Title: Object-selective cortex exhibits performance-independent repetition suppression

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ABSTRACT

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 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 ROI and one experimental condition. Thus, repetition suppression appears 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 sec), while in a second experiment durations were close to the minimum time required for recognition (67-101 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 (Kourtzi and Kanwisher, 2001; Grill-Spector, 2003) and fusiform regions (Kanwisher et al., 1997; 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 fMRI BOLD response in object-selective cortex is consistently lower for repeated versus novel images (Henson, 2003; Grill-Spector, et al., 1999; Epstein, et al., 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 et al. 1999, Grill-Spector and Malach, 2001), 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 (Schacter and Buckner, 1998; Wiggs and Martin, 1998, Dobbins 2004, Lustig 2004). Conversely, it may relate to classical adaptation effects found in earlier visual areas (Boynton and Finney, 2003; Tolias et al., 2001; Bradley et al., 1988), 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
Repetition suppression 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). Further, RS is used as an experimental tool to characterize the selectivity of neuronal populations (Grill-Spector and Malach 2001; Kourtzi and Kanwisher, 2001; Vuilleumier et al., 2002; Avidan 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 investigate priming associates RS with performance changes, while 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. Further, 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, 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
(housecats, lions and tigers) or not feline (horses, donkeys and dogs) and compared neuroimaging and behavioral data (Figure 1). Half of the repeated objects were felines and 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+ sec). 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). Further, 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 (~100ms) 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 sec), while in the second experiment we presented stimuli for a short duration (67, 85, or 101ms) and masked them. We masked the briefly-presented images with scrambled images, which reduce neural activity in object selective cortex (Kovacs et al., 1995; Grill-Spector et al., 2000). The duration of presentation in our
second experiment was determined separately for each subject to achieve at least 85% accuracy in the classification task (see Figure 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 (Figure 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 two-second trials that included: 43 fixation trials, 36 nonrepeated images that were shown once, and six repeated images, which were shown a total 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: half of the images (both repeated and non repeated) were felines and the rest were other 4-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:** used the same basic design as Experiment 1, with the exception that images were presented briefly (67, 85, or 101ms) and then were followed by a masking stimulus. The masking stimulus was a scrambled image (randomly-assigned object image broken into 100 tiles which were randomly shuffled). Prior to 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 Figure 1. The exposure duration used during scanning is shown in red. 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 months.

**Subjects.** Eight subjects (3 female, ages 21-35) participated in Experiment 1. Seven subjects (3 female, ages 21-44) 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 5 scans due to 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.** MR imaging was performed on a research-only GE 3T Signa scanner, using a custom transmit-received occipital quadrature RF surface coil (Nova
Medical, Inc., Wilmington, MA, USA). The dimensions of the coil are: interior dimension left/right = 9 inches, exterior dimension left/right = 10 1/8 inches; height= 5 1/4 inches; length = 7.5 inches. Subjects lay supine with the coil positioned beneath the head, and a front-angled mirror mounted overhead for viewing the stimulus.

Data were collected from sixteen oblique slices, positioned perpendicularly to the calcarine sulcus, with a slice thickness of 4 mm. First, a set of anatomical inplane images was collected using a T1-weighted SPGR pulse sequence (TR = 1000 ms, min TE, FA = 45°, 2 NEX, FOV = 200 mm), with an inplane resolution of 0.78 x 0.78 mm. Then, 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 = 1000 ms, FA = 60°, FOV = 200 mm, 16 slices which were 4-mm thick and with effective inplane pixel size = 3.125 x 3.125 mm). Functional volumes were collected with a time resolution of 1 second. Since there is a tradeoff between temporal and spatial resolution, we chose to use a relatively high temporal resolution (TR = 1 second) 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 (Figure 2).

**Stimuli.** We used 192 gray level images of felines and 192 images of other 4-legged animals that subtended a visual angle of 11.9 degrees. All stimuli were programmed in
MATLAB (The Mathworks, Inc., Natick, MA, version 5.1) 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 through an angled first-surface mirror positioned 3” in front of their eyes.

