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Sayres, Rory and Kalanit Grill-Spector. Object-selective cortex exhibits performance-independent repetition suppression. *J Neurophysiol* 95: 995–1007, 2006. First published October 19, 2005; doi:10.1152/jn.00500.2005. Object-selective cortical regions exhibit a decreased response when an object stimulus is repeated [repetition suppression (RS)]. RS is often associated with priming: reduced response times and increased accuracy for repeated stimuli. It is unknown whether RS reflects stimulus-specific repetition, the associated changes in response time, or the combination of the two. To address this question, we performed a rapid event-related functional MRI (fMRI) study in which we measured BOLD signal in object-selective cortex, as well as object recognition performance, while we manipulated stimulus repetition. Our design allowed us to examine separately the roles of response time and repetition in explaining RS. We found that repetition played a robust role in explaining RS: repeated trials produced weaker BOLD responses than nonrepeated trials, even when comparing trials with matched response times. In contrast, response time played a weak role in explaining RS when repetition was controlled for: it explained BOLD responses only for one region of interest (ROI) and one experimental condition. Thus repetition suppression seems to be mostly driven by repetition rather than performance changes. We further examined whether RS reflects processes occurring at the same time as recognition or after recognition by manipulating stimulus presentation duration. In one experiment, durations were longer than required for recognition (2 s), whereas in a second experiment, durations were close to the minimum time required for recognition (85–101 ms). We found significant RS for brief presentations (albeit with a reduced magnitude), which again persisted when controlling for performance. This suggests a substantial amount of RS occurs during recognition.

INTRODUCTION

A large extent of human occipital and temporal cortex responds more strongly to intact object images over other visual stimulation (Grill-Spector 2003; Malach et al. 1995). This object-selective cortex contains a number of functionally defined regions of interest (ROIs), including the lateral occipital complex (Grill-Spector 2003; Kourtzi and Kanwisher 2001) and fusiform regions (Grill-Spector et al. 2000). These ROIs are implicated in object recognition (Grill-Spector et al. 2000) and have been shown to correlate with the perception of different classes of objects (Grill-Spector et al. 2004; Tong et al. 1998).

The functional MRI (fMRI) BOLD response in object-selective cortex is consistently lower for repeated versus novel images (Epstein et al. 2003; Grill-Spector et al. 1999; Henson 2003; Koutstaal et al. 2001; Winston et al. 2004). This phenomenon has been referred to as repetition suppression (Henson 2003), functional magnetic resonance adaptation (Grill-Spector and Malach 2001; Grill-Spector et al. 1999), and repetition-priming (Schacter and Buckner 1998). Here, we will use the term repetition suppression (RS) to refer to reduced activation in object-selective cortex with repeated object presentation.

Interest in RS has been motivated by several (possibly overlapping) interpretations of this phenomenon. It is thought to reflect priming, performance improvement (faster response times and greater accuracy) that is often observed in conjunction with stimulus repetition (Dobbins et al. 2004; Lustig and Buckner 2004; Schacter and Buckner 1998; Wiggs and Martin 1998). Conversely, it may relate to classical adaptation effects found in earlier visual areas (Boynton and Finney 2003; Bradley et al. 1988; Tolias et al. 2001), which tend to correlate with impaired task performance (Boynton and Finney 2003; Bradley et al. 1988), although they sometimes facilitate certain fine discriminations (Clifford and Wenderoth 1999). RS may also reflect memory processes, which may be independent from performance changes (Jiang et al. 2000; Ranganath and Rainer 2003) and may relate to similar effects found using electrophysiology in macaque inferotemporal cortex (Miller and Desimone 1994). Furthermore, RS is used as an experimental tool to characterize the selectivity of neuronal populations (Avidan et al. 2002; Grill-Spector and Malach 2001; Kourtzi and Kanwisher 2001; Vuilleumier et al. 2002; Winston et al. 2004). Finally, it may reflect changes in the nature of object representations as a consequence of repetition (Wiggs and Martin 1998). These studies indicate that RS is a useful measure and may provide information on many aspects of object representation and behavior.

Different interpretations of RS focus on distinct factors that may contribute to this phenomenon. For instance, the use of RS to study priming associates RS with performance changes, whereas the examination of mnemonic processes relates RS to repetition independently of performance changes. Although repetition and performance changes are known to be correlated, they may not coincide under all conditions. Furthermore, RS may reflect only one of these factors but not the other. For instance, RS may be driven by changes in response time (e.g., shorter response times may produce lower BOLD), but not repetition. Variations in response time to different nonrepeated stimuli might produce the same sort of changes in the BOLD signal as variations caused by repetition. If this is the case,

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interpretations relying on the relationship between RS and repetition would be difficult to justify.

To examine whether stimulus-specific repetition, performance, or both contribute to RS, we conducted a set of rapid event-related fMRI experiments. We imaged object-selective cortex in an MRI scanner while subjects classified these images as feline (house cats, lions, and tigers) or not feline (horses, donkeys, and dogs) and compared neuroimaging and behavioral data (Fig. 1). One-half of the repeated objects were felines, and one-half were other four-legged animals. The presentation of repeated images included parametric variations of several repetition parameters: presentation number of images (1–8 presentations or 7 repetitions), number of intervening images between repeats (0–16+), and time between repeats (0–32+ s). This design allows for a better characterization of RS and provides multiple ways to examine the relationship between RS and performance (see Buracas et al. 2005). Furthermore, by measuring both repetition and performance information for each trial, we could separate out the effects of each factor to examine whether one or both contribute to RS.

A related consideration is whether RS represents changes in neural activity occurring during the process of recognition or whether it reflects changes after recognition occurs. Under most conditions, recognition reflects only a small part of the time period from which the BOLD signal is derived. Human observers can recognize briefly presented (~100 ms) and masked stimuli (Grill-Spector and Kanwisher 2005; Zago et al. 2005), yet the BOLD response integrates temporally over several seconds. As a consequence, the observed changes in the BOLD signal associated with RS may result from processes that occur well after the subject has recognized the object.

To address this question, we manipulated stimulus presentation duration across two experiments. In the first experiment, the duration was substantially longer than required for recognition (2 s), whereas in the second experiment, we presented stimuli for a short duration (67, 85, or 101 ms) and masked them. We masked the briefly presented images with scrambled images, which reduce neural activity in object-selective cortex (Grill-Spector et al. 2000; Kovacs et al. 1995). The duration of presentation in our second experiment was determined separately for each subject to achieve ≥85% accuracy in the classification task (see Fig. 1 and METHODS). Varying the presentation time allowed us to examine whether the factors that explain RS are the same for early periods in a trial, when recognition is taking place, versus later periods that occur after the subject has recognized the object.

METHODS

We conducted two experiments that had the same basic design but varied in stimulus presentation durations (Fig. 1).

