Brief Communications

Dissociating Task Performance from fMRI Repetition Attenuation in Ventral Visual Cortex

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Repeated visual stimuli elicit reduced neural responses compared with novel stimuli in various brain regions (repetition attenuation). This effect has become a powerful tool in fMRI research, allowing researchers to investigate the stimulus-specific neuronal representations underlying perception and cognition. Repetition attenuation is also commonly associated with behavioral priming, whereby response accuracy and speed increase with repetition. This raises the possibility that repetition attenuation merely reflects decreased processing time. Here, we report a full dissociation between repetition attenuation and behavioral performance by varying the task performed on identical visual stimuli. In the scene task, observers judged whether two photographs came from the same scene, and in the image task, they judged whether the two photographs were identical pixel for pixel. The two tasks produced opposite patterns of behavioral performance: in the scene task, responses were faster and more accurate when the photographs were very similar, whereas, in the image task, responses were faster and more accurate when the photographs were less similar. However, in the parahippocampal place area (PPA), a scene-selective region of ventral cortex, identical repetition attenuation was observed in both tasks: lower neural responses for the very similar pairs relative to the less similar pairs. Whereas the PPA was impervious to task modulation, responses from two frontal regions mirrored behavioral performance, consistent with their role in decision-making. Thus, although repetition attenuation and performance are often correlated, they can be dissociated, suggesting that attenuation in ventral visual areas reflects stimulus-specific processing independent of task demands.

Key words: **repetition attenuation; fMRI-adaptation; repetition suppression; parahippocampal place area; repetition priming; decision making**

Introduction

The repetition attenuation effect in functional magnetic resonance imaging (fMRI), also known as fMRI-adaptation or repetition suppression, refers to the decreased blood oxygenation level-dependent (BOLD) response observed when a stimulus is repeated (Schacter and Buckner, 1998; Wiggs and Martin, 1998; Henson, 2003; Grill-Spector et al., 2006). This effect has been widely used to study neuronal selectivity in different regions of ventral visual cortex (Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2001; Epstein et al., 2003; Rotshtein et al., 2005), and to explore the impact of attention on visual representations (Murray and Wojciulik, 2004; Yi et al., 2004; Yi and Chun, 2005). By repeating a stimulus over multiple intervening items and longer delays, repetition attenuation has also been used to study repetition priming, a form of implicit memory (Buckner et al., 1998; Dobbins et al., 2004; Wig et al., 2005; Turk-Browne et al., 2006).

Because repetition attenuation may reflect changes in stimulus-selective neuronal subpopulations, it affords greater spatial resolution than other fMRI designs (Grill-Spector et al., 2006). Accordingly, it has spurred new discoveries about the specificity of representations in different ventral regions. For example, object representations in the lateral occipital complex reflect perceived shapes rather than simple contours (Kourtzi and Kanwisher, 2001) and are relatively invariant to changes in size and location (Grill-Spector et al., 1999), scene representations in the parahippocampal place area (PPA) are viewpoint-specific (Epstein et al., 2003), and face representations in the fusiform face area are invariant to certain physical changes as long as identity is preserved (Rotshtein et al., 2005).

When stimuli are repeated, however, tasks performed on them become easier, resulting in decreased response times. This repetition priming effect is often correlated with the degree of repetition attenuation in frontal and temporal regions (Maccotta and Buckner, 2004; Wig et al., 2005; Zago et al., 2005; Turk-Browne et al., 2006). Because of this correlation, previous studies and existing models of repetition attenuation (Grill-Spector et al., 2006) have been unable to determine whether attenuation in ventral regions per se facilitates behavioral performance, or whether such attenuation is the result of facilitated behavioral performance. In other words, repetition attenuation may reflect an overall shorter processing time or reduced effort for any repeated stimulus, rather than stimulus-specific neuronal changes. This issue is especially important for understanding how top-

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down feedback contributes to repetition attenuation (Friston, 2005).

If repetition attenuation reflects perceptual processes independent of task demands, comparable repetition attenuation should be observed even in a task where repeated stimuli elicit slower responses. In contrast, if repetition attenuation solely reflects the amount of stimulus processing required to reach a task decision, then attenuation should reverse in concert with behavioral response latencies. A third possibility is that perceptual and task-related processes will interact, and attenuation should be reduced when the behavioral response pattern reverses. By varying the task performed on identical visual stimuli, here we report a full dissociation between repetition attenuation and behavioral performance in the scene-selective region of the ventral cortex, the PPA.

Materials and Methods

Observers viewed pairs of very similar and less similar scene photographs. Given scene-selectivity in the PPA (Epstein and Kanwisher, 1998; Epstein et al., 2003), two very similar photographs should produce a lower BOLD response than two less-similar photographs, reflecting greater baseline repetition attenuation. We manipulated behavior by choosing two tasks that would produce opposite patterns of performance given identical stimuli. Because repetition attenuation depends on attention to both initial and repeated stimuli (Yi and Chun, 2005), we used tasks that required observers to attend and compare both photographs in a pair. In the scene task, observers judged whether two photographs came from the same scene, and in the image task, they judged whether the two photographs were identical pixel for pixel. We examined repetition attenuation in the PPA under both tasks.

Participants

Eight paid observers (five females) were recruited from the Yale University community. All were right handed and had normal or corrected-to-normal vision. Informed consent was obtained from all observers and the study was approved by the Human Investigation Committee of the Yale University School of Medicine.

Design and procedure

Main experiments. Each trial in the main experiment consisted of a sequential presentation of two scene photographs. Each photograph was immediately followed by a phase-scrambled scene mask. All images subtended 9.4 × 9.4° of visual angle.

In the two experimental conditions, the two photographs of a given trial were parts of the same scene, and they covered either a very similar area of the scene with 83% image overlap (very similar) (see Fig. 1*A*, left), or somewhat different areas of the scene with 50% image overlap (less similar) (see Fig. 1*A*, right). Different trials used photographs depicting completely different scenes and a given scene was never repeated in the experiment. Two filler conditions were included to reduce response bias in the experimental conditions: one filler condition contained a repetition of the same scene photograph and there was, thus, 100% image overlap between the two photographs in the trial (identical, example not shown); and a second filler condition contained two photographs from two different scenes, and there was 0% overlap between the two photographs in the trial (different, example not shown). In the scene task, observers had to judge, with both speed and accuracy emphasized, whether the two photographs originated from the same scene. The correct response was "yes" for the very similar, less similar, and identical conditions, and "no" for the different condition. In the image task, observers had to judge, also with speed and accuracy, whether the two photographs were identical. The correct response in this task was "yes" for the identical condition and "no" for the very similar, less similar, and different conditions. Thus, the correct response was always the same for the two experimental conditions of interest, with both requiring "yes" responses in the scene task and "no" responses in the image task. Observers made keypress responses with their right index finger or their right middle finger. Key assignment was counterbalanced across observers to eliminate finger-related differences in response speed. Although we did not include the two filler conditions (i.e., the identical and the different conditions) in our main analyses because of differences in response demands, results from these filler conditions are consistent with our main results and conclusions. These data are reported in supplemental Figures 1–3 and supplemental Results (available at www.jneurosci.org as supplemental material).

Each stimulus trial lasted 3 s and consisted of 500 ms of blank screen with fixation, 200 ms presentation of the first scene photograph without fixation, 50 ms presentation of a phase scrambled scene mask without fixation, 350 ms presentation of a blank screen with fixation, 200 ms presentation of the second scene photograph without fixation, 50 ms presentation of a different phase scrambled scene mask without fixation, and 1650 ms presentation of a blank screen with fixation, during which responses were collected. The fixation dot was not presented with either the photographs or the masks to encourage observers to attend to the stimuli globally (i.e., to prevent observers from only encoding and detecting a relative change in position between the fixation dot and the surrounding region of the photograph in the image task). Eye movements were unlikely in this design because stimuli were presented too briefly for a saccade to be completed before the photograph was removed. We also included fixation trials in which only the fixation dot was present during the 3 s trial period. Each scanning run consisted of, in order, a 3 s fixation period, four practice trials (the last two serving to counterbalance trial history at the beginning of the run), 125 event-related trials, two filler trials (to counterbalance trial history at the end of the run), and a 6 s fixation period at the end. The practice trials, filler trials, and fixation periods were excluded from the analysis. There were 25 event-related trials for each of the five conditions. As in previous studies (Kourtzi and Kanwisher, 2001), the presentation order of the different trial types was counterbalanced within each run such that trials from each condition, including the fixation trials, were preceded and followed equally often by trials from each of the other conditions two trials back and two trials forward. To further balance for order effects, five different orders were created by rotating the conditions. Each observer was scanned with four of the five orders; the run sequence was further rotated across observers. In two of the four runs, observers performed the scene task and in the other two runs, they performed the image task. Task order was counterbalanced across different observers. Each scan lasted 6 min and 42 s.

We used four sets of scene photographs, each containing 100 different indoor scenes and 100 different outdoor scenes. The four sets were assigned to the four functional runs (two for the scene task and two for the image task). For each observer and each functional run, we first randomized the order of the scenes in a set and then assigned them according to the randomized order to each stimulus trial of the run. To prevent observers from adapting to the scene mask and suppressing it, we generated 200 different phase-scrambled scene masks and randomly chose two different masks for each trial.

PPA localizer scan. To localize the PPA, we presented observers with blocks of grayscale scene and face photographs (Aguirre et al., 1996; Epstein and Kanwisher, 1998). The scene photographs resembled those used in our main experiments but never appeared in the main experiment. There were 18 16 s stimulus blocks within a scan, including six scene blocks, six face blocks, and six blocks of phase scrambled scenes. There were also three 8 s fixation blocks interleaved between every nine stimulus blocks. Each stimulus block contained 20 different exemplars of the same stimulus category, each presented for 750 ms followed by a 50 ms blank interval. To ensure attention on the displays, observers fixated at the center fixation dot and detected a slight spatial jitter, occurring randomly in one of every 10 photographs. The localizer scan lasted 5 min and 12 s.

The phase-scrambled scenes were included to contrast with the intact scenes in an attempt to localize regions in the lateral occipital cortex that may be involved in scene processing. In five of our eight observers, we failed to obtain any significant activation in the lateral occipital cortex under this contrast. Consequently, following previous conventions, we focused our region of interest (ROI)-based analysis on the PPA.

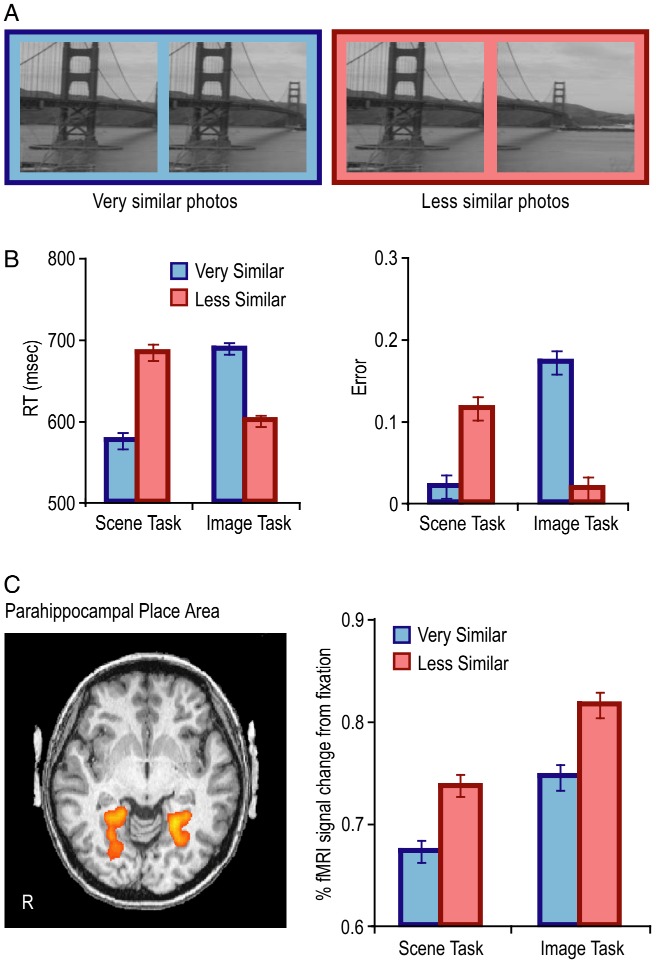

Figure 1. ***A***, Example stimuli used. Each trial consisted of a sequential presentation of two scene photographs that were immediately masked. The two photos were very similar (83% overlap, left) or less similar (50% overlap, right). In the scene task, observers judged whether the two photographs originated from the same scene. In the image task, observers judged whether the two photographs were identical. ***B***, Behavioral performance from the scene and image tasks. Response times from the correct trials are shown on the left and error rates are shown on the right. In the scene task, observers were faster and more accurate when the two photographs were very similar than when they were less similar. In the image task, the pattern of performance was reversed. Error bars reflect SEs of the differences between less similar and very similar conditions across observers (henceforth referred to as within-subject SEs). ***C***, fMRI responses from the parahippocampal place area. Left, The bilateral PPA ROI from an example observer. Right, PPA responses for the scene and image tasks. In both tasks, PPA responses were greater for the less similar image pairs than for the very similar image pairs, showing a repetition attenuation effect that is independent of stimulus processing time. Error bars indicate within-subject SEs.

MRI procedures

Data acquisition. Observers laid on their backs inside a Siemens (Erlangen, Germany) Trio 3T scanner and viewed the back-projected liquid crystal display with a mirror mounted inside the head-coil. Stimulus presentation and behavioral response collection were controlled by an Apple (Cupertino, CA) PowerBook G4 running Matlab with PsychToolbox extensions (Brainard, 1997; Pelli, 1997). Standard protocols were followed to acquire the anatomical images. The same gradient echo pulse sequence (echo time, 25 ms; flip angle, 90°; matrix, 64×64) was used for the main experiment and the localizer scan, with repetition times of 1.5 s and 2.0 s, respectively. Twenty-four 5-mm-thick (3.75×3.75 mm in-plane, 0 mm skip) axial slices parallel to the anterior commissure–posterior commissure line were collected; 268 and 156 volumes were acquired for the main and the localizer scans, respectively.

Data analysis. fMRI data were analyzed using BrainVoyager QX (Brain Innovation, Maastricht, Netherlands). Data preprocessing included slice acquisition time correction, three-dimensional motion correction, linear trend removal, and Talairach space transformation (Talairach and Tournoux, 1988).

Multiple regression analyses were performed separately on each observer to model data from the PPA localizer run. Individual bilateral PPA ROIs (Fig. 1*C*, left) were defined as regions in the left and the right parahippocampal gyrus and collateral sulcus whose activation was greater for scenes than for faces ($p < 0.001$, uncorrected) (Epstein et al., 2003). The PPA ROI was identified in each observer (mean Talairach coordinates were right +23/−43/−4, and left −22/−43/−4). Using the same contrast, we were also able to localize an additional bilateral scene-selective region in the transverse occipital sulcus/intraparietal sulcus in six of our observers. The data from this region are reported in supplemental Figure 2 and supplemental Results (available at www.jneurosci.org as supplemental material). Another scene-selective region sometimes observed in scene versus face contrasts is the retrosplenial cortex. However, we were only able to localize this region bilaterally in four of our observers and, thus, the results were not interpretable.

We overlaid each individual's PPA ROI onto the data from the main experiment and extracted the averaged time course over all voxels in the ROI for the two conditions of interest, separately for the scene and the image tasks. For each run of the main experiment, the averaged BOLD signal across the 25 trials of each condition at 10 peristimulus time points (totaling 15 s) was calculated. As in previous studies (Kourtzi and Kanwisher, 2001), these event-related responses were converted to percent signal change for each stimulus condition by subtracting and dividing by the corresponding value of the fixation condition. The peak responses were then derived by collapsing the event-related responses of all conditions and determining the time point of greatest signal amplitude. Peak responses were extracted for each individual and condition, and combined into second-level statistical analyses.

In the whole brain, we used a random-effects general linear model (GLM) in an exploratory manner to identify regions that mirrored the behavioral response pattern. We also identified brain regions that showed a main effect of image similarity (greater response for the less similar than the very similar photograph pairs in both tasks) using a second random-effects GLM.

Results

In the scene task, behavioral responses were faster and more accurate when the two photographs were very similar than when they were less similar (p values < 0.05) (Fig. 1*B*). In the image task, the opposite pattern of responses was observed: responses were slower and less accurate when the two photographs were very similar than when they were less similar (p values < 0.05) (Fig. 1*B*). There were significant crossover interactions between task and response time and between task and response accuracy (p values < 0.001); however, the overall response time and accuracy did not differ between the two tasks (p values > 0.17).

To examine scene-related repetition attenuation in the PPA, we conducted an ROI-based analysis. Overall, neither peak PPA response amplitude nor its response latency differed between the two tasks (p values > 0.23). The lack of overall differences in neural and behavioral responses suggests that task difficulty and task demands were well matched between the two tasks.[a] In both

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[a] Our scene task required the observers to attend to and comprehend the scene images as a whole, whereas our image task required the matching of scene images pixel by pixel. Thus, more holistic and global processing would be necessary for the scene task and more featural and local processing would be necessary for the image task. As a result, observers might have used different strategies in the two tasks. For example, they might have attended more to the edges of the scene photographs to help them perform pixel-by-pixel matching of the scenes in the image task, and attend more to the overall scene photographs in the scene task. Although observers were explicitly instructed to fixate at the center and the stimulus presentation was brief to prevent eye movements, we did not measure eye movements and therefore could not know exactly where observers looked during the two tasks and whether they changed their direction of gaze across trials/tasks. Despite these uncertainties and differences associated with the two tasks, we obtained comparable overall PPA responses for the two tasks. If anything, the overall PPA response was slightly higher in the image than in the scene task, despite more in-depth scene processing in the scene task. Thus, differences in eye gaze and strategy in the two tasks, if they existed, did not seem to affect PPA response in a significant way.

tasks, PPA response amplitudes were significantly higher for the less similar than the very similar conditions (p values < 0.05), and there was no interaction between task and stimulus condition ($p > 0.77$). Thus, repetition attenuation for scenes in the PPA was the same for both tasks, although there was a full crossover interaction, that is, a complete reversal, in behavioral responses.

In a whole-brain random-effects analysis, we identified two brain regions that mirrored the behavioral response pattern (greater response amplitude for the less similar than the very similar conditions in the scene task, and lower response amplitude for the less similar than the very similar conditions in the image task): one in the anterior cingulate cortex (ACC) and the other in the left insula (Fig. 2*A*,*B*). Both of these regions have previously been linked to decision-related processes (Miller and Cohen, 2001; Maccotta and Buckner, 2004; Wig et al., 2005). Peak response latencies did not differ between the two tasks in either frontal region (p values > 0.68). Response amplitudes in these regions during the scene task were similar to the PPA (i.e., higher for the less similar image pairs than for the very similar image pairs; ACC, $p < 0.01$; left insula, $p = 0.05$). However, during the image task, these regions demonstrated the reverse pattern: the very similar image pairs showed a greater response amplitude than the less-similar image pairs (p values < 0.05), in line with the behavioral responses, and different from the PPA. A region of the posterior cingulate cortex showed the opposite interaction (scene task, very similar > less similar; image task, less similar > very similar), consistent with its role in the default network (see supplemental Fig. 3 and supplemental Results, available at www.jneurosci.org as supplemental material).

In a second whole-brain random-effects analysis, we found that only one region on the right parahippocampal gyrus showed a main effect of similarity (less similar > very similar) across task (Fig. 2*C*). This parahippocampal region was part of the individually defined PPA ROI in three of the eight observers and was adjacent to the remainder observers' PPA ROIs (when we lowered the threshold from $p < 0.001$ to $p < 0.005$, the right parahippocampal region identified in our whole-brain analysis overlapped with the individually defined PPA ROIs in seven of our eight observers). Consistent with our PPA ROI-based analysis, responses in this region were lower for the very similar than for the less similar conditions in both tasks (p values < 0.05), and there was no interaction between scene similarity and task ($p > 0.67$).

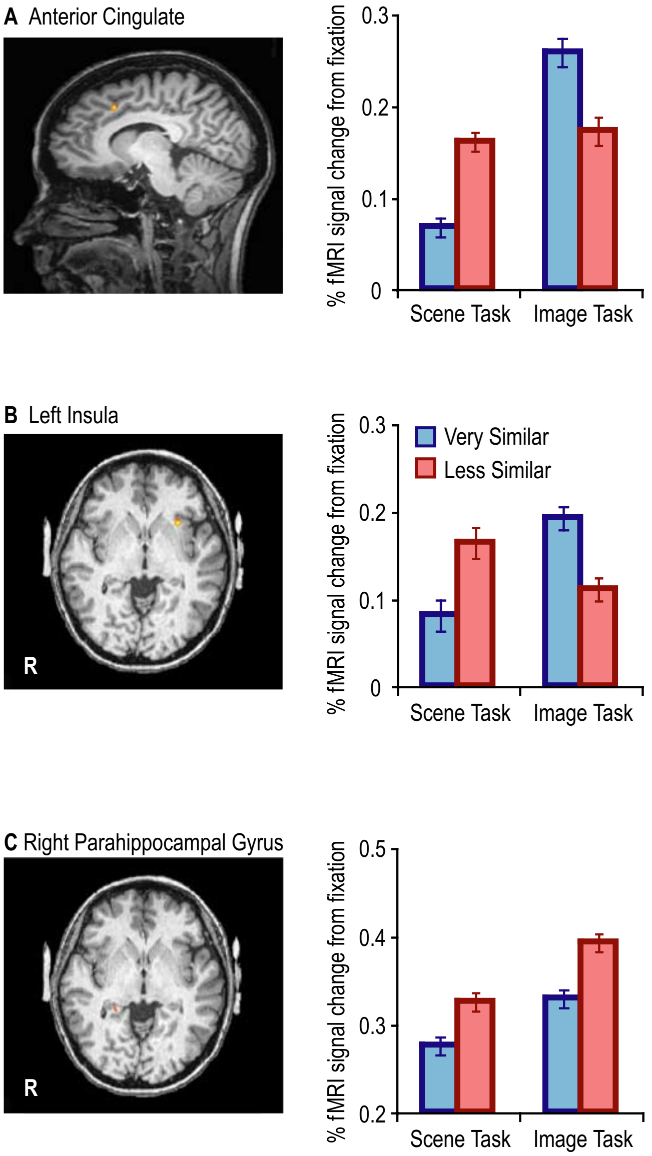

Figure 2. ***A***, ***B***, Brain regions identified in a random effects whole brain analysis ($p < 0.001$) that mirrored the behavioral response pattern. In both the anterior cingulate cortex (***A***; +9/+17/+40) and the left insula (***B***; −27/+14/0), responses were lower for the very similar than for the less similar photograph pairs in the scene task, and were greater for the very similar than for the less similar photograph pairs in the image task, showing an fMRI response pattern that was modulated by task and decision related processes (error bars indicate within-subject SEs). ***C***, A brain region identified in a random-effects whole-brain analysis ($p < 0.001$) that tracked scene similarity in both tasks. In the right parahippocampal gyrus (+24/−37/+1), responses were lower for the very similar than for the less similar scene photograph pairs in both tasks, consistent with results from the ROI-based PPA analysis in Figure 1*C*. Error bars indicate within-subject SEs. For illustration purposes, statistical maps are depicted at $p < 0.005$.

Discussion

We have thus found evidence for both task-independent fMRI repetition attenuation in ventral visual cortex and task-dependent fMRI responses in the frontal cortex. These results provide some of the strongest evidence to date that repetition attenuation measures stimulus-specific neuronal representations in the ventral visual cortex, rather than reduced processing time or effort. These results also indicate that the neural mechanisms underlying fMRI repetition attenuation may be different across brain regions, consistent with Schacter et al. (2007).

When observers had to decide that two very similar photographs were different in the image task or that two less similar photographs were from the same scene in the scene task, more processing of the photographs was required to reach a task decision. Because the degree (and specificity) of processing in the visual cortex has been directly related to the speed and accuracy of perceptual decision making (Ditterich et al., 2003; Heekeren et al., 2004), we might have expected to find greater PPA activity in the two slowest conditions. But we did not. Thus, although repetition attenuation in the ventral visual cortex can facilitate processing, which leads to behavioral priming, decision-related processes do not always modulate stimulus processing in the ventral visual cortex in a top-down feedback manner. In other words, information processing in our task involved discrete, rather than interactive, stages of operation. When information processing was completed by perceptual mechanisms in the ventral cortex, it was passed on to decision mechanisms in the frontal/prefrontal cortex with minimal feedback to the ventral cortex. As a result, our manipulation of task difficulty only influenced activity within these subsequent stages of information processing.

Consistent with this idea, although task difficulty did not modulate repetition attenuation in ventral visual cortex, other factors that affect the initial input into these cortical regions can modulate repetition attenuation. Modulatory factors include attention, emotion, and context (Dobbins et al., 2004; Eger et al., 2004; Ishai et al., 2004; Murray and Wojciulik, 2004; Yi et al., 2004; Vuilleumier et al., 2005; Yi and Chun, 2005). For example, attention to the initial and the repeated presentations of a stimulus is necessary for repetition attenuation to be observed (Yi and Chun, 2005).

Additional evidence that repetition attenuation in the ventral visual cortex is task independent has been reported by Sayres and Grill-Spector (2006) (see also Ganel et al., 2006). They found significant repetition attenuation when response times for repeated and nonrepeated stimuli were matched. However, because different stimulus sets were used for repeated and nonrepeated conditions, inherent stimulus differences may have contributed to this result. Our manipulation allowed us to completely dissociate behavioral performance and repetition attenuation. Consequently, we were able to observe both task-independent fMRI repetition attenuation in the ventral visual cortex and task-dependent fMRI responses in the frontal cortex.

In summary, our results indicate that the mechanisms involved in forming perceptual representations in category-selective regions of ventral visual cortex may be mostly impervious to subsequent task-related processes, whereas those that use the output of these areas may not. With our task manipulations, the information processing stages of perception and decision-making were thus discrete rather than interactive.

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