**Block-design localizer scans.** We used an independent localizer scan to define object-selective cortex (see ROI selection below). Subjects were presented with gray-level images of animals, novel objects (abstract sculptures), empty scenes, and scrambled objects (Grill-Spector et al., 2004). Stimuli were presented at rate of 1Hz in blocks for 16 seconds. 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 which extended 10° in visual angle from the fovea, and which rotated for 6 cycles of 32 sec/cycle, for at least two scans for each subject (one clockwise and one counterclockwise rotation; 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 then 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. 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 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 2 of our 7 subjects in the second experiment. The fusiform data from that experiment therefore derives from the other 5 subjects.

**Sorting Data by Repetition Parameters.** All data were sorted according to several criteria. Sortings included: (a) Repeated vs. nonrepeated: All repeated trials across all conditions were collapsed into one bin. This analysis measures the basic RS effect (Figure 3). (b) 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. (c) Sorting by intervening stimuli: We grouped repeated trials into 4 bins based on number of animal images between repeats: the bins had 0, 1-3, 4-7, and ≥ 8 intervening images. (d) Time between repeats (inter-stimulus interval): We grouped repeated trials into 4 bins based on the time that elapsed between
repeats: 0, 2-6, 8-14, and ≥ 16 seconds. Analyses b-d examine the effect of repetition parameters on RS (Figures 4, 5). (e) 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 (Figure 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. Further, this sorting also allowed us to calculate separate regressions between RT and the fMRI signal on the nonrepeated and repeated data (Figure 6).

We also performed a similar sorting to (e) above by first binning all response times into four bins, 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 non-repeated trials in each bin. Results of the second analysis were similar to the analysis in Figure 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 then 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:
\[ y(t) = \sum_{i=1}^{n} h_i(t) \ast x_i(t) + n(t) \]

\( y(t) \) 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 seconds before stimulus onset to 17 seconds after onset, at discrete intervals of 1 second. 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. Since this analysis only considers activation around the peak point — although differences may be present across the entire time course— we have 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** (Grill-Spector et al., 1999): To measure the magnitude of repetition suppression we calculated the RS ratio: \( \% \text{Signal}_{\text{Repeated}} / \% \text{Signal}_{\text{Nonrepeated}} \). The signal was measured as the average response of the peak of the hemodynamic response (4-6s 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 less than one indicate suppression of the response to repeated stimuli compared to nonrepeated stimuli.
Repetition suppression ratios were calculated for individual voxels (Figure 3c) and for region of interest (ROI) analyses (Figures 4,5).

**Priming Ratio:** To measure the level of priming, we calculated an analogous priming ratio from the average response time (RT) for repeated and nonrepeated trials. The priming ratio was defined as: \( \frac{RT_{\text{repeated}}}{RT_{\text{nonrepeated}}} \). A ratio of 1 indicates no priming and values that are significantly less than one reflect priming (faster performance for repeated trials).

**Regression Analyses:** We performed a linear regression analysis of the priming ratio vs. RS ratio for repeated trials. The RS ratio was calculated from the mean response across the left and right hemispheres. Results reported in Table I 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 regions of interest (ROIs) for each subject using an independent block-design localizer scan (see Methods). Figure 2 illustrates 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 Figure 2) (Grill-Spector et al., 2003; Grill-Spector et al., 2000; Grill-Spector et al., 1999).

**Basic Repetition Suppression Effect**

We observed significant RS (nonrepeated > repeated images, $p < 0.001$, t-test) for each subject in both of our object-selective ROIs (Figure 3). This RS was observed for the majority of the voxels in both ROIs (Figure 3c). 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 SEM in LO and a mean of 0.70±0.011 in pFus. Both distributions were significantly less than one 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 (Figure 3b, 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 out of 14 hemispheres at $p < 0.05$, uncorrected. After applying Bonferroni correction for multiple comparisons, only 1/14 comparisons was 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 SEM; 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
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studies (Grill-Spector et al. 1999, Grill-Spector and Malach 2001) and validate the notion that RS in object selective cortex is distinct from adaptation phenomena observed in early visual cortex (Engel and Furmanski, 2001, Boynton and Finney, 2003).

Whether a given image was a target or non-target (feline or non-feline) did not affect the level of RS. This was assessed by applying a 2-way ANOVA on the data from each ROI, using as factors repeated vs. nonrepeated trials, and target vs. 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, \( p > 0.49 \)), nor an interaction between the type of image (target/non target) 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-tests 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, \( p = 0.193 \)), nor 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 inter-stimulus interval may include fixation trials without any
images). For both behavioral and fMRI data, we used responses for correct trials only.

