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fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex

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The way information about objects is represented in visual cortex remains controversial. It is unclear, for example, whether information is processed in modules, specialized for different categories of objects or whether information is represented in a distributed fashion across a large network of overlapping visual areas. In this study, we used fMR-adaptation to investigate the extent to which 'specialized' regions of visual cortex are involved in representing information about inanimate objects and places. We found adaptation in the object-selective lateral occipital complex (LOC) following repeated presentations of the same inanimate object. However, we also found fMR-adaptation to inanimate objects in fusiform face area (FFA) and the parahippocampal place area (PPA). Furthermore, this adaptation was not affected by changes in the size of the stimulus. In the second part of the experiment, we found adaptation to repeated images of places in the place-selective PPA, which was both size- and viewpoint-invariant. fMR-adaptation to repeated images of places was also observed in the LOC, but not in the FFA. These results suggest that the representation of inanimate objects and places is not restricted to those regions showing maximal responses to these particular categories of objects, but is distributed across human visual cortex and can include 'face-selective' regions such as the FFA.

Keywords: FFA; LOC; PPA; OFA; Temporal lobe; Ventral stream

Introduction

Visual areas involved in object recognition form a ventral processing stream that projects toward the temporal lobe (Ungerleider and Mishkin, 1982; Milner and Goodale, 1995). Lesions to this region of the brain often result in difficulties in recognizing, identifying, and naming different categories of objects (Farah, 1990). The concept that discrete areas of the human temporal lobe are specialized for different categories of objects is supported by a number of physiological studies. For example, a region in the fusiform gyrus has been shown to be more responsive to faces than to other complex objects (Allison et al., 1994; Kanwisher et al., 1997; see however, Gauthier et al., 1999, 2000). Similar category-specific visual responses have been found for inanimate objects (Malach et al., 1995), buildings and scenes (Epstein and Kanwisher, 1998), human body parts (Downing et al., 2001), and letter strings (Allison et al., 1994). These results are consistent with single-neuron recordings in humans that have also revealed category-specific responses for faces, natural scenes, houses, and animals (Fried et al., 1997).

Selectivity of neural response need not, however, imply that the perception of different categories of objects is only coded by a particular neuronal population. This is because the neural response to any category of object is not restricted to the area that responds maximally to that particular category; many brain regions show significant responses to many different categories of objects (Ishai et al., 1999; Andrews and Schluppeck, 2004; Andrews and Ewbank, 2004). Thus, the functional significance of neural responses to 'non-preferred' stimuli is unclear (Cohen and Tong, 2001; Andrews, 2005). An alternative model of object perception proposes that information about different object categories is represented by a widely distributed population response in which both strong and weak responses play a central role in recognition (Haxby et al., 2001). The implication is that specialized regions of visual cortex, such as the fusiform face area (FFA), could also be contributing to the perception of object categories such as inanimate objects and places.

However, it remains unclear whether non-preferred responses play an important role in perception or just reflect a non-specific activation of the visual system that does not lead to recognition (Spiridon and Kanwisher, 2002; Andrews and Schluppeck, 2004). To address this issue, we previously used fMR-adaptation (the reduction in fMRI activity that follows the repeated presentation of identical images; Grill-Spector and Malach, 2001) to ask how different face- and object-selective regions of visual cortex contribute to specific aspects of face perception (Andrews and Ewbank, 2004). We found that activity in the

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FFA was reduced following repeated presentations of the same face. However, despite the fact that object- and place-selective regions of visual cortex responded to photographs of faces, we failed to find adaptation to face images. Although this finding challenges the view that faces are coded by a distributed representation across all regions of the ventral visual pathway, it is not clear whether other categories of objects are represented in a similar way.

Here, we used fMR-adaptation to determine how inanimate objects and places are represented in visual cortex. Imaging studies have revealed a region in the lateral occipital lobe (LOC) that responds more strongly to whole objects than to scrambled images or textured patches (Malach et al., 1995; Grill-Spector and Malach, 2001; Moore and Engel, 2001). Whereas a region in the medial temporal lobe, known as the parahippocampal place area (PPA), has been shown to respond more strongly to scenes depicting places and buildings than to other kinds of visual stimuli (Epstein and Kanwisher, 1998). Previous studies have reported fMR-adaptation to inanimate objects in the LOC (Grill-Spector et al., 1998; Kourtzi and Kanwisher, 2001) and to places in the PPA (Avidan et al., 2002; Epstein et al., 2003). While these results are consistent with a modular view of cortical processing, adaptation to inanimate objects and places has also been reported in brain regions that are not selective for these object categories (Avidan et al., 2002). However, it could be argued that the reduced activity in non-selective regions of visual cortex might not reveal high-level object recognition, but may simply reflect adaptation to low-level features of the stimulus. To address these issues, we have determined whether a reduction in response to repeated presentations of the same image is specific to particular regions of the brain and also whether this adaptation is evident when low-level attributes (such as the size or the viewpoint) of the images are changed.

Methods

Subjects

Thirteen subjects participated in both the object and place adaptation experiments. All observers had normal or corrected to normal visual acuity. Informed consent was obtained from all subjects and the study was approved by COREC 98.161. Stimuli (approximately 9° × 9°) were back-projected (Focus LP1000, Unicol Engineering, Oxford UK) on to a screen placed at a distance of 280 cm from the subject's eyes. Subjects lay supine in the magnet bore and viewed the back-projection screen outside the bore with mirror glasses.

Imaging parameters

All experiments were carried out using the Siemens-Varian 3-T MRI scanner at the FMRIB centre in Oxford. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage, radio-frequency coil tuned to 127.4 MHz. A gradient-echo EPI sequence was used to collect data from 16 contiguous axial slices (TR 2 s, TE 30 ms, FOV 224 × 224 mm, in-plane resolution 3 × 3.5 mm, slice thickness 6 mm). T1-weighted structural images were acquired with a 3D Turbo Flash Sequence at a resolution of 3 mm × 3 mm within slice and 3 mm between slices. The statistical maps were registered onto a standard image in Talairach space using FLIRT (http://www.fmrib.ox.ac.uk/fsl).

Localizer scan

To discriminate regions of visual cortex that are selectively activated by faces, inanimate objects, and places, a localizer scan was carried out for each subject. Each scan contained 16 stimulus blocks. The stimuli in each block were either gray-scale photographs of (i) inanimate objects, (ii) places (buildings, indoor scenes, and natural landscapes), (iii) faces, (iv) or textures. Photographs of inanimate objects, places, and textures were obtained from various sources including commercial clip-art collections (CorelDraw, Microsoft). Images of faces were taken from the PICS database (http://www.pics.psych.stir.ac.uk/) and were not familiar to any of the subjects. Each stimulus block contained 10 images with each image being presented for 800 ms followed by a 200-ms blank screen. Subjects were instructed to perform a contrast decrement detection task using a response box. One image in each block was presented at a reduced contrast (25%), and subjects were required to respond, via a button press, when they saw this image. Each stimulus condition was repeated four times in a counterbalanced block design. Blocks were separated by periods of fixation when a gray screen, of the same average luminance, was viewed for 10 s.