Experiment 1

We presented gray level pictures of animals in a rapid event-related design intermixed with blank fixation trials. Each scan consisted of 127 2-s trials that included 43 fixation trials, 36 nonrepeated images that were shown once, and 6 repeated images that were shown a total

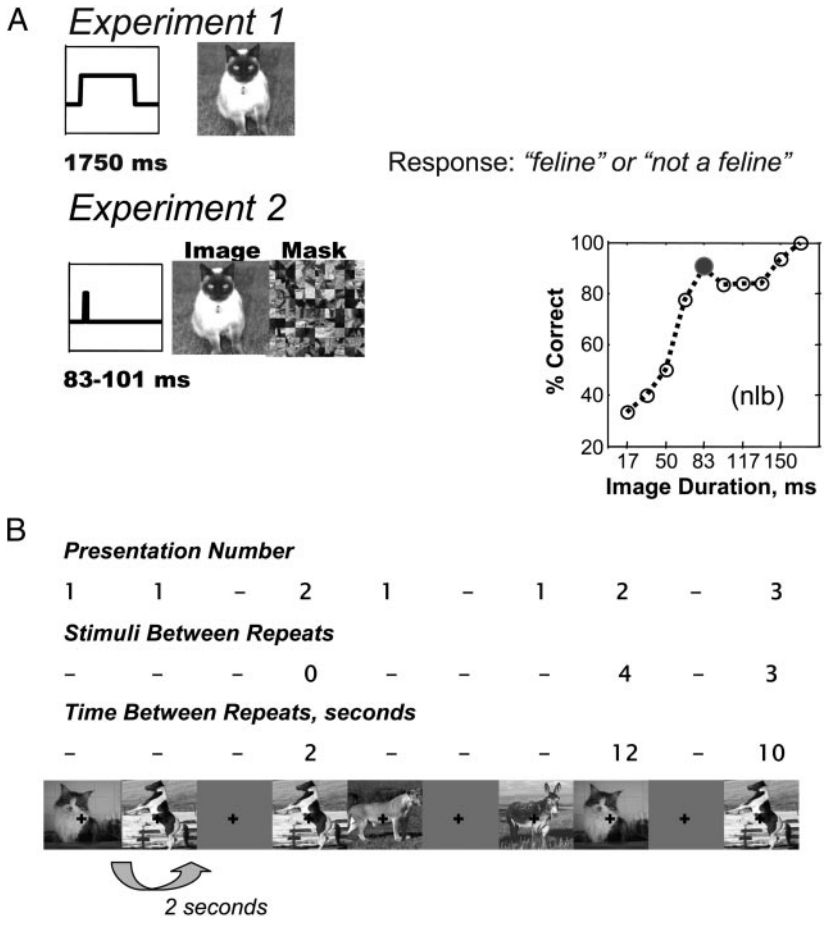

FIG. 1. Experimental design. *A*: example trial: *experiment 1*: each trial lasted 2 s: 1,750 ms in which an image appeared with a 250-ms blank period between trials. *Experiment 2*: each trial lasted 2 s: images were presented briefly and were followed by a random scrambled pattern for the remainder of the trial. Duration of the image was determined separately for each subject. An example psychophysical curve for 1 subject is shown at *right*. Red circle indicates duration used during scanning. *B*: repetition parameters: behavioral performance and functional MRI (fMRI) responses were analyzed according to the image presentation number, number of intervening stimuli between repeats, and time between repeats. Value of each parameter for each image is indicated above the image.

of eight times each. The nonrepeated condition included both nonrepeated distractors and the first presentation of repeated images. Stimuli consisted of gray level images of animals: housecats, lions, tigers, dogs, horses, and donkeys. Subjects were instructed to classify whether the animal was feline (cat, lion, or tiger) or not (horse, donkey, or dog) while fixating. The classification task was independent of repetition: one-half of the images (both repeated and nonrepeated) were felines, and the rest were other four-legged animals. During fixation trials, subjects were instructed to press a button for brief (~50 ms) fixation flickers, to ensure consistent attention throughout the scan. The order of repeated, nonrepeated, and fixation conditions was counterbalanced for each scan, and images did not repeat across scans. The order of image presentation within the repeated condition was determined by an algorithm that optimized counterbalancing for number of intervening trials between repeats. Subjects performed at ceiling for this task (mean accuracy, ≥94% for all subjects).

Experiment 2

Experiment 2 used the same basic design as *experiment 1*, with the exception that images were presented briefly (67, 85, or 101 ms) and were followed by a masking stimulus. The masking stimulus was a scrambled image (randomly assigned object image broken into 100 tiles that were randomly shuffled). Before scanning, subjects participated in a psychophysical experiment in which we determined the minimum exposure duration for 85% correct performance (Grill-Spector and Kanwisher 2005). This duration was used during the fMRI scans. A psychophysical performance curve from one subject is shown in Fig. 1. The exposure duration used during scanning is indicated by the black disk. The same animal images were used as *experiment 1*, except that a different subset of images were repeated (48 images randomly selected from a set of 384 total images). Five subjects who participated in *experiment 1* also participated in *experiment 2*. The average time that had elapsed between experiments was 16 mo.

Subjects

Eight subjects (3 female, ages 21–35 yr) participated in *experiment 1*. Seven subjects (3 female, ages 21–44 yr) participated in *experiment 2*. Five subjects participated in both experiments. All subjects were right-handed and had normal or corrected-to-normal vision. Each subject participated in one scanning session per experiment, which included eight scans of the experiment and a reference scan to define object-selective cortex. For one subject on the first experiment, data were only collected for five scans because of subject movement. The experiments were undertaken with the written consent of each subject, and procedures were approved in advance by the Stanford Internal Review Board on Human Subjects Research. Subject initials were changed to protect their privacy.

fMRI data collection

MRI was performed on a research-only GE 3T Signa scanner, using a custom transmit-received occipital quadrature RF surface coil (Nova Medical, Wilmington, MA). The dimensions of the coil were as follows: interior dimension left/right, 9 in; exterior dimension left/right, 10.125 in; height, 5.25 in; length, 7.5 in. Subjects laid supine with the coil positioned beneath the head and a front-angled mirror mounted overhead for viewing the stimulus.

Data were collected from 16 oblique slices, positioned perpendicularly to the calcarine sulcus, with a slice thickness of 4 mm. First, a set of anatomical in-plane images was collected using a T1-weighted spoiled GRASS (SPGR) pulse sequence (TR = 1,000 ms, min TE, FA = 45°, 2 NEX, FOV = 200 mm), with an inplane resolution of 0.78 × 0.78 mm. Functional scans were collected in the same slices, using a one-shot, T2*-sensitive, spiral-trajectory (Glover 1999) gradient-recalled-echo pulse sequence (TE = 30 ms, TR = 1,000 ms, FA = 60°, FOV = 200 mm, 16 slices that were 4-mm thick and with effective inplane pixel size = 3.125 × 3.125 mm). Functional volumes were collected with a time resolution of 1 s. Because there is a trade-off between temporal and spatial resolution, we chose to use a relatively high temporal resolution (TR = 1 s) to get accurate deconvolution of rapid event-related data, but only covered posterior regions of the brain at this resolution. Our slice prescription covered occipito-temporal cortex and posterior parietal cortex.

Behavioral responses were collected during scanning using a magnet-compatible button box connected to the stimulus computer. In addition, a whole brain anatomical scan was run on each subject during a separate session. The anatomical images from this scan were segmented into gray and white matter to restrict activation patterns to gray matter and for creating surface-based visualizations (Fig. 2).

Stimuli

We used 192 gray level images of felines and 192 images of other four-legged animals that subtended a visual angle of 11.9°. All stimuli were programmed in MATLAB (version 5.1, The Mathworks, Natick, MA) using the Psychophysics Toolbox (Brainard 1997). Stimuli were projected on to a screen mounted on the cradle for the coil. Subjects lay on their backs in the bore of the MR scanner and viewed the screen

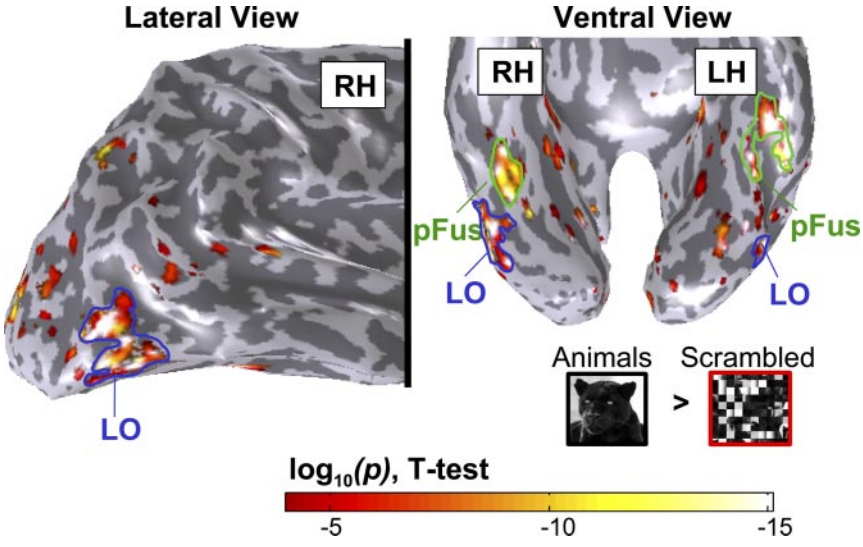

FIG. 2. Object-selective regions and region of interest (ROI) location on the inflated brain of 1 subject. Inflated brain of a representative subject showing regions that responded more strongly to animal images than scrambled animal images. Color maps are the negative log base 10 of the significance value of a 2-sided *t*-test (thresholded at $P < 10^{-5}$). LO, lateral occipital; pFus, posterior fusiform.

through an angled first-surface mirror positioned 3 in in front of their eyes.