Repetition suppression progressively increased with successive repetitions,
plateauing at about the fifth repetition (Figure 4b, top). Repetition suppression was
strongest after no intervening trials and zero seconds ISI (Figures 4b, 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 (Figure 4a) and follow a
similar trend.

**Repetition Suppression During Brief Image Presentations**

The results described so 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 which is not
required for classification, or which 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 msec after the onset of the mask (Kovacs et al.,
1995; Keysers and Perret, 2001, 2002). Further, 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.

Prior to scanning, we determined the minimum presentation duration required for 85% correct performance for each subject, and used this duration in the scanner (Figure 1, Methods). This performance level was optimal because it was significantly above chance performance, but also measurably 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 (Figure 5a). 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 \( p = 0.32 \); two-tailed t test). Since 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 (Figure 5b) 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 (Figure 5). However, for brief presentations we did not find maximal adaptation for the shortest intervals between
repeats or for no intervening stimuli between repeats, (Compare Figures 4 and 5).

We observed lower RS levels for briefly-presented images (67, 85, or 101 ms) compared to long presentations (2 sec). 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 to the second (one-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 afterwards. However, because of the greater level of RS during the first experiment, some post-recognition processes may contribute to the magnitude of the RS effect when stimuli are present for a long time.

Quantitative Analysis of the Relationship between Repetition Suppression 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 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.

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 Ia). 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 Ib) 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 Repetition suppression**

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 non-repeated trials (Figure 6). We found that, for long image presentations, LO response correlated with response time even for nonrepeated data (Figure 6a). 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). Since 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 then performed an analysis of variance on our data taking as factors trial type (repeated/nonrepeated) and reaction time (RT) bin. 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 to 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). By 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 (Figure 6). However, there was no significant effect for pFus in
Experiment 1 or any effect in either ROI in Experiment 2 (F(3,92) ≤ 0.89, \( p \geq 0.45 \); Table II). Finally, we found no significant interaction between repetition and response times in any of the ROIs or experiments (Table II).

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.

DISCUSSION

Dynamics of Repetition Suppression

The repetition suppression 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 to later repetitions (Figure 4). This measured dependence of RS on repetition parameters is qualitatively similar to effects reported in single units in macaque 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 the current study (e.g., passive viewing or a 1-back matching, see Grill-Spector et al., 1999; Grill-Spector and Malach, 2001) and with event-related fMRI studies examining the effect of repetition parameters (Jiang et al., 2000; Henson et al., 2004; Henson 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. Our present 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 Repetition Suppression**

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 non-object masks reduce the firing rates of shape-selective cells. Similar effects of masking on BOLD signal have been reported in human object-selective cortex (Zago et al., 2005; Grill-Spector et al., 2000). It has also been demonstrated that the response in these ROIs to the scrambled objects used as a mask are small compared to the response to objects (Malach et al., 1995; Grill-Spector et al., 2003). 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 Zago et al., 2005; James et al., 2000). Evidence from primate neurophysiology suggests that the recognition process may contain several distinct stages (Tamura and Tanaka, 2001; Sugase et al., 1999) that allow for progressively finer discriminations of object identity. These studies find an early component between ~50-150 ms and a later component between ~150-500 ms. While there may be persistent activity in object-selective cortex after the appearance of the mask, recent data by Keysers and Perrett (2001, 2002) suggest that this persistent activity shuts down within 60ms 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 127-150ms 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 (250-1900 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 (Figure 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 (Tamura and Tanaka, 2001; Sugase et al., 1999).

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 (Figure 1), the second experiment may include later components of recognition, and therefore differences between experiments would relate to post-recognition 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 sub-threshold stimuli that were repeated, compared to 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.

Since 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 due to masking, there may be additional suppression from having viewed the images during the first experiment. However, on average 16 months had elapsed between Experiments 1 and 2 for each subject. Given that long-term RS has not been reported for durations longer than three 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 which parametrically varied contrast (Avidan et al., 2002) or stimulus duration (Zago et al., 2005), or which 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 (compare Figures 5 and 4); 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 Repetition Suppression 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., Buckner and Schacter, 1998, Wiggs and Martin 1998, Koutstall et al. 2001, Henson 2003, Lustig and Buckner 2004, 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 Repetition suppression**

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, since 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. Repetition suppression 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; Miller 1993); and/or reduced amplitude of neuronal response (Miller and Desimone, 1994). Since 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, Henson, Martin, 2006). Using parametric manipulations such as in the present study, future experiments may be able to further reveal the complex relationship between these functional neuronal dynamics and behavior.