Statistical analysis of the localizer scans was carried out using FEAT (http://www.fmrib.ox.ac.uk/fsl). The initial 8 s of data from each scan were discarded to minimize the effects of magnetic saturation. Motion correction was carried out using MCFLIRT (http://www.fmrib.ox.ac.uk/fsl), followed by spatial smoothing (Gaussian, FWHM 5.0 mm) and temporal high-pass filtering (cutoff, 0.01 Hz). Z-statistic images based on the contrast between different events were generated using resel (corrected Bonferroni) thresholding ($P < 0.05$). To determine the temporal characteristics of the response, the time series of the resulting filtered MR data at each voxel was converted from units of image intensity to fractional signal change (% change in MR signal) by subtracting and then normalizing by the mean response of each scan ($[x - \text{mean}] / \text{mean}$). All voxels in a given ROI were then averaged to result in one time series for each ROI in each subject. Individual trial blocks were normalized by subtracting every time point by the zero point for that trial block. The normalized data were then averaged to obtain the mean time course for each stimulus condition. Repeated-measures ANOVA was used to determine the significance of the response to each stimulus condition.

Object and place adaptation

Gray-scale images of objects and places were obtained from 3D models composed using Strata 3D Plus design software. We determined which regions of visual cortex showed fMR-adaptation to images of inanimate objects and places in separate scans. The MR response when subjects viewed the same image from a particular category (same) was compared with the response to different exemplars of that category (different). To determine whether the response to objects and places was size-invariant, we varied image size in some stimulus blocks (3 × 3°, 6 × 6° and 9 × 9°). We also determined whether the response to objects and places was view-invariant by varying the direction of viewpoint in the object and place images. Changes in viewpoint were presented in a naturalistic manner (approximately 15°), analogous to the sequence that would typically occur when an observer moves around a scene. However, it is important to note that these changes did not lead to the perception of object motion or self-induced movement.

In total, we monitored MR activity for the following six stimulus conditions for each category (inanimate objects and places): (1) same-image, (2) different-image, (3) vary-size same-image, (4) vary-size different-image, (5) vary-viewpoint same-image, (6) vary-viewpoint different-image. Each stimulus condition lasted for 12 s and contained 12 images. Each image was presented for 800 ms followed by a 200-ms blank screen. Subjects were instructed to perform a contrast detection task using a response box, with one image in each block being presented at a reduced contrast. Each stimulus condition was repeated four times in a counterbalanced block design giving a total of 24 stimulus blocks in each scan. Blocks of images were separated by periods of fixation when an equiluminant gray screen was viewed for 10 s. The exemplars of inanimate objects and places were balanced across all same and different conditions. In this way, we were able to control for any change in neural response that may be due to differences in object features or semantic attributes. For each region of interest, we

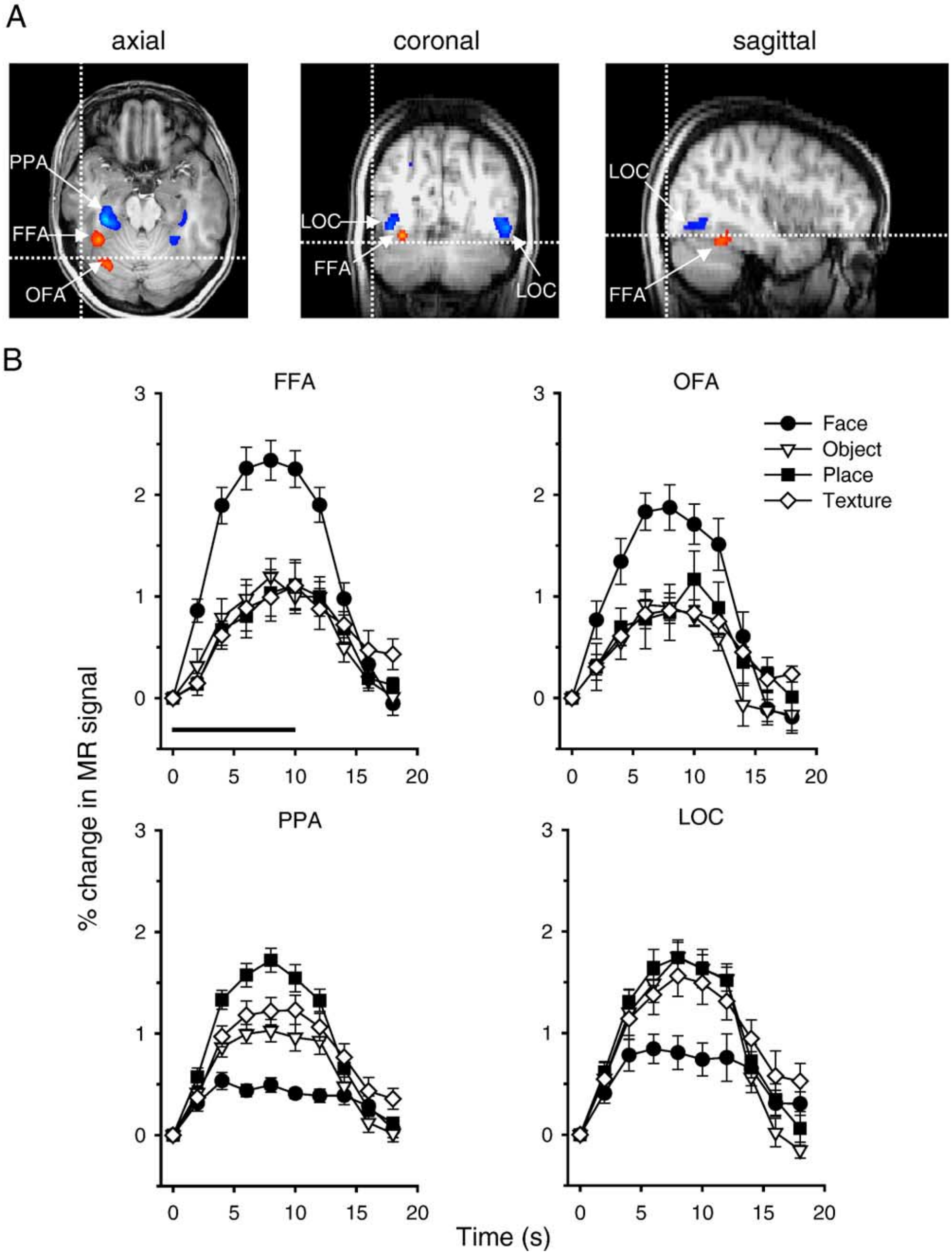

Fig. 1. Localizer scan. Regions of interest were defined by their anatomical location and their functional responses to different object categories. (A) Location of areas in visual cortex that showed selective responses to faces (red), objects (blue) in one subject (FFA = fusiform face area, OFA = occipital face area, LOC = lateral occipital complex, PPA = parahippocampal place area). These scan images follow radiological convention, with the left hemisphere shown on the right. The dashed line in each image shows the spatial relation of the three slices. (B) MR time course showing activity averaged across subjects in object-, place-, and face-selective regions, to faces, objects, places, and textures. The horizontal bar represents the duration of each block. Error bars represent ±1 standard error.