Block-design localizer scans

We used an independent localizer scan to define object-selective cortex (see *ROI selection*). Subjects were presented with grayscale images of animals, novel objects (abstract sculptures), empty scenes, and scrambled objects (Grill-Spector et al., 2004). Stimuli were presented at rate of 1 Hz in blocks for 16 s. Subjects were asked to covertly name the stimuli while fixating.

Retinotopic mapping scans

We defined visual area V1 using separate retinotopic mapping scans. Retinotopic ROIs were imported into the event-related sessions by aligning both sessions to a high-resolution volume anatomy for each subject. The stimuli for these scans consisted of a 30° wedge containing object images that extended 10° in visual angle from the fovea and that rotated for six cycles of 32 s/cycle for at least two scans for each subject (1 clockwise and 1 counterclockwise; details in Grill-Spector and Malach 2004). Visual areas were defined by counting phase reversals at representations of the vertical/horizontal meridians, as described previously (Sereno et al. 1995). The ROIs defining these visual regions were restricted to those voxels that showed a response to our object stimuli (object stimuli $>$ blank baseline; *t*-test, $P < 0.01$). For one subject in *experiment 1*, the imaging prescription did not extend posterior enough to include all of V1, so this subject was excluded from the V1 analyses.

Data analysis

Data were analyzed using the mrVista analysis package (http://white.stanford.edu/software/) for MATLAB (version 6.5), and SurfRelax segmentation/visualization software (Larsson 2001). Event-related analyses, including application of general linear models and hypothesis tests to generate contrast maps, were performed as outlined in Dale and Buckner (1997) and Burock and Dale (2000).

ROI selection

We defined all ROIs on a subject-by-subject basis lateral occipital (LO) and fusiform ROIs were selected based on a conjunction of functional and anatomical cues. ROIs had to be in the appropriate anatomical location [near the lateral occipital sulcus for LO, within the fusiform gyrus for posterior fusiform pFus], respond significantly more to intact images of animals versus scrambled images (Malach et al. 1995), and remain centered in the same place at different statistical thresholds. The minimum threshold for a voxel being considered responsive to animal images more than scrambled animals was $P < 10^{-3}$ (*t*-test on the contrast animals $>$ scrambled).

Bilateral LO and pFus ROIs were defined in all subjects for both experiments. However, because of low signal strength during the masked experiment (*experiment 2*) combined with the drop off from our surface coil, we were not able to get reliable data from the pFus ROIs from two of our seven subjects in the second experiment. The fusiform data from that experiment therefore derives from the other five subjects.

Sorting data by repetition parameters

All data were sorted according to several criteria. Sortings included the following. *1*) Repeated versus nonrepeated: all repeated trials across all conditions were collapsed into one bin. This analysis measures the basic RS effect (Fig. 3). *2*) Sorting by presentation number: the first presentation was the nonrepeated condition, the second presentation was the first time the stimulus was repeated, etc., up to the eighth occurrence of the image. *3*) Sorting by intervening stimuli: we grouped repeated trials into four bins based on number of animal images between repeats. The bins had zero, one to three, four to seven, and eight or more intervening images. *4*) Time between repeats (interstimulus interval): we grouped repeated trials into four bins based on the time that elapsed between repeats: 0, 2–6, 8–14, and $\geq$16 s. Analyses 2–4 examine the effect of repetition parameters on RS (Figs. 4 and 5). *5*) Sorting by response time and repetition: nonrepeated and repeated trials were separately grouped into four bins according to the response time of each trial, from fastest to slowest trials (Fig. 7). By first separating trials to repeated and nonrepeated conditions and then binning the data by response time (RT), each bin contained the same number of correct trials. Furthermore, this sorting also allowed us to calculate separate regressions between RT and the fMRI signal on the nonrepeated and repeated data (Fig. 6).

We also performed a similar sorting to *5*) above by first binning all response times into four bins and then subdividing each bin into nonrepeated and repeated trials. Because the distribution of response times was different for repeated and nonrepeated trials, this sorting included different numbers of repeated and nonrepeated trials in each bin. Results of the second analysis were similar to the analysis in Fig. 7.

Time series processing

Functional time series were detrended using a temporal high-pass filter to remove scanner signal drift and converted to percent signal by dividing each voxel's time series by its mean intensity. We deconvolved each voxel's time series according to each sorting (Burock and Dale 2000; Dale and Buckner 1997). This method does not assume a shape for the hemodynamic response to each condition; rather, it uses a general linear model to estimate the mean and variance of response at each time point for each condition.

The hemodynamic response at each voxel to the same stimulus presented several times over an experiment is assumed to be governed by the following linear time invariant system

$$y(t) = \sum_{i=1}^{n} h_i(t) \times x_i(t) + n(t)$$

$y(t)$ is the estimated time course for each voxel; $x_i(t)$ is the presentation sequence for condition i; h_i is the estimated response for condition i; and $n(t)$ is additive noise distributed with a white noise distribution. We estimated responses $h_i(t)$ for a time window ranging from 4 s before stimulus onset to 17 s after onset, at discrete intervals of 1 s. The estimates were computed using a generalized least mean squares solution.

From the deconvolved time-courses, we calculated the mean amplitude of each condition as the average response of the peak and two surrounding time points relative to the fixation baseline. Because this analysis only considers activation around the peak point—although differences may be present across the entire time-course—we also repeated our analyses using a relative fMRI amplitude as used by Ress et al. (2000). This measure uses the dot product of each deconvolved time-course relative to the mean response of all time-courses, and thus uses information across the entire time-course. These relative amplitudes produced the same changes with repetition parameters as using the peak response. Therefore only results using the peak response metric are depicted in the figures.

Repetition suppression ratio

To measure the magnitude of repetition suppression, we calculated the RS ratio: % $\text{Signal}_{\text{Repeated}}$/% $\text{Signal}_{\text{Nonrepeated}}$ (Grill-Spector et al. 1999). The signal was measured as the average response of the peak of the hemodynamic response (4–6 s after trial onset) relative to the

fixation baseline. This ratio varies from 0 (complete RS) to 1 (no RS). Repetition suppression ratios that are significantly <1 indicate suppression of the response to repeated stimuli compared with nonrepeated stimuli. Repetition suppression ratios were calculated for individual voxels (Fig. 3*C*) and for ROI analyses (Figs. 4 and 5).

Priming ratio

To measure the level of priming, we calculated an analogous priming ratio from the average RT for repeated and nonrepeated trials. The priming ratio was defined as: $RT_{repeated}/RT_{nonrepeated}$. A ratio of 1 indicates no priming, and values that are significantly <1 reflect priming (faster performance for repeated trials).

Regression analyses

We performed a linear regression analysis of the priming ratio versus RS ratio for repeated trials. The RS ratio was calculated from the mean response across the left and right hemispheres. Results reported in Table 1 reflect data combined from all subjects in each experiment. Each data point in this analysis represents data from one subject and one level of a repetition parameter (e.g., when sorting by repetition number, the regression contains 7 points per subject for repetitions 2–8). Regressions were performed using data from correct trials.

