Spatially Specific fMRI Repetition Effects in Human Visual Cortex

Scott O. Murray,[1] Cheryl A. Olman,[2] and Daniel Kersten[2]
[1]*Department of Psychology, University of Washington, Seattle, Washington; and* [2]*Department of Psychology, University of Minnesota, Minneapolis, Minnesota*

Murray, Scott O., Cheryl A. Olman, and Daniel Kersten. Spatially specific fMRI repetition effects in human visual cortex. *J Neurophysiol* 95: 2439–2445, 2006. First published January 4, 2006; doi:10.1152/jn.01236.2005. The functional MRI (fMRI) response to a pair of identical, successively presented stimuli can result in a smaller signal than the presentation of two nonidentical stimuli. This "repetition effect" has become a frequently used tool to make inferences about neural selectivity in specific cortical areas. However, little is known about the mechanism(s) underlying the effect. In particular, despite many successful applications of the technique in higher visual areas, repetition effects in lower visual areas [e.g., primary visual cortex (V1)] have been more difficult to characterize. One property that is well understood in early visual areas is the mapping of visual field locations to specific areas of the cortex (i.e., retinotopy). We used the retinotopic organization of V1 to activate progressively different populations of neurons in a rapid fMRI experimental design. We observed a repetition effect (reduced signal) when localized stimulus elements were repeated in identical locations. We show that this effect is spatially tuned and largely independent of both interstimulus interval (100–800 ms) and the focus of attention. Using the same timing parameters for which we observed a large effect of spatial position, we also examined the response to orientation changes and observed no effect of an orientation change on the response to repeated stimuli in V1 but significant effects in other retinotopic areas. Given these results, we discuss the possible causes of these repetition effects as well as the implications for interpreting other experiments that use this potentially powerful imaging technique.

INTRODUCTION

It has been widely observed that the functional MRI (fMRI) blood oxygen level–dependent (BOLD) response to a repeated stimulus is smaller than a nonrepeated stimulus. This "repetition effect" has become a commonly used tool in functional imaging experiments. Application of the effect—sometimes referred to as "priming" (Buckner et al. 1998; Henson 2003; Henson and Rugg 2003; Naccache and Dehaene 2001; Schacter and Buckner 1998) or "adaptation" (Grill-Spector and Malach 2001; Tolias et al. 2002) based on the assumed underlying neural mechanism—has been used to infer neural selectivity with resolution finer than a single voxel. For example, in a typical fMRI adaptation experiment, an initial stimulus is shown that is presumed to adapt the population of neurons processing that stimulus. After removal of the adapting stimulus, a second stimulus is presented that is either identical to the adapter or transformed in some dimension (e.g., orientation). If the fMRI signal is larger for the transformed stimulus compared with the identical stimulus, neural sensitivity to that dimension is inferred because the transformed stimulus is thought to be accessing a separate, unadapted neural population.

While the use of the effect has been particularly prevalent in higher visual areas of the temporal cortex, repetition effects have also been observed in lower visual areas, such as primary visual cortex (V1). For example, Huettel and McCarthy (2000) showed in retinotopic cortex that the fMRI response to successive presentations of a large checkerboard stimulus is significantly smaller than what would be predicted from the response to a single presentation. It is unclear whether their observed nonlinearity was caused by a neural mechanism such as adaptation or some other component of the BOLD signal. Evidence for a neural mechanism would, at the least, require some form of stimulus specificity.

While there does seem to be some evidence to suggest that neural adaptation is a possible mechanism for repetition effects in V1 (Huettel et al. 2004; Kourtzi et al. 2003b; Tootell et al. 1998), other data call this into question. For example, in several of the repetition studies with large effects in higher visual areas, there have been no associated changes in V1 when, based on the adaptation logic, effects should have also been measured (Grill-Spector et al. 1999; Kourtzi and Kanwisher 2000, 2001; Murray and Wojciulik 2004). In addition, Boynton and Finney (2003) directly examined rapid repetition effects in retinotopic cortex. They used successive presentations of oriented gratings and showed a larger signal for different versus same orientations in extrastriate visual areas, consistent with an adaptation mechanism, but did not observe any differences in V1. The lack of stimulus-specific repetition effects in V1 in the Boynton and Finney study was surprising given the ease with which feature-selective repetition effects have been observed in higher visual areas, the substantial evidence that primate V1 is sensitive to stimulus orientation, and the neurophysiological evidence of pattern-specific adaptation in V1 (Carandini et al. 1998; Movshon and Lennie 1979; Müller et al. 1999; Sclar et al. 1989).