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Competing Interests

The authors declare that they have no competing financial interests.
FIGURE LEGENDS

Figure 1. Experimental design a) Example trial: Experiment 1: Each trial lasted 2 seconds: 1750 ms in which an image appeared with a 250 ms blank period between trials. Experiment 2: Each trial lasted 2 seconds: images were presented briefly and were followed by a random scrambled pattern for the remainder of the trial. The duration of the image was determined separately for each subject. An example psychophysical curve for one subject is illustrated at right. The red circle indicates the duration used during scanning. b) Repetition parameters: Behavioral performance and fMRI responses were analyzed according to the image presentation number, number of intervening stimuli between repeats, and time between repeats. The value of each parameter for each image is indicated above the image.

Figure 2. Object-selective regions and ROI location on the inflated brain of one subject. Inflated brain of a representative subject demonstrating regions which responded more strongly to animal images than scrambled animal images. Color maps are the negative log base 10 of the significance value of two-sided t-tests (thresholded at $p < 10^{-5}$). Abbreviations: LO: lateral occipital; pFus: posterior fusiform.

Figure 3. Adaptation Effect in Experiment 1. a-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 standard error of the mean (SEM) 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 SEM across subjects. c) Distribution of repetition suppression ratios across voxels in three ROIs. X-axis denotes the RS ratio. Dashed line indicates RS ratio of 1 (no RS).

Figure 4. Effect of repetition parameters on RS and priming summarized for
Experiment 1. a) Mean response time; b) BOLD response amplitude for pFus (center), and LO (right). Error bars indicate standard error of the mean between subjects. BOLD responses are averaged across hemispheres. Asterisks indicate significantly lower than first presentation at p<0.05; Dashed line indicates the response to the first presentation. Top: Data sorted by presentation number; Middle: Sorting by intervening stimuli between repeats. Bottom: Sorting by time between repeats.

Figure 5. Effect of repetition parameters on RS and priming summarized for Experiment 2. a) Mean behavioral responses; b) BOLD response amplitude for pFus (center) and LO (right). Error bars represent standard error of the mean across subjects. Conventions are the same as Figure 4.

Figure 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 the data for one subject and one response-time bin.

Figure 7. Dual repetition / response-time analysis. Data are sorted first into repeated and nonrepeated correct trials, then grouped into four response time bins for each subject. The first response time bin represents the fastest quartile of correct trials for each subject. Error bars indicate SEM across subjects. a) Results across subjects for Experiment 1. b) Results across subjects for Experiment 2.

TABLE CAPTIONS
Table I. Summary of regression analysis results across all experiments, ROIs, and sortings of the data. Regression analyses were run on data pooled across subjects. Slope: slope of best-fit (least-squares) regression line. Rows in italic indicate statistically-significant regressions a) Results for Experiment 1; b) Results for Experiment 2.

Table II. Results of ANOVA analysis on joint response-time, repetition sorting of data
from both experiments. Sum Sq. = sum of squares, d.f. = degrees of freedom, Mean Sq. = mean squared. a) Results for Experiment 1; b) Results for Experiment 2.
REFERENCES


Epstein R, Graham KS, Downing PE Viewpoint-specific scene representations in


A  

**Experiment 1**

![Image 1]  
1750 ms  

Response: “feline" or “not a feline"

**Experiment 2**

![Image 2]  
83-101 ms

B

**Presentation Number**

|   | 1 | 1 | - | 2 | 1 | - | 1 | 2 | - | 3 |

**Stimuli Between Repeats**

|   |   |   | 0 |   |   | 4 |   | 3 |

**Time Between Repeats, seconds**

|   |   |   | 2 |   |   | 12 |   | 10 |

Image Mask

Sayres & Grill-Spector  Figure 1
Sayres & Grill-Spector Figure 2
Sayres & Grill-Spector  Figure 3
Sayres & Grill-Spector Figure 4
A. Experiment 1

Nonrepeated

Repeated

Subject

B. Experiment 2

Nonrepeated

Repeated

Subject
A. Experiment 1

B. Experiment 2

Sayres & Grill-Spector Figure 7
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