calculated the mean time course across all repeats of all stimulus conditions in all subjects. This average response profile was used as a model to extract response amplitudes in the different stimulus conditions: we projected the response time courses of individual blocks onto this model. (This corresponds to a least-squares fit of the model response to the data.) The model response scaled by the mean projected amplitude is shown (line) superimposed on the average data for the two different conditions (symbols, Figs. 2–7). A multi-factorial ANOVA was used to determine the main effects of Category (inanimate object, place) Identity (same, different), Appearance (no change, vary size, vary viewpoint), and Region (FFA, OFA, PPA, LOC). To assess whether the reduction in amplitude was statistically significant for particular regions, we performed a two-sample t test on the amplitude estimates across subjects. Finally, we calculated an adaptation index (AI) to quantify the reduction in response amplitudes during same image blocks compared to different image blocks: AI = Response[same] / Response[different]. This measure was used to give an indication of the effect of adaptation, but this ratio was not used in the analysis.

Results

Localizer scan

We characterized four different regions in the occipital and temporal cortex (Fig. 1; Table 1): (1) a region on the lateral aspect of the occipital lobe (LOC) responded more to images of inanimate objects than to faces or textures (Malach et al., 1995); (2) a region in the medial temporal lobe (PPA) was more active when subjects viewed images of places compared to faces and textures (Epstein and Kanwisher, 1998); (3) a region of the fusiform gyrus (FFA) showed significant activation for images of faces versus non-face objects (Kanwisher et al., 1997); (4) a more posterior region on the lateral surface of the occipital lobe was also found to be more active for faces compared to objects and is likely to correspond to the occipital face area (OFA) (Gauthier et al., 2000). These regions were defined for each individual. All further analyses were performed on the mean time courses of voxels in these regions of interest.

The average time courses of activation in the different regions of interest are shown in Fig. 1B. Consistent with the FEAT analysis, an ANOVA revealed that the LOC was significantly activated by images of objects ($F = 31.2$, $P < 10e{-}6$) and the PPA was significantly activated by images of places ($F = 75.2$, $P < 10e{-}6$). However, significant activations following images of inanimate objects and places were not restricted to these regions. The PPA ($F = 36.1$, $P < 10e{-}6$), FFA ($F = 20.2$, $P < 10e{-}6$), and OFA ($F = 14.3$, $P < 10e{-}5$) all responded significantly to images of inanimate objects. In addition, the LOC ($F = 38.2$, $P < 10e{-}6$), FFA ($F = 15.6$, $P < 10e{-}6$), and OFA ($F = 12.4$, $P < 10e{-}6$) all showed a significant response to images of places.

Table 1
Mean Talairach coordinates of object-, place-, and face-selective regions of interest

Region	Hemisphere	n	x	y	z
LOC	Right	8	33	−66	5
	Left	8	−41	−70	−1
PPA	Right	13	25	−42	−19
	Left	13	−26	−44	−18
FFA	Right	12	36	−47	−20
	Left	11	−33	−57	−19
OFA	Right	7	25	−66	−10
	Left	3	−18	−64	−6

Object and place adaptation

A 4-factor ANOVA 2 × 2 × 3 × 4 (Category, Identity, Appearance, Region) revealed a significant main effect for Identity (i.e., adaptation) ($F = 10.1$, $P < 0.05$) and Region ($F = 11.3$, $P < 0.001$), but no effect for Appearance (size, viewpoint) ($F = 0.13$, $P = 0.74$) or Category ($F = 0.05$, $P = 0.82$). There was a significant interaction between Identity × Region ($F = 4.2$, $P < 0.03$) that implies adaptation to objects and places was specific to particular regions. Furthermore, a significant interaction between Identity × Region × Category ($F = 5.9$, $P < 0.01$) suggests that this region-specific adaptation differs for objects and places.

Object adaptation

A 3-factor ANOVA 2 × 3 × 4 (Identity, Appearance, Region) showed a significant main effect for Identity ($F = 12.46$, $P < 0.05$) and Region ($F = 6.85$, $P < 0.001$), but not for Appearance ($F = 0.07$, $P = 0.93$) of objects. The interaction between Identity × Region failed to reach significance ($F = 2.85$, $P = 0.08$), but suggests some region-specific adaptation. To determine whether adaptation to images of objects occurred in the different regions of interest, we compared the responses to repeated presentations of the same object (same-object) with the responses to images of different objects (different-object) (Fig. 2). Our prediction was that areas involved in object recognition would be less active during the same-object condition compared to the different-object condition. We found a reduction in the response amplitude to the same object compared to different objects in the object-selective LOC [AI = 0.68 ± 0.07; $t(8) = 3.5$, $P < 0.01$]. However, we also found a significantly reduced response in both the PPA [AI = 0.57 ± 0.07; $t(12) = 5.2$, $P < 0.001$] and FFA [AI = 0.64 ± 0.20; $t(12) = 2.7$, $P < 0.05$]. The OFA failed to show adaptation to images of objects ($P = 0.54$). Behavioral data indicated that subjects were performing the contrast detection task successfully during the object-adaptation scan (94.2 ± 3.8% correct).

To determine whether adaptation to inanimate objects in the LOC, PPA, and FFA was sensitive to changes in image size, we compared the response to repeated presentations of images of the same object that varied in size (vary-size same-object) with the response to images of different objects that also varied in size (vary-size different-object) (Fig. 3). A significantly lower response to images of the same object was apparent in LOC [AI = 0.77 ± 0.10; $t(8) = 2.6$, $P < 0.05$], PPA [AI = 0.62 ± 0.10; $t(12) = 3.1$, $P < 0.01$], and FFA [AI = 0.64 ± 0.13; $t(12) = 2.9$, $P < 0.05$].

Finally, we asked whether adaptation to inanimate objects would occur if we changed the viewpoint of the object. We compared the peak MR response to repeated presentations of the same object that varied in viewpoint (vary-viewpoint same-object) to images of different objects that also varied in viewpoint (vary-viewpoint different-object) (Fig. 4). The results show that there were no differences between the vary-viewpoint same-object and vary-viewpoint different-object conditions in either the LOC [$t(8) = 0.9$, $P = 0.39$], PPA [$t(12) = 1.4$, $P = 0.17$], or FFA [$t(12) = 0.3$, $P = 0.77$]. A previous study (Vuilleumier et al., 2002) reported

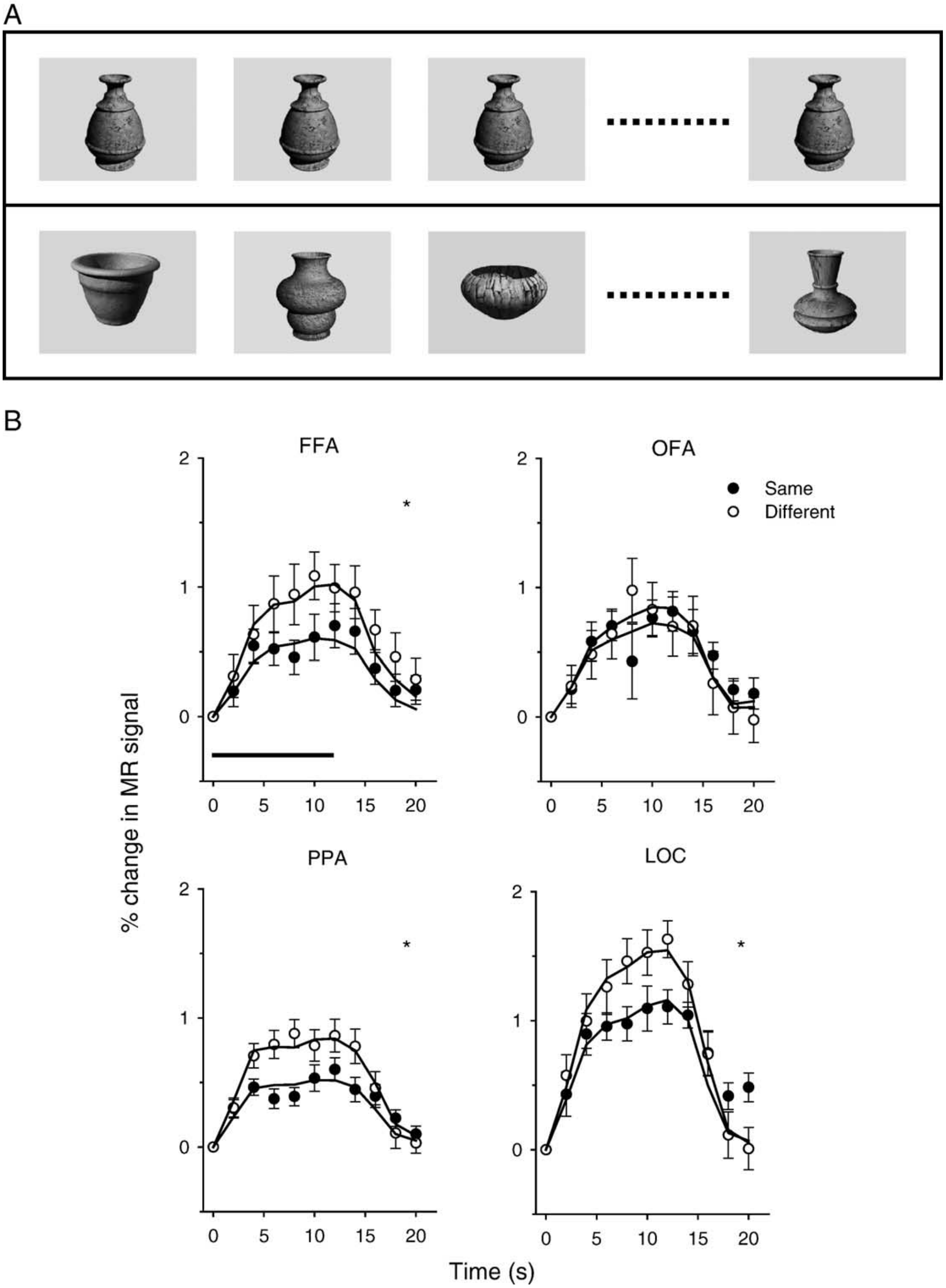

Fig. 2. Object adaptation experiment. (A) Examples of images from the same-object (top) and different-object (bottom) conditions. (B) Average time course in different regions across subjects. Symbols, mean ± standard error across subjects. Line, model fit (mean across subjects, see Methods). *Reduction in response amplitude was statistically significant (*t* test, $P < 0.05$).

viewpoint-invariant adaptation to objects in the fusiform region of the left, but not the right hemisphere. We reanalyzed our data for hemispheric effects, but found no significant difference between the vary-viewpoint same-object and vary-viewpoint different-object conditions in either hemisphere: LOC (RH: $t = 1.7$, $P = 0.14$; LH: $t = 0.89$, $P = 0.40$); PPA (RH: $t = 1.1$, $P = 0.29$; LH: $t = 1.2$, $P = 0.24$); FFA (RH: $t = 1.8$, $P = 0.10$; LH: $t = 0.01$, $P = 0.99$).

Place adaptation

A 3-factor ANOVA 2 × 3 × 4 (Identity, Appearance, Region) failed to show a main effect for Identity ($F = 4.68$, $P = 0.09$). However, we found a significant interaction between Identity × Region ($F = 7.98$, $P < 0.05$), suggesting that adaptation to places was apparent in some, but not all regions of

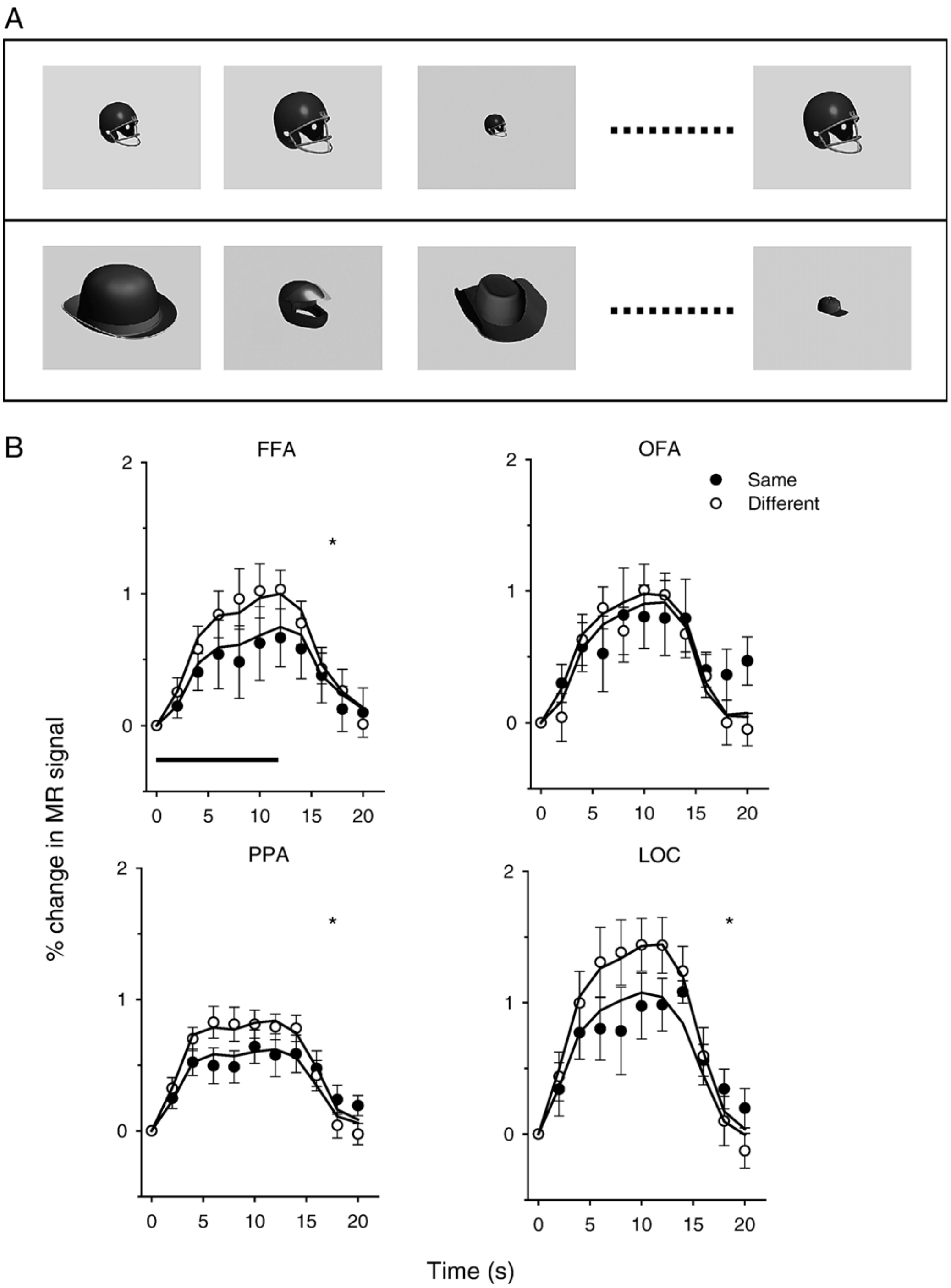

Fig. 3. Object adaptation (vary size) experiment. (A) Examples of images from the vary-size same-object (top) and vary-size different-object (bottom) conditions. (B) Average time course in different regions across subjects. Symbols, mean ± standard error across subjects. Line, model fit. *Reduction in response amplitude was statistically significant (t test, $P < 0.05$).

interest. There was no main effect for Appearance ($F = 0.25$, $P = 0.79$), but there was a main effect for Region ($F = 14.2$, $P < 0.001$). Next, we examined the response to images of places within the previously defined regions. We compared the peak response to repeated presentations of the same place (same-place) with images of different places (different-place) in the different regions of interest (Fig. 5). The results show a significant reduction in response to the same place compared to different places in the place-selective PPA [AI = 0.61 ± 0.07; $t(12) = 4.5$, $P < 0.001$]. Adaptation to images of places was also apparent in the object-selective LOC [AI = 0.66 ± 0.14; $t(8) = 2.3$, $P < 0.05$]. However, no reduction in activity to repeated presentations of the same place image was evident in the FFA [$t(12) = 0.08$, $P = 0.93$] or in the OFA [$t(7) = -0.23$, $P = 0.81$]. As in the other stimulus conditions, subjects were performing the contrast detection task (98.3 ± 1% correct).

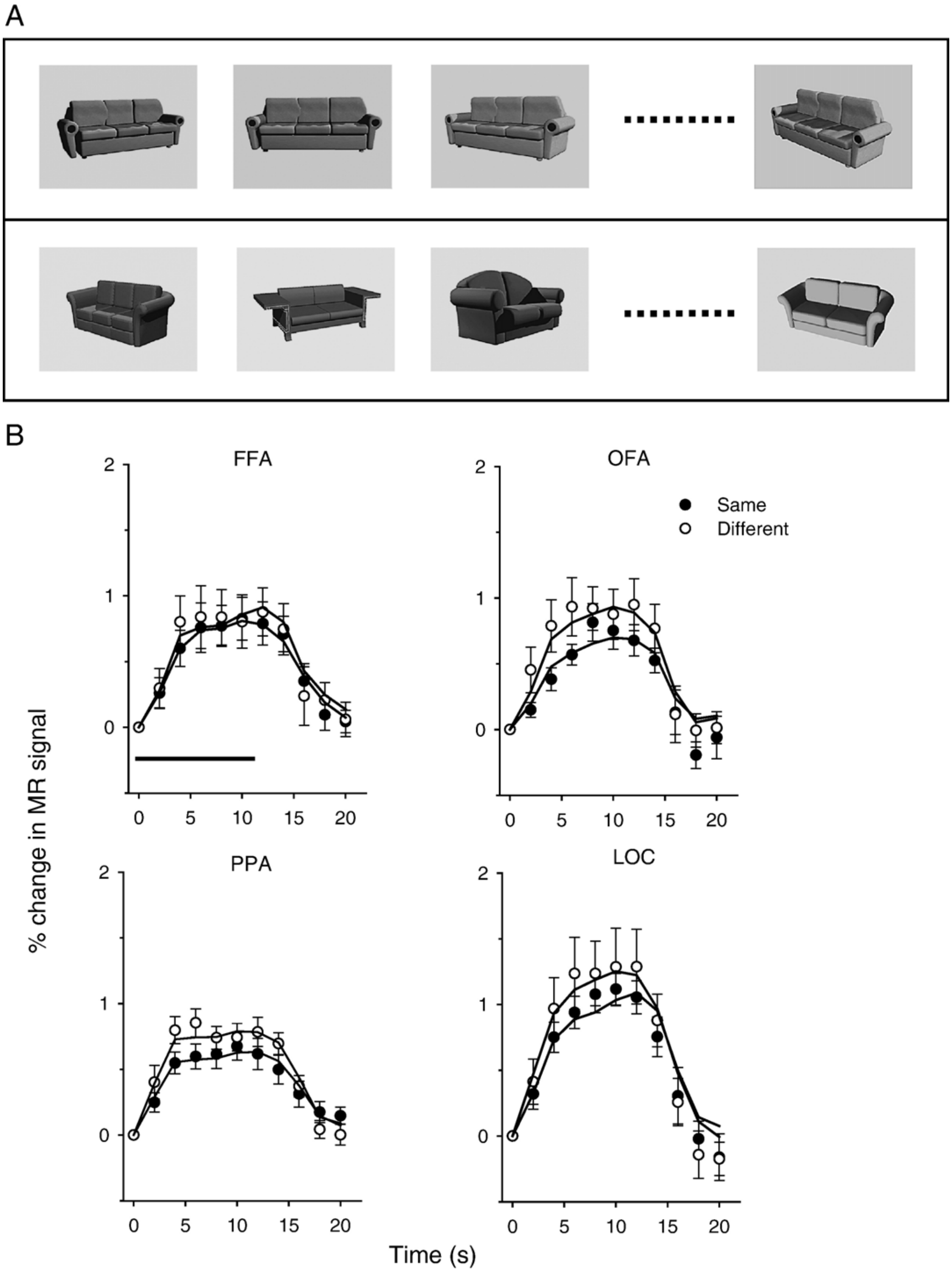

Fig. 4. Object adaptation (vary viewpoint) experiment. (A) Examples of images from the vary-viewpoint same-object (top) and vary-viewpoint different-object (bottom) conditions. (B) Average time course in different regions across subjects. Symbols, mean ± standard error across subjects. Line, model fit.

To determine whether adaptation to images of places in the PPA and LOC was invariant to changes in image size (Fig. 6), we compared peak MR activity for repeated presentations of images of the same place that varied in size (vary-size same-place) with images of different places that also varied in size (vary-size different-place). We found a significantly reduced response to images of the same place compared to different places in the PPA [AI = 0.61 ± 0.08; $t(12) = 4.3$, $P < 0.001$], but not in the LOC [$t(8) = 1.7$, $P = 0.12$]. Finally, we asked whether adaptation to places was sensitive to changes in the viewpoint of the image (Fig. 7). We compared peak MR activity to repeated presentations of images of the same place that varied in viewpoint (vary-viewpoint same-place) to images of different places that also varied in viewpoint (vary-viewpoint different-place). Despite these changes in viewpoint, we found significant adaptation effects in both the PPA [AI = 0.76 ± 0.05; $t(12) = 2.6$, $P < 0.05$] and the LOC [AI = 0.74 ± 0.05; $t(8) = 2.7$, $P < 0.05$].

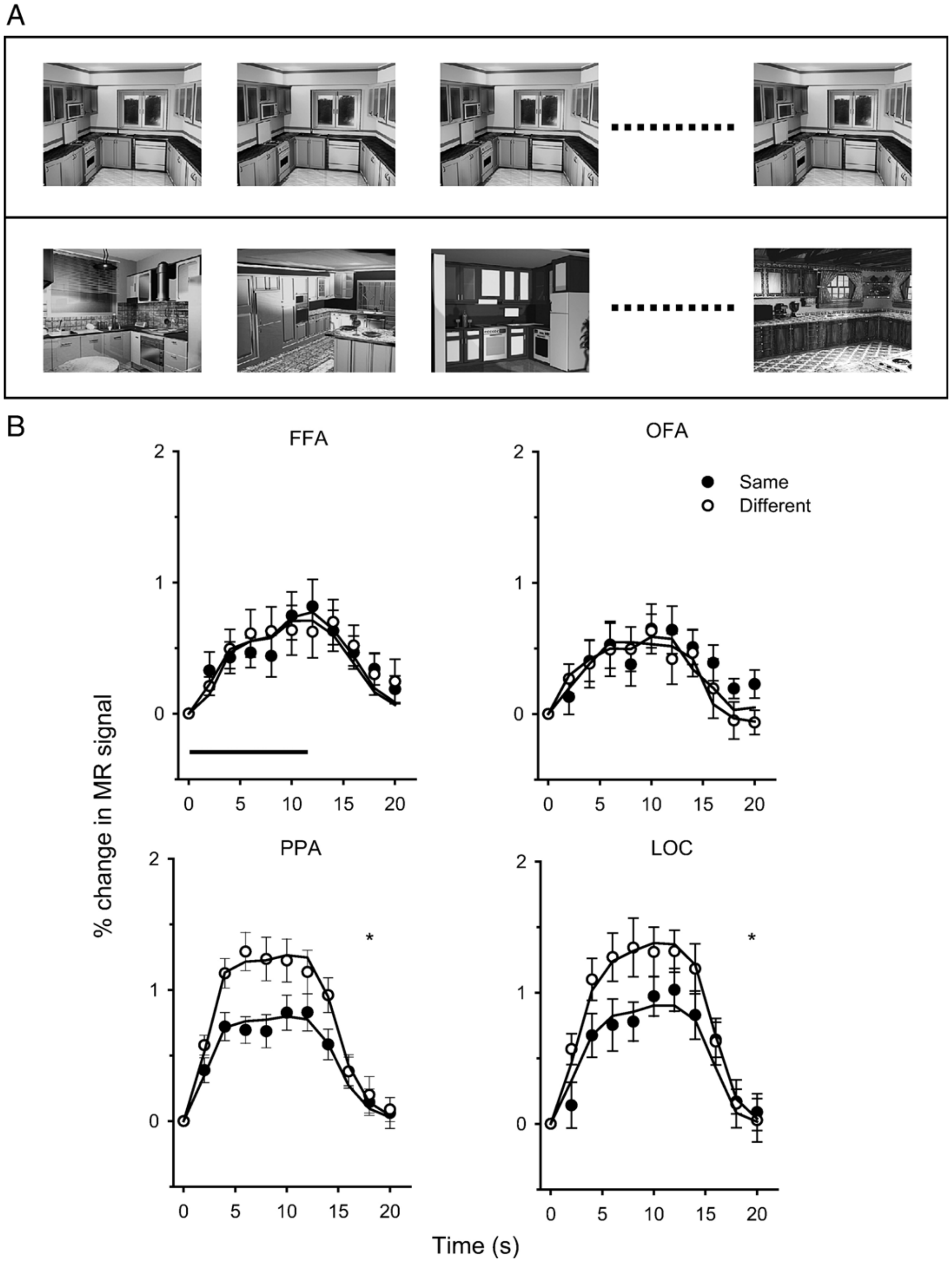

Fig. 5. Place adaptation experiment. (A) Examples of images from the same-place (top) and different-place (bottom) conditions. (B) Average time course in different regions across subjects. Symbols, mean ± standard error across subjects. Line, model fit. *Reduction in response amplitude was statistically significant (t test, $P < 0.05$).

Adaptation in early visual areas

To determine whether responses in early visual areas could explain the data, we measured the responses of a region in the medial occipital lobe that responded more to textures than to faces (Fig. 8). This region overlapped with the calcarine sulcus and is, therefore, likely to contain visual areas V1 and V2 (Andrews et al., 1997). We found no significant adaptation for objects or places in this region of visual cortex [objects: $t(11) = 0.56$, $P = 0.59$; places: $t(11) = 1.11$, $P = 0.29$].

Discussion

The aim of this study was to determine how information about inanimate objects and places is represented in visual

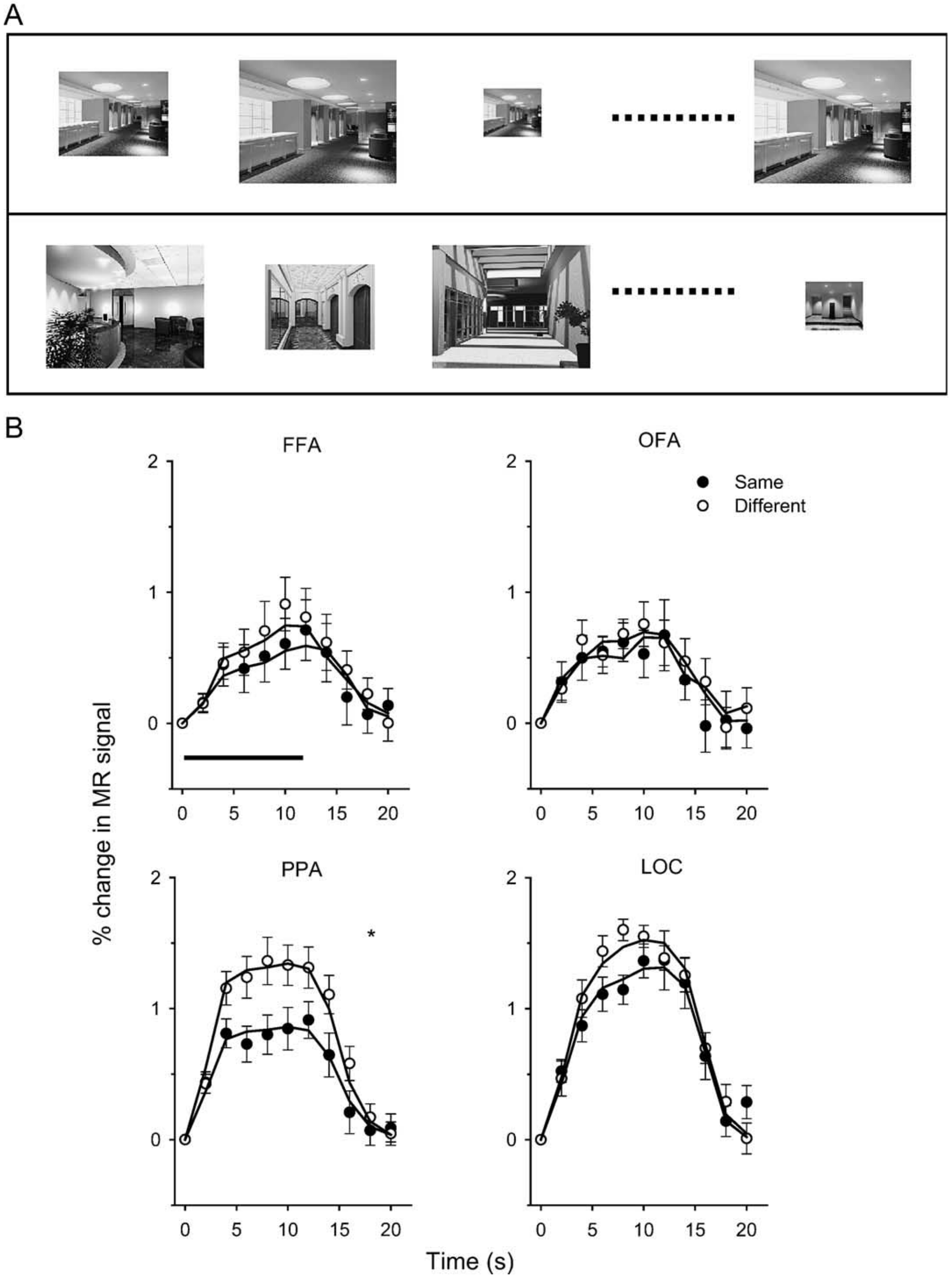

Fig. 6. Place adaptation (vary size) experiment. (A) Examples of images from the vary-size same-place (top) and vary-size different-place (bottom) conditions. (B) Average time course in different regions across subjects. Symbols, mean ± standard error across subjects. Line, model fit. *Reduction in response amplitude was statistically significant (*t* test, $P < 0.05$).

cortex. We specifically asked whether the neural representation of inanimate objects and places is restricted to those regions showing maximal response to those particular object categories or whether the representation is distributed throughout visual cortex. Using fMR-adaptation, we report a distributed representation of inanimate objects and places that is not restricted to areas showing maximal responses to these object categories.

The principle of fMR-adaptation is that neuronal populations that represent particular categories of visual information will show a decrease in response for presentations of the same object compared to when different exemplars of that object category are viewed (Grill-Spector and Malach, 2001). However, it is also possible that a reduced response to repeated presentations of the same image could just reflect a reduced attentional load. We argue that this is unlikely in this study for the following reasons: First,

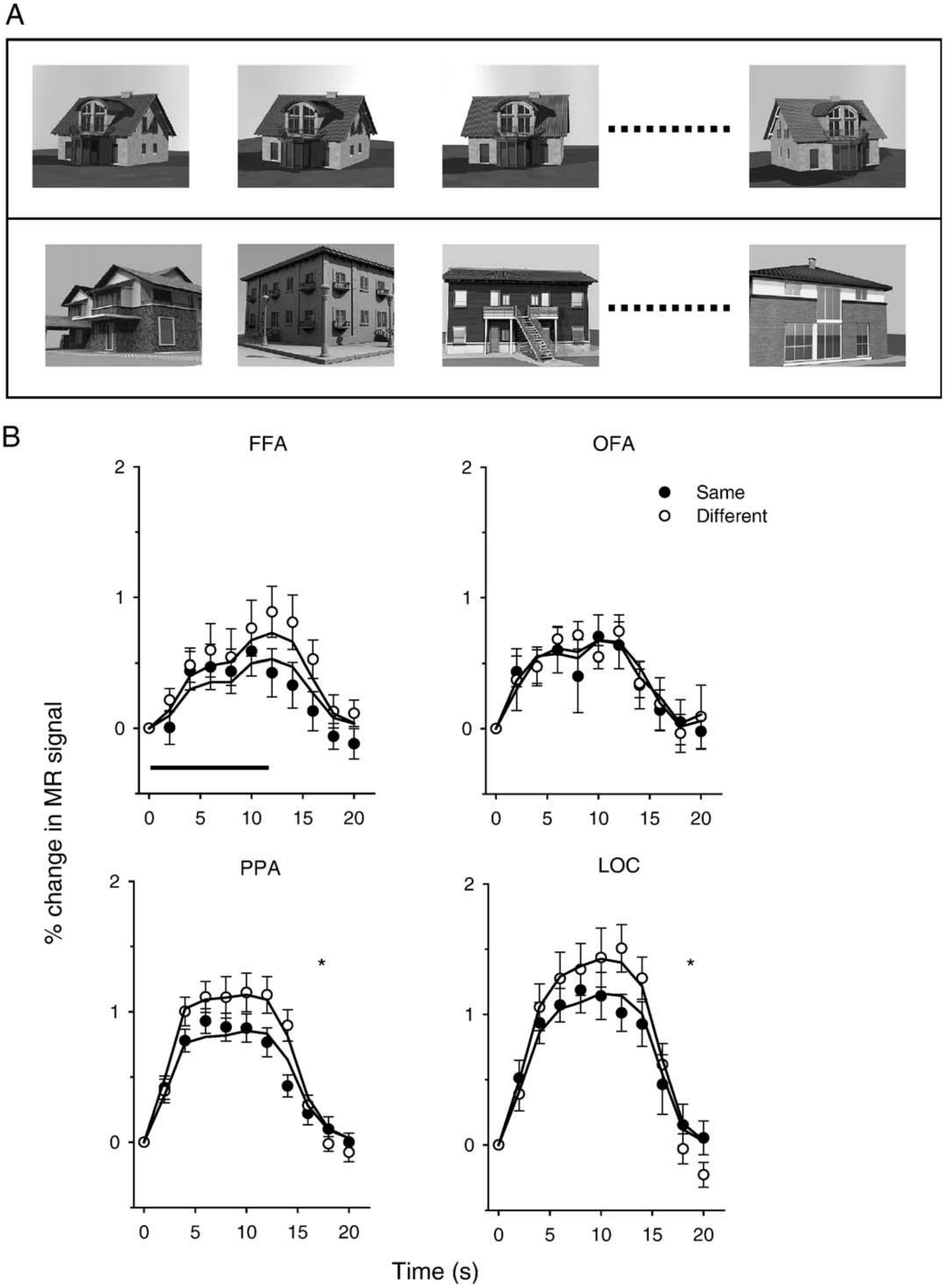

Fig. 7. Place adaptation (vary viewpoint) experiment. (A) Examples of images from the vary-viewpoint same-place (top) and vary-viewpoint different-place (bottom) conditions. (B) Average time course in different regions across subjects. Symbols, mean ± standard error across subjects. Line, model fit. *Reduction in response amplitude was statistically significant (*t* test, $P < 0.05$).

the task (to detect a low contrast image) was unrelated to whether the images were the same or different. Second, a non-selective effect of attention should have produced a general lowering in response throughout visual cortex; the adaptation we observed was restricted to only a few regions of interest and was not evident in primary visual areas. Finally, different patterns of adaptation were observed during the object and place scans, suggesting that the reduction in neural response was specifically related to object category and not to differing attentional demands.

We found adaptation to repeated presentations of inanimate objects in the lateral occipital complex (LOC). Consistent with previous studies (Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2001), we found that adaptation in this region was not affected by low-level changes in the stimulus (such as image size). The implication of these studies is that the LOC represents higher-

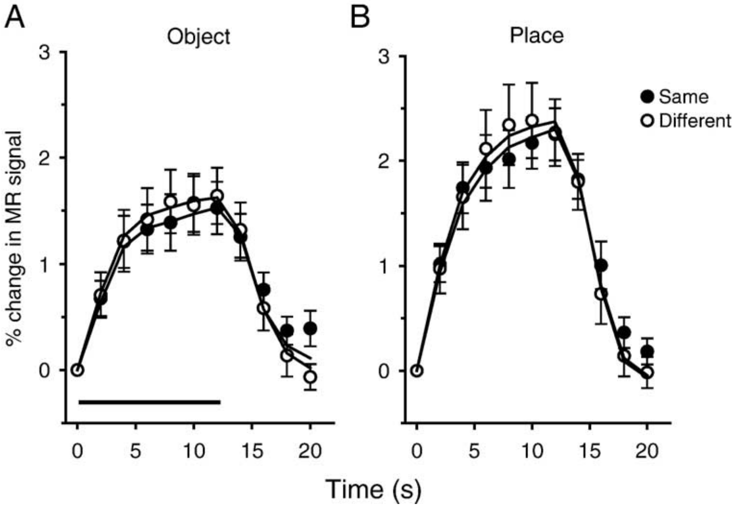

Fig. 8. Average time course across subjects in V1/V2 to presentations of (A) the same and different object images or (B) the same or different place images. Symbols, mean ± standard error across subjects. Line, model fit.

level shape information, that leads to object recognition, rather than simple image features. However, we also report that the LOC failed to adapt when the same object was shown from different viewpoints (see also Grill-Spector et al., 1999; although see Vuilleumier et al., 2002). Together, these data support a viewer-centered (Bulthoff and Edelman, 1992), rather than an object-centered (Marr, 1982; Biederman, 1987), representation for inanimate objects in the LOC. Behavioral support for this position comes from a report in which recognition of objects falls off with increasing angle of rotation from a familiar view (Palmer et al., 1981).

Adaptation to inanimate objects was not specific to the LOC but was also apparent in other areas. For example, we found adaptation to inanimate objects in the FFA, but not in other face-selective regions such as the OFA. Like the LOC, the adaptation in the FFA was invariant to low-level stimulus features such as changes in the size of the image. These findings are relevant to the debate about whether processing in the FFA is specific to faces (Spiridon and Kanwisher, 2002; Andrews and Schluppeck, 2004; Andrews and Ewbank, 2004; Grill-Spector et al., 2004; Yovel and Kanwisher, 2004), or whether it is selective for a broader range of objects that are recognized at the subordinate level (Tarr and Gauthier, 2000). For example, Gauthier et al. (1999) showed that the FFA responses to images of unfamiliar objects were increased when subjects learnt to recognize these objects. Similarly, the FFA responses to images of birds and cars in (bird and car) experts were greater than that of non-experts (Gauthier et al., 2000). This result concurs with a recent study that showed that the recognition of images of birds and cars in non-experts correlated with activity in the FFA, albeit to a lesser extent than the recognition of faces (Grill-Spector et al., 2004). In this study, we compared different exemplars from the same category (i.e., cars, tools) with one repeated exemplar of that category. It is conceivable therefore that the difference in response within the FFA to the same-object versus different-object condition may not reflect a reduction in response to the same-object condition, but rather an increased response in the different-object condition due to subordinate level processing. Further experiments will be necessary to determine whether the MR response to repeated presentations of the same inanimate object is less than to exemplars of different categories of inanimate objects.

Adaptation to inanimate objects was also evident in the place-selective PPA (see also Avidan et al., 2002) and was not affected by changes in the size of the images. Why does the place-selective PPA contain a representation for inanimate objects? A possible explanation could be that objects rarely occur in isolation, but are usually embedded within visual scenes (Palmer, 1975). Indeed, objects that play an important role in navigation or have strong associations to particular spatial contexts have been shown to selectively activate the PPA (Janzen and Van Turennout, 2004; Bar and Aminoff, 2003). Together, these results suggest that the information represented in PPA may not be restricted to the configural properties of scenes and buildings, but also includes other object categories that contain information about the spatial layout of the visual environment.

Next, we used fMR-adaptation to determine how information about places is represented in visual cortex. We found that repeated presentations of the same scene led to a reduced response in the PPA. Furthermore, this adaptation was not sensitive to changes in the size or viewpoint of the images. Previous studies have revealed fMR-adaptation to scenes within PPA (Avidan et al., 2002; Epstein et al., 2003). However, our findings differ from those of Epstein et al. (2003) who reported that adaptation in the PPA does not occur when the same scene is observed from different viewpoints. One explanation for this discrepancy could be that the changes in viewpoint used in Epstein et al. (2003) may have been greater than in our paradigm, where the viewpoint was changed gradually to generate a sequence of images that one would typically experience when navigating a scene (see Fig. 7). Our results are, however, consistent with Epstein et al. (1999) who reported that activation in the PPA was significantly lower when subjects were shown an ordered sequence of images taken from a camera moving though an unchanging environment compared to a sequence of unrelated scenes. We take these findings as evidence for a viewpoint-invariant representation of places in the PPA. Adaptation to places was also evident in the object-selective LOC. This may reflect the fact that scenes are composed of objects. In contrast, we found no adaptation to images of places in the FFA. This finding concurs with other studies (Spiridon and Kanwisher, 2002; Grill-Spector et al., 2004; Yovel and Kanwisher, 2004) that have reported activity in this region does not discriminate between images of places.

In conclusion, these findings show that the way in which information is represented in ventral stream visual areas varies for different categories of objects. Previously, we reported that adaptation to faces was restricted to face-selective regions of visual cortex (Andrews and Ewbank, 2004). These findings suggest that inanimate objects and places are represented in a more distributed fashion, encompassing not only object-selective and place-selective regions, but also 'face-selective' regions such as the FFA.

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