Despite its frequent use as a tool to study visual processing, little is known about the underlying mechanism(s) of fMRI repetition effects. For example, a wide range of timing parameters has been used (hundreds of milliseconds to multiple days; van Turennout et al. 2000), suggesting that there are multiple mechanisms involved. Given the relatively few direct neurophysiological studies of repetition effects (Miller et al. 1991; Müller et al. 1999; Priebe and Lisberger 2002; Priebe et al. 2002), the limited understanding of the relationship between neural activity and the BOLD signal, the wide range of timing parameters that have been used, as well as the varied results in

V1, it is likely that the underlying mechanism(s) are not simple.

One neural property that is well characterized in early visual areas is the mapping of visual field locations to specific areas of the cortex (i.e., retinotopy), making it a good starting point for a systematic study of fMRI repetition effects in early visual cortex. In this study, we used a rapid, event-related design to measure the summed response to successively presented stimulus arrays with local elements in either identical or slightly different retinotopic positions. We examined a range of parameters including the spatial and temporal separation of the repeated elements, whether the elements were attended or unattended, and the orientation relationship of the elements. In choosing the specific values for these parameters, we made few a priori assumptions about the mechanism(s) underlying repetition effects. Instead, our strategy was to use well-established stimulus dimensions (e.g., spatial position), relatively well-understood cortical areas (retinotopic cortex), and parameter values (e.g., stimulus durations) that are typically used in other repetition experiments. We show that rapid repetition effects in V1 are spatially tuned, exist over a range of timing and task parameters, but are not orientation-specific—a pattern of results that suggests there may be nonneural mechanisms underlying rapid repetition effects in V1 measured with fMRI.

METHODS

Subjects

A total of four volunteers (2 female) participated in this study. All had normal or corrected-to-normal vision and were experienced psychophysical observers and included two authors (S. O. Murray and C. A. Olman). Subjects gave informed consent, according to procedures approved by the Institutional Review Board of the University of Minnesota. Each subject participated in four to eight separate imaging sessions (1 session/day) each consisting of 6–10 functional scans.

fMRI acquisition

Scanning was done on a 3-T Siemens Trio scanner at the Center for Magentic Resonance Research at the University of Minnesota. An echo planar sequence [repetition time (TR) = 1 s, echo time (TE) = 30 ms] was used. Ten axial slices (64 × 64 matrix, 220-mm field-of-view, 5 mm thick), where the bottom slice was positioned at the bottom of the temporal lobes, were acquired using a high resolution eight-channel head array coil. The functional data were corrected for head motion using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). All subsequent analyses were performed using a combination of Brain-Voyager (coregistering anatomical and functional scans, conversion of functional data to standardized Talairach space, statistical analyses of localizer scans, and visualization) and custom Matlab code (for generating event-related averages).

Stimuli

In *experiment 1* (position repetition), each stimulus was composed of 16 sparsely distributed, 100% contrast, oriented broadband elements (disks with a diameter of 0.45° that were half black and half white) on a mean gray background (Fig. 1). A minimum of 1.5° separated each of the elements. The elements were distributed within an annulus between 3° and a maximum of 7° from fixation. Each element changed position either inward or outward (randomly determined) with respect to the fixation dot. This maintained spatial separation from the other elements and eliminated any perceived global change (e.g., contraction or expansion). On each trial, the initial
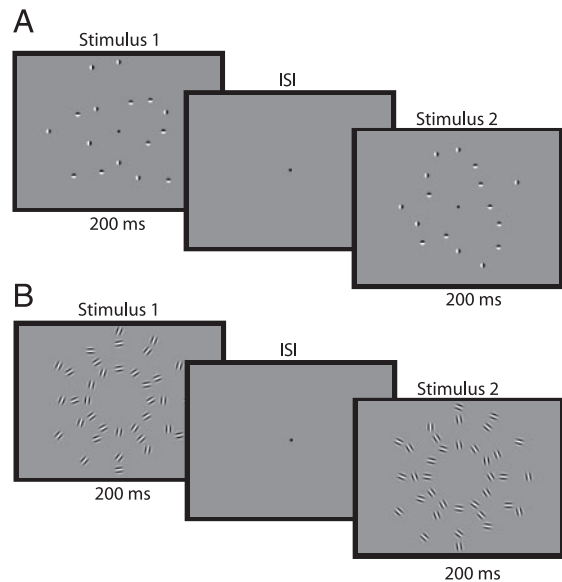

FIG. 1. Schematic of the event-related design and stimuli. *A*: array of oriented, broadband elements was presented for 200 ms, followed by an interstimulus interval (ISI) and presentation of a 2nd stimulus array. In *experiment 1*, "single stimulus" refers to presentation of only 1 array (i.e., no ISI or stimulus 2). Parameters that were varied included amount of spatial displacement of array elements between stimulus 1 and stimulus 2 (0.0, 0.5, and 1.0°), duration of ISI, and whether elements in array were attended or ignored. *B*: 2 arrays of randomly oriented Gabors were presented for 200 ms each and separated by a 200-ms ISI. Each of the Gabors in the 2nd array could either be in identical orientation, rotated ±45°, or rotated ±90°.

starting position of the elements was randomly determined to help avoid any across-trial interaction effects. For *experiment 2* (pattern repetition), a denser array (36 elements) of randomly oriented Gabors (diameter = 2°, spatial frequency = 3 cycles/°) was used. Visual stimuli were displayed with a PC running Presentation software (http://www.neurobs.com) through a LCD projector onto a rear projection screen located behind the head of the subjects and viewed with an angled mirror located above the coil.

For all experiments, a rapid fMRI design was used that presented a trial every 3 s similar to the design of other rapid repetition experiments (Altmann et al. 2004; Epstein et al. 2003; Kourtzi and Kanwisher 2000, 2001; Kourtzi et al. 2003a; Murray and Wojciulik 2004). Trials were ordered using m-sequences (Buracas and Boynton 2002). These are pseudo-random sequences that have the advantage of being perfectly counterbalanced n-trials back (we tested ≤10 trials back), so that trials from each condition, including the fixation condition, were preceded equally often by trials for each of the other conditions. For each of the experiments, there were three trial types (conditions) plus fixation "trials" where no stimulus was presented, serving as a baseline. Each scan consisted of 32 trials per condition and, for each condition described below, each subject was run on a total of four, 400-s scans, resulting in 128 trials per condition.

Experiment 1: position repetition

PART 1: SPATIAL DEPENDENCE. The first part of *experiment 1* tested whether there were spatially dependent repetition effects in V1. The three experimental conditions included *1*) a single stimulus array presented for 200 ms, "single stimulus," *2*) two arrays each presented for 200 ms with elements in the identical positions, "same position," or *3*) two arrays each presented for 200 ms with elements moved to a new location 1° away, "different position." For same position and different position trials, each stimulus was separated by a 200-ms interstimulus interval (ISI). In this initial experiment, subjects were asked to simply indicate whether one or two arrays had been presented

for each trial. The effects of task demands are explored in later manipulations. This first part of *experiment 1* included all four subjects each participating in a single imaging session.

