bizzi, 2004). Thus, object information in LOC is both fine-grained enough to allow the differentiation of very similar objects, and general enough to allow humans to act in a changing environment. This result may be explained in different ways. Greater shape differences between objects belonging to different categories may be the underlying reason (Haushofer et al., 2008; Op de Beeck et al., 2008c; Drucker and Aguirre, 2009). Equally possible, LOC might contain category information that is independent of visual appearance (Kriegeskorte et al., 2008).

LOC contains location information independent of object identity

Our results question a common view of the visual system as divided into two pathways: a location-tolerant "what" pathway and an identity-tolerant "where" pathway (Ungerleider and Mishkin, 1982). Recent studies reported information about object identity in the "where" pathway (Sereno and Maunsell, 1998; Konen and Kastner, 2008). Complementary, we found that LOC in the "what pathway" contained location information independent of object identity. Our result concurs with recent studies that found location information in the "what pathway," in particular in LOC (Carlson et al., 2009; Schwarzlose et al., 2008). This is also in line with the observation that LOC represents visual angle in a retinotopic fashion (Brewer et al., 2005; Larsson and Heeger, 2006; Sayres and Grill-Spector, 2008) and exhibits an eccentricity bias (Levy et al., 2001; Malach et al., 2002; Hasson et al., 2002). Location information about locations that span the vertical meridian was to be expected on the basis of the contralateral field bias in LOC both in BOLD activation and in object information levels (Grill-Spector et al., 1998, 1999; Niemeier et al., 2005; Hemond et al., 2007; MacEvoy and Epstein, 2007; Kravitz et al., 2010). However, an additional analysis that controlled for mean activation differences suggests that patterns of activations also contain information about location independent on mean activation differences in LO and FUS (Supplementary Analysis 2). In conjunction, our data cast further doubt on the location tolerance of the "what" pathway. Instead, it favors a view of the visual system which allocates identity and location information to both visual pathways (Milner and Goodale, 2008).

Conclusion

In summary, using high-resolution fMRI in combination with multivariate pattern classification we found a mixture of location-tolerant object information and object-tolerant location information in LOC. Importantly, tolerance may be a more desirable goal for object representation by the visual system than invariance. Invariance would allow either only location or only object information to be encoded. In contrast, tolerance allows the encoding of both types of information. The joint presence of both types of information might help to avoid a binding problem (Riesenhuber and Poggio, 1999; Treisman, 1999), to allow disambiguation between multiple objects (Li et al., 2009), and to allow coding of the relative position of object parts (Missal et al., 1999; Edelman and Intrator, 2000). Thus, our results further elucidate and strengthen the tight link between object recognition and object representations in LOC.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.09.044.

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