RESULTS

Definition of object-selective cortex

We defined object-selective ROIs for each subject using an independent block-design localizer scan (see METHODS). Figure 2 shows the location and extent of object-selective regions, primarily within the lateral occipital complex (LOC; Malach et al. 1995). This complex is defined as a region within the lateral part of the occipital and posterior temporal lobes that preferentially activates to intact images of objects versus scrambled images. Our lateral occipital ROIs activated significantly more strongly for animals than scrambled animals, were in the correct anatomical location for the LOC, and remained centered in the same location for a range of statistical thresholds. Because this does not reflect the entirety of the LOC, we will refer to this ROI simply as LO. ROIs that passed the same criterion, but were located in posterior fusiform and inferior temporal regions of cortex will be referred as pFus (see Fig. 2) (Grill-Spector 2003; Grill-Spector et al. 1999, 2000).

Basic RS effect

We observed significant RS (nonrepeated > repeated images; $P < 0.001$, *t*-test) for each subject in both of our object-selective ROIs (Fig. 3). This RS was observed for the majority of the voxels in both ROIs (Fig. 3*C*). We quantified the amount of repetition suppression by defining a suppression ratio, which varies from 0 (complete RS) to 1 (no RS; see METHODS). The observed RS was distributed with a mean of 0.67 ± 0.029 (SE) in LO and a mean of 0.70 ± 0.011 in pFus. Both distributions were significantly <1 as verified with a one-sided *t*-test (LO: $P < 10^{-28}$; pFus: $P < 10^{-27}$).

In contrast, we observed a minimal level of RS in early visual cortex (Fig. 3*B, right*). A *t*-test on the mean V1 time-course across subjects revealed no significant difference between repeated and nonrepeated trials ($P = 0.22$). Most individual subjects did not show RS effects in V1: we found significant RS only in 4 of 14 hemispheres at $P < 0.05$

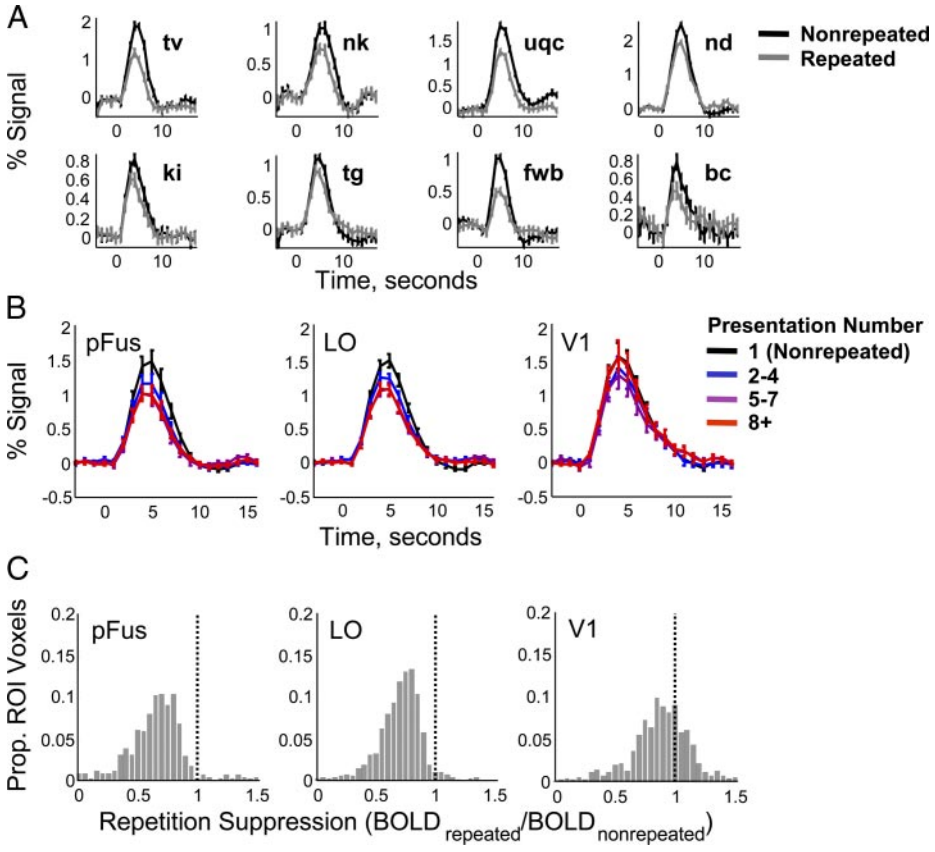

FIG. 3. Adaptation effect in *experiment 1*. *A* and *B*: deconvolved time-courses from *experiment 1*. Activities are measured in percent signal change relative to fixation baseline; time is measured in seconds relative to onset of trial. *A*: deconvolved time-courses from LO for each subject (indicated by initials). Black curves, nonrepeated images; gray curves, repeated. Error bars indicate SE across trials. *B*: average time-courses across subjects for LO (*left*) and posterior fusiform (pFus, *middle*), and V1 (*right*) ROIs. Black, nonrepeated images; color, repeated images by binned presentation number. Error bar indicates SE across subjects. *C*: distribution of repetition suppression ratios across voxels in 3 ROIs. *x*-axis denotes the repetition suppression (RS) ratio. Dashed line indicates RS ratio of 1 (no RS).

(uncorrected). After applying Bonferroni correction for multiple comparisons, only 1/14 of comparisons were significant. In contrast, 15/16 individual comparisons were significant in LO and 14/16 in pFus after this correction. The mean suppression ratio across voxels in V1 was 0.90 ± 0.016, which was significantly greater than that for LO ($P < 10^{-10}$) or pFus ($P < 10^{-10}$; 1-tailed *t*-test). These results are consistent with previous studies (Grill-Spector and Malach 2001; Grill-Spector et al. 1999) and validate the notion that RS in object-selective cortex is distinct from adaptation phenomena observed in early visual cortex (Boynton and Finney 2003; Engel and Furmanski 2001).

Whether a given image was a target or nontarget (feline or nonfeline) did not affect the level of RS. This was assessed by applying a two-way ANOVA on the data from each ROI, using as factors repeated versus nonrepeated trials and target versus nontarget images. We found a significant repetition effect in LO [$F(1,31) = 18.88$, $P < 10^{-3}$] and in pFus [$F(1,31) = 9.08$, $P = 0.0038$] ROIs, but there was no effect of the target [LO: $F(1,31) = 0.15$, $P = 0.70$; pFus: $F(1,31) = 0.48$, $P > 0.49$] or an interaction between the type of image (target/nontarget) with the repetition effect [LO: $F(1,15) = 0.30$, $P = 0.59$; pFus: $F(1,15) = 0.06$, $P = 0.81$]. One-sided *t*-test between target and nontarget responses also failed to reveal a difference in either direction (LO: $P = 0.36$; pFus: $P = 0.25$, for testing target > nontarget).

For both object-selective ROIs, overall BOLD response as well as RS were similar between left and right hemispheres. A two-way ANOVA using repetition and hemisphere as factors revealed a main effect of repetition [LO: $F(1,31) = 184.55$, $P < 10^{-5}$; pFus: $F(1,31) = 72.26$, $P < 10^{-4}$] but not hemisphere [LO: $F(1,31) = 0.40$, $P = 0.54$; pFus: $F(1,31) = 2.07$, $P = 0.193$] or interaction with repetition [LO: $F(1,15) = 1.05$, $P = 0.34$; pFus: $F(1,15) = 0.01$, $P = 0.97$].

Effect of repetition parameters

Our stimulus presentation sequence allowed us to separately examine different repetition parameters that may affect RS (see METHODS). Figure 4 summarizes the dependence of fMRI response and task performance on repetition parameters: the presentation number of an image, the number of intervening object stimuli between repeats, and the total time between repeats [this is distinct from the number of intervening stimuli since a given interstimulus interval (ISI)may include fixation trials without any images]. For both behavioral and fMRI data, we used responses for correct trials only.

RS progressively increased with successive repetitions, plateauing at about the fifth repetition (Fig. 4*B, top*). RS was

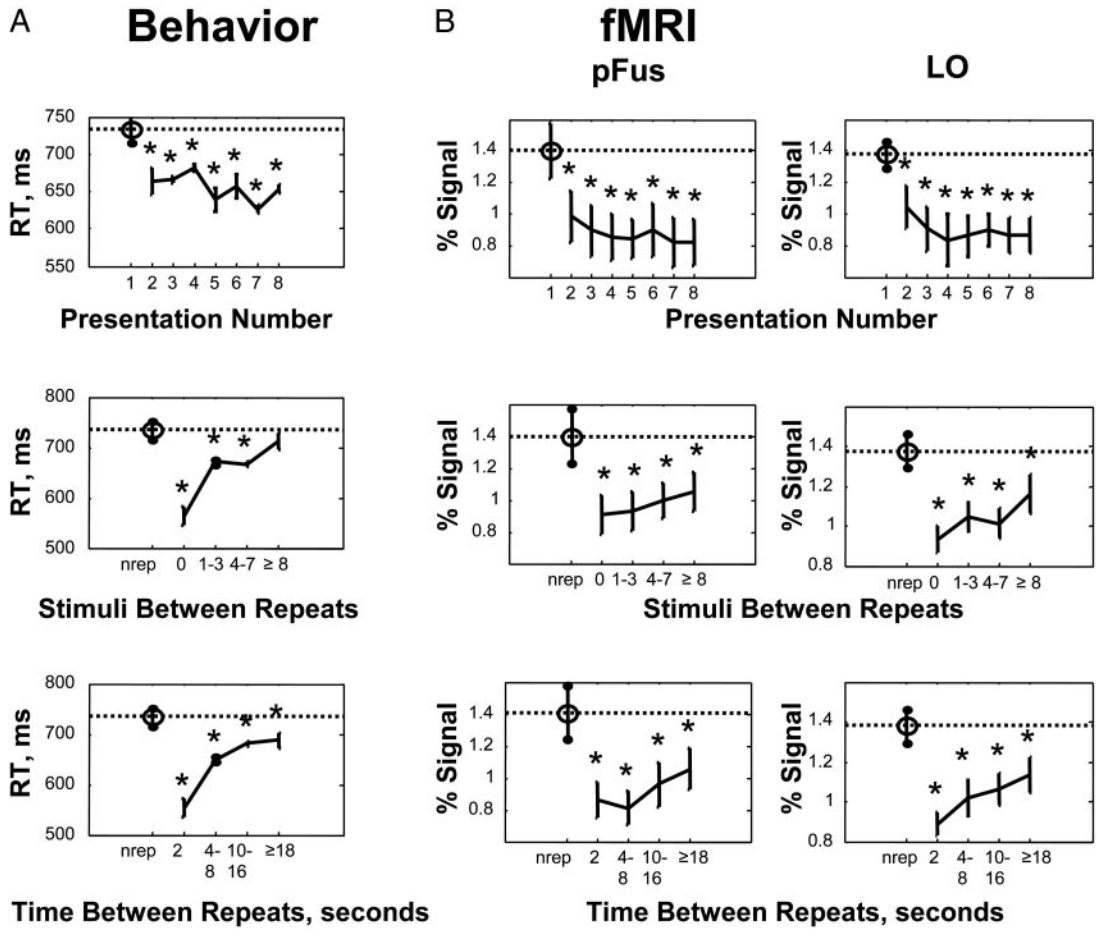

FIG. 4. Effect of repetition parameters on RS and priming summarized for *experiment 1*. *A*: mean response time. *B*: BOLD response amplitude for pFus (*middle*) and LO (*right*). Error bars indicate SE between subjects. BOLD responses are averaged across hemispheres. *Significantly lower than 1st presentation at $P < 0.05$. Dashed line indicates response to the 1st presentation. *Top*: data sorted by presentation number. *Middle*: sorting by intervening stimuli between repeats. *Bottom*: sorting by time between repeats.

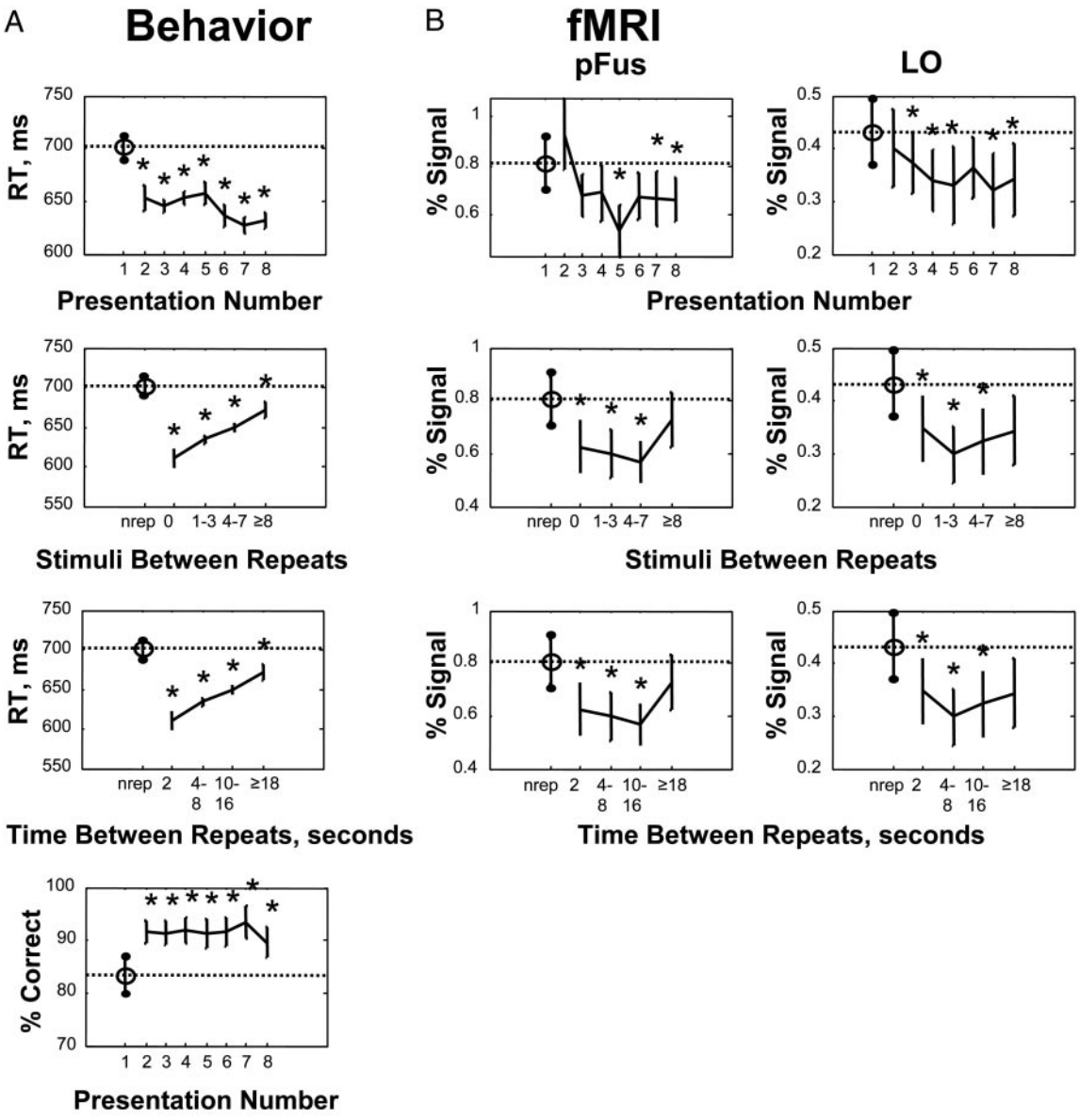

FIG. 5. Effect of repetition parameters on RS and priming summarized for *experiment 2*. *A*: Mean behavioral responses. *B*: BOLD response amplitude for pFus (*middle*) and LO (*right*). Error bars represent SE across subjects. Conventions are the same as Fig. 4.

strongest after no intervening trials and zero seconds ISI (Fig. 4*B, middle* and *bottom*) and gradually recovered with more intervening trials and greater ISI. These effects of repetition parameters can also be seen in the response time data (Fig. 4*A*) and follow a similar trend.

RS during brief image presentations

The results described thus far pertain to an experimental design in which stimuli were present well beyond the time required to classify the objects and respond to them. In this time period, object-selective cortex may engage in additional processing that is not required for classification or that may reflect a later, distinct stage of recognition (Kovacs et al. 1995; Sugase et al. 1999; Tamura and Tanaka 2001; Zago et al. 2005). To examine the factors that affect RS on the early component of the MR response during recognition, we conducted a second experiment that used a masking paradigm in which stimuli were presented briefly and immediately masked (see METHODS). Such masks have been shown to curtail firing rates of shape-selective neurons in putatively homologous macaque inferotemporal cortex within 60 ms after the onset of the mask (Keysers and Perret 2002; Keysers et al. 2001; Kovacs et al. 1995). Furthermore, progressively shorter presentation durations of masked stimuli reduce both recognition performance and BOLD signal in object-selective ROIs in humans (Grill-Spector and Kanwisher 2005; Grill-Spector et al. 2000). This indicates that the presence of masks reduces neural processing in object-selective cortex to a briefly presented image.

Before scanning, we determined the minimum presentation duration required for 85% correct performance for each subject, and used this duration in the scanner (see Fig. 1 and METHODS). This performance level was optimal because it was significantly above chance performance but also measurably

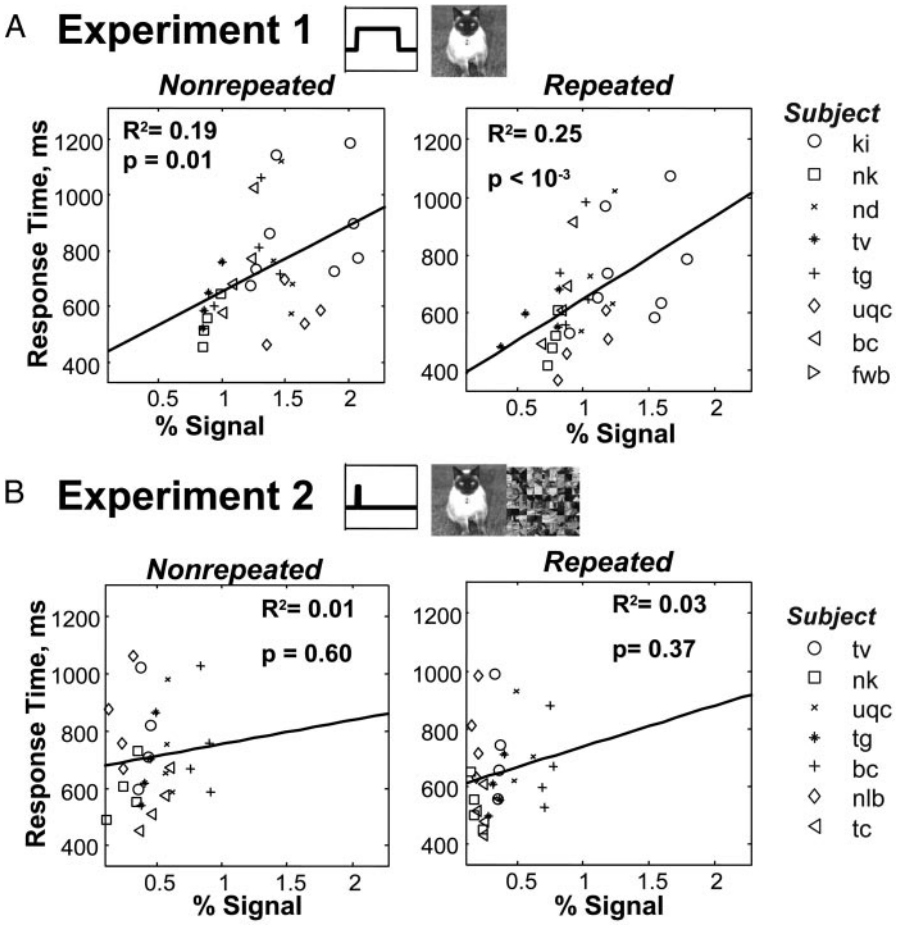

FIG. 6. Regression analyses between RT and BOLD response in LO for repeated and nonrepeated trials. *A*: data from *experiment 1* (long presentation durations). *B*: data from *experiment 2* (short presentation durations). Data are binned in each subject by response time quartiles. Each point represents data for 1 subject and 1 response-time bin.

below ceiling performance. It also provided for a reasonable number of correct trials from which to derive event-related time-courses. Finally, these presentation durations are significantly shorter than response times in the first experiment, allowing for potential dissociations between response time and image presentation time in determining the level of RS.

When objects were briefly presented, we found significant RT priming (Fig. 5*A*). The magnitude of the priming effect did not decrease with brief presentations (there were no significant differences between priming ratios between experiments: all subjects $P = 0.23$; 5 subjects in both experiments $P = 0.32$; 2-tailed *t*-test). Because subjects were not performing at ceiling, we could also assess changes in recognition accuracy with repetition parameters. We found that the percent of correct responses increased for repeated trials (in which RT decreased). However, accuracy did not exhibit the same monotonic increase with repetition as response time priming.

Consistent with the results of *experiment 1*, we found significant RS in object-selective cortex (Fig. 5*B*) for brief presentations and a similar dependence of RS on repetition parameters: the level of RS increased with presentation number and decreased when many intervening stimuli occurred between repetitions (Fig. 5). However, for brief presentations, we did not find maximal adaptation for the shortest intervals between repeats or for no intervening stimuli between repeats (cf. Figs. 4 and 5).

We observed lower RS levels for briefly presented images (67, 85, or 101 ms) compared with long presentations (2 s). RS was not significant for the second presentation of an object or when more than 8 intervening stimuli occurred between image repetitions, although it was significant for subsequent repetitions and with fewer intervening stimuli. We compared the level of RS between experiments by calculating the RS ratios from the five subjects who participated in both experiments. This analysis revealed a significantly greater level of RS (lower RS ratio) for the first experiment compared with the second (1-sided *t*-test, LO: $P = 0.008$; pFus: $P = 0.003$). This may result from a smaller dynamic range of BOLD response in the second experiment, owing to the shortened presentation time. Alternatively, it may also indicate that processes occurring both during and after object recognition contribute to the RS effect observed in *experiment 1*.

The consistent RS and priming present in both experiments suggests that a significant component of these processes occur while subjects recognize objects, rather than afterward. However, because of the greater level of RS during the first experiment, some postrecognition processes may contribute to the magnitude of the RS effect when stimuli are present for a long time.

Quantitative analysis of the relationship between RS and priming

Results of our experiments indicate that the level of RS and priming depends on repetition parameters. We next examined whether repetition parameters have the same effect on RS and

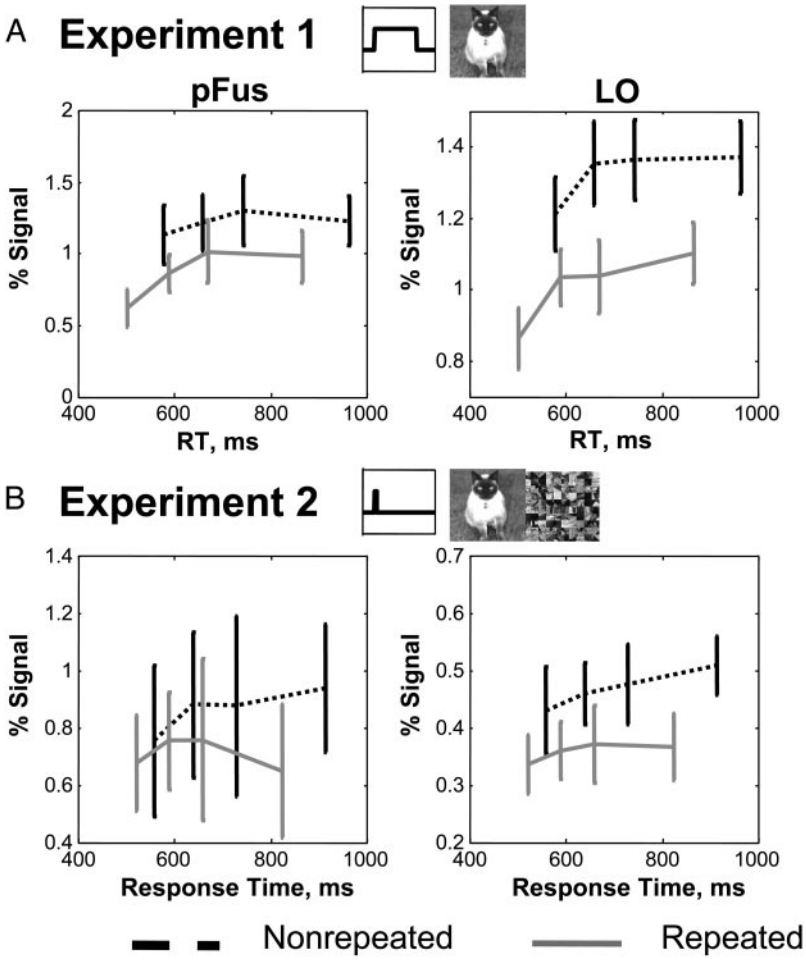

FIG. 7. Dual repetition/response-time analysis. Data are sorted 1st into repeated and nonrepeated correct trials and then grouped into 4 response time bins for each subject. The 1st response time bin represents fastest quartile of correct trials for each subject. Error bars indicate SE across subjects. *A*: results across subjects for *experiment 1*. *B*: results across subjects for *experiment 2*.

priming. Therefore we performed a series of regression analyses of the priming ratio against the RS ratio.

Regressions were performed for all repetition parameters for data from all subjects (see METHODS). Table 1 summarizes regression results for both experiments.

TABLE 1. *Performance-independent RS in object cortex*

(ROI, Sorting)	Slope	R^2	F	P
Experiment 1				
LO, presentation number	0	0.001	0.063	0.80
LO, stimuli between repeats	0.44	0.319	14.061	<10e-4
LO, time between repeats	0.37	0.306	13.244	<10e-3
pFus, presentation number	0	0.004	0.221	0.64
pFus, stimuli between repeats	0.42	0.27	11.077	<10e-3
pFus, time between repeats	0.34	0.244	9.698	<10e-3
V1, presentation number	−0.01	0.005	0.258	0.61
V1, stimuli between repeats	0.19	0.046	1.25	0.27
V1, time between repeats	0.05	0.007	0.193	0.66
Experiment 2				
LO, presentation number	0.01	0.011	0.533	0.47
LO, stimuli between repeats	0.02	0.016	0.415	0.53
LO, time between repeats	0.02	0.016	0.415	0.53
pFus, presentation number	0	0.001	0.031	0.86
pFus, stimuli between repeats	0.03	0.016	0.289	0.60
pFus, time between repeats	0.03	0.016	0.289	0.60
V1, presentation number	0.01	0.006	0.242	0.63
V1, stimuli between repeats	0.01	0.005	0.067	0.80
V1, time between repeats	0.01	0.005	0.067	0.80

For long exposures (*experiment 1*), when sorting by either stimuli between repeats or time between repeats, we found significant correlations between priming and RS for both LO and pFus ROIs (all $R^2 \geq 0.23$, all $P \leq 0.02$; Table 1). However, no significant correlation was found when sorting data by presentation number. Additionally, no significant correlation was found between V1 activation and priming, regardless of the sorting method used (all $R^2 \leq 0.04$, $P \geq 0.32$).

For brief presentations (*experiment 2*), we did not find significant correlations between priming and RS (all $R^2 < 0.02$; $P > 0.45$; Table 1) for any ROI. Thus while both priming and RS suppression occur during brief presentations, priming is not significantly correlated with RS in object-selective cortex.

Dissociable effects of response time and repetition on RS

In examining the correlation between RS and priming, we compared changes in two potentially distinct factors: stimulus repetition and response time. However, it may be that decreased response time alone drives signal decreases (even among nonrepeated trials). Or, it may be that stimulus repetition alone causes a change, and the correlation with priming conflates response time with repetition. In addition, it is possible that one or both factors drive responses in *experiment 1* but only one factor in *experiment 2*. Therefore in the following

analyses, we examined the separate contributions of response time and repetition on RS.

We assessed the direct contribution of response time to BOLD signal by performing regressions between the BOLD amplitude and response times separately for repeated and nonrepeated trials (Fig. 6). We found that, for long image presentations, LO response correlated with response time even for nonrepeated data (Fig. 6*A*). However, there were no correlations between BOLD and RT for either repeated or nonrepeated data from LO for brief image presentations nor in pFus data for any presentation duration ($R^2 \leq 0.09$ and $P \geq 0.06$ for all regressions). Because response times contribute to RS in LO only for long stimulus presentations, this factor likely reflects processing that occurs after recognition.

Next, we assessed the contributions of both response time and repetition to RS by performing a further sorting of our data from both experiments, taking both factors into account. For this sorting, we first separated trials into repeated and nonrepeated conditions. For each condition, we ranked each subject's trials according to response time and grouped the trials into four equally sized bins (see METHODS). We performed an ANOVA on our data, taking as factors trial type (repeated/nonrepeated) and RT. The result was that we could dissociate between repetition and response time effects and also test whether the two interact.

Figure 7 shows the mean BOLD response across subjects using this sorting, plotted against the mean response time across subjects for each bin. Responses to repeated trials were consistently reduced compared with nonrepeated trials even when response times were equated between conditions. Importantly, for both experiments and all object-selective ROIs, we found a significant effect of repetition independent of response time [$F(1,94) \geq 8.7$, $P < 10^{-3}$ for all ANOVAs]. In contrast, we did not see strong effects of response time independent of repetition. There was a weak, statistically significant effect in LO during *experiment 1* [$F(3,92) = 3.0$, $P < 0.03$], consistent with our regression analyses (Fig. 6). However, there was no significant effect for pFus in *experiment 1* or any effect in either ROI in *experiment 2* [$F(3,92) \leq 0.89$, $P \geq 0.45$; Table 2]. Finally, we found no significant interaction between repetition and response times in any of the ROIs or experiments (Table 2).

Taken together, these analyses reveal that RS robustly reflects stimulus-specific repetition, even when performance is matched between repeated and nonrepeated objects and when stimuli are presented close to the minimum time required for recognition.

TABLE 2. *Performance-independent RS in object cortex*

Source	Sum Sq.	df	Mean Sq.	*F*	*P* > *F*
LO, experiment 1					
Repetition	3.13	1	3.13	48.71	6.1e-10
RT	0.89	3	0.30	4.60	0.005
Repetition × RT	0.01	3	0.00	0.06	0.98
Error	5.46	85	0.06		
Total	23.09	127			
LO, experiment 2					
Repetition	0.34	1	0.34	19.82	3.0e-05
RT	0.05	3	0.02	0.89	0.45
Repetition × RT	0.01	3	0.00	0.20	0.90
Error	1.28	74	0.02		
Total	5.77	111			
pFus, experiment 1					
Repetition	4.11	1	4.11	17.82	6.1e-05
RT	0.78	3	0.26	1.13	0.34
Repetition × RT	0.09	3	0.03	0.13	0.94
Error	19.59	85	0.23		
Total	41.38	127			
pFus, experiment 2					
Repetition	0.47	1	0.47	8.25	0.006
RT	0.14	3	0.05	0.81	0.49
Repetition × RT	0.13	3	0.04	0.77	0.51
Error	2.96	52	0.06		
Total	12.52	79			

DISCUSSION

Dynamics of RS

The RS described in this study was a consistent phenomenon that appeared in all subjects. The magnitude of RS depended on repetition parameters: it increased gradually with the number of repetitions and was largest when no intervening stimuli occurred between image repetitions. The first several repetitions produce a greater reduction in signal strength compared with later repetitions (Fig. 4). This measured dependence of RS on repetition parameters is qualitatively similar to effects reported in single units in macaque inferotemporal (IT) cortex (Li et al. 1993).

Our RS curves are consistent with our previous reports on the effect of presentation number in block design experiments using different tasks than this study (e.g., passive viewing or a 1-back matching, see Grill-Spector and Malach 2001; Grill-Spector et al. 1999) and with event-related fMRI studies examining the effect of repetition parameters (Henson et al. 2000, 2004; Jiang et al. 2000). The similar dependence of RS on repetition parameters for both block and event-related designs suggests that these reflect the same phenomenon. These results indicate that many presentations of the same stimulus without intervening stimuli yield the largest RS, and as a consequence, RS in block design experiments will be stronger than event-related designs.

Effects of presentation duration on RS

Several lines of evidence indicate that the mask in our second experiment reduces neural activity in object-selective cortex. Kovacs et al. (1995) showed in macaque inferotemporal cortex that nonobject masks reduce the firing rates of shape-selective cells. Similar effects of masking on BOLD signal have been reported in human object-selective cortex (Grill-Spector et al. 2000; Zago et al. 2005). It has also been shown that the response in these ROIs to the scrambled objects used as a mask are small compared with the response to objects (Grill-Spector 2003; Malach et al. 1995). This strongly suggests that the smaller BOLD responses in our second experiment reflect a shorter period of neural activity in these regions.

The masking paradigm we adopted can be useful to help distinguish contributions from times during and after recognition or from different stages of recognition (see also James et al. 2000; Zago et al. 2005). Evidence from primate neurophysiology suggests that the recognition process may contain several distinct stages (Sugase et al. 1999; Tamura and Tanaka 2001) that allow for progressively finer discriminations of object identity. These studies find an early component between ~50 and 150 ms and a later component between ~150 and 500

ms. While there may be persistent activity in object-selective cortex after the appearance of the mask, recent data by Keysers and Perrett (2002) and Keysers et al. (2001) suggest that this persistent activity shuts down within 60 ms after the onset of the mask. Therefore it is likely that during our second experiment, most of the BOLD signal derives from activity during the first 127–150 ms after the appearance of the object image. In humans, Zago et al. (2005) found differential effects on RS of shorter (40–250 ms) and longer (250–1,900 ms) stimulus presentations, which may reflect the contributions of these distinct components. Different effects of early and late processes on RS may relate to the differences we observed between our two experiments.

Results from our second experiment differed from the first experiment in the following ways: lower overall RS; absence of a response-time component to BOLD signal in LO (Fig. 6); and a lack of correlation between priming and RS (Table 1). Effects present in the first experiment, but reduced or absent in the second experiment, may reflect one of two factors. First, they may reflect processes unrelated to recognition. For instance, longer time spent looking at objects for novel than repeated images may cause varying temporal windows of integration for the BOLD signal during long presentations. Second, they may reflect a later component to recognition, which is used for finer discriminations but not required to perform classification (Sugase et al. 1999; Tamura and Tanaka 2001).

Comparison to previous studies suggests that our presentation durations of 67–101 ms may reflect an early component only. However, because our 85% masking threshold allowed subjects to classify images fairly well above chance (Fig. 1), the second experiment may include later components of recognition, and therefore differences between experiments would relate to postrecognition processes. Recent work by James and Gauthier (2005) measured BOLD response to objects when the repeated presentation was below detection threshold, using a combination of backward masking, and low contrast. Somewhat surprisingly, they found a stronger response to subthreshold stimuli that were repeated compared with objects shown for the first time. This suggests that neural activity during repeated trials may be occurring very early in a trial, even before subjects accumulate enough evidence to recognize the object. This further implies that the RS observed in our masking experiment occurs during the process of recognition.

Because the stimuli were kept constant between experiments, long-term suppression effects (van Turennout and Martin 2001) may also contribute to the different levels of RS between *experiments 1* and *2*. In addition to reduced signals caused by masking, there may be additional suppression from having viewed the images during the first experiment. However, on average, 16 mo had elapsed between *experiments 1* and *2* for each subject. Given that long-term RS has not been reported for durations >3 days, it seems unlikely that long-term effects explain differences in the level of RS between *experiments 1* and *2*.

Finally, it is possible is that the level of RS may depend on the initial response. Evidence that the level of RS is proportional to the initial activation has been found in studies that parametrically varied contrast (Avidan et al. 2002) or stimulus duration (Zago et al. 2005) or that manipulated attention to different objects (Eger et al. 2004; Yi and Chun 2005). In our data, the magnitude of response to nonrepeated images was lower for brief presentations (cf. Figs. 4 and 5); at the same time, both overall RS and the repetition effect were reduced. These reductions may reflect different degrees of the same process, rather than reflecting the contribution of distinct processes.

Relationship between RS and visual priming

While both priming and RS occurred in both experiments, they did not always correlate quantitatively. The correlation was sensitive to the regression parameters in *experiment 1* and was not significant in *experiment 2*. While there is a vast literature suggesting that RS reflects priming (e.g., Henson 2003; Koutstall et al. 2001; Lustig and Buckner 2004; Schacter and Buckner 1998; Wiggs and Martin 1998; Zago et al. 2005), our results suggest that these phenomenon may co-occur without being directly linked. Indeed, RS has been reported in anesthetized macaques using fMRI (Tolias et al. 2001), as well as single unit recordings in IT (Miller and Desimone 1993), in which behavioral response is not an issue. Thus the relationship between task performance and BOLD response should be carefully considered before attributing a behavioral change to a change in localized neural activity (Buracas et al. 2005).

Stimulus-specific repetition and RS

Across our manipulations, the most consistent factor in explaining RS was the presentation history of a stimulus. Repeated stimuli were associated with a reduced response in object-selective cortex, regardless of response time and regardless of the presentation duration. The persistence of the repetition effect for brief presentations suggests that at least part of this effect occurs at the same time as recognition processes.

This result is particularly relevant for the use of RS to probe the functional properties of neural subpopulations within cortical regions (Grill-Spector and Malach 2001), because it shows that the effect is stimulus-specific and reflects the presentation history of the stimulus. Failure to observe such an effect would have raised concerns about the use of this technique, because other explanatory factors for RS such as response mapping (Dobbins et al. 2004) may not be stimulus-specific. While our findings do not directly validate this technique, the robust stimulus-specific repetition effect allows us to rule out the most likely alternative explanations. It further suggests that RS occurs within specific neural populations within our voxels, enabling the functional characterization of neural subpopulations within fMRI voxels.

Finally, while our data provide several insights about the factors explaining RS, the underlying mechanisms remain largely unknown. RS may be caused by multiple aspects of change in the neural response: spatial changes, e.g., fewer neurons respond (Wiggs and Martin 1998); temporal changes, e.g., shorter period of response (Sobotka and Ringo 1996); and/or reduced amplitude of neuronal response (Miller and Desimone 1994). Because the BOLD response pools over neurons and time, lesser neural activation or shorter neural activation will yield a lower BOLD response for repeated stimuli (Grill-Spector et al. 2005). Using parametric manipulations such as in this study, future experiments may be able to further reveal the complex relationship between these functional neuronal dynamics and behavior.

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