PART 2: SPATIAL TUNING, ISI, AND ATTENTION.   The second part of *experiment 1* addressed three questions. The first was whether the repetition effect was spatially tuned. That is, does the repetition effect depend on the amount of spatial separation of the elements in the repeated stimulus arrays? In all of the manipulations described next, there were three spatial conditions: the elements in the arrays could change positions by 0.0, 0.5, or 1.0°. Based on published estimates of the human cortical magnification factor in V1 (Engel et al. 1997), a 0.5° shift in the visual field results in a position change on the cortex of 2 mm at 4° and 1 mm at 6.5° eccentricity. These estimates of cortical distance in V1 can be compared with our voxel size of 3.4 × 3.4 × 5 mm. Thus on average, the 0.5° position changes are very likely confined to a single voxel in the native resolution of the fMRI images.

The second question addressed was whether the repetition effect was dependent on the amount of time between stimulus pairs. Two ISIs were used: 100 and 800 ms. The third question addressed was whether the repetition effects are affected by task demands. Previous research in temporal-cortical visual areas has shown that there is a much larger repetition effect when attention is directed to the stimulus (Murray and Wojciulik 2004). Within an imaging session, there were two attention conditions. One task (elements "unattended") was a demanding same-different matching task of the perceived brightness of the fixation dot which could change during the presentation of the array elements. During the ISI and between trials, the fixation dot was black. Performance on the fixation task was 80% and 74% for the 100- and 800-ms ISI conditions, respectively. When the elements were unattended, all subjects (including those in later experiments) reported having little awareness of the array elements and reported being completely unaware of whether the elements of the image pair were in the same or different position. The second task was a position discrimination task that required indicating whether the array elements were in the same or different spatial positions (elements "attended"). Performance for the 0.0, 0.5, and 1.0° shifts was 98, 78, and 100%, 100-ms ISI, and 96, 91, and 97%, 800-ms ISI.

Three subjects participated in two separate imaging sessions (the 2 ISI conditions were collected on different days). Each session consisted of nine functional scans lasting 400 s each. There were four scans for each of the attention conditions plus an additional retinotopic localizer scan.

Experiment 2: pattern repetition

Experiment 2 was designed to test whether the repetition effects observed with position could be extended to stimulus orientation—another dimension known to be represented in primary visual cortex. The design was made to be as similar as possible to the position experiments. Because the elements were not changing positions (only orientation), it was possible to have more stimulus elements in the display, helping to increase any signal differences between conditions. Because attention was not shown to have a measurable effect in the position experiments (see RESULTS), the fixation task was used to help promote eye fixation. Similar timing parameters as the position experiments were used—200-ms presentation times for the stimulus arrays and a 200-ms ISI. In choosing these parameters, we did not presume a specific mechanism underlying short-term repetition effects. For example, the duration of the initial stimulus is at least an order of magnitude shorter than what might be used in a typical psychophysical orientation-adaptation experiment. Instead, the timing parameters were chosen to directly compare results to the position experiments and previous rapid fMRI repetition experiments. Two subjects participated in two separate imaging sessions and a total of 12 functional scans for a total of 384 trials/condition/subject.

Data analysis

The analysis of the event-related data followed previous studies using a similar design (Kourtzi and Kanwisher 2000, 2001; Murray and Wojciulik 2004). The time course of MR signal intensity was extracted by averaging the data from all the voxels within the independently defined regions of interest (ROIs). For each scan, the signal intensity across each trial type at each of 12 time-points was averaged. These event-related time-courses of signal intensity were converted to percent signal change by subtracting the corresponding value for the fixation condition and dividing by that value. The resulting time-course for each condition was averaged across trials and subjects. The peak in activity (time-point 4 s after stimulus presentation to allow for the hemodynamic delay) served as the measured response for each condition and used in a repeated-measures ANOVA.

Defining visual areas

Early retinotopic areas were delineated for each subject in separate scanning sessions using standard techniques (Engel et al. 1997; Sereno et al. 1995) identifying vertical and horizontal meridian representations. We were able to reliably localize V1, V2d/V2v, and V3d/VP. Our slice positioning, which was optimized for scanning V1, did not reliably measure V4 or V3A. The data from each experimental session were coregistered to these retinotopic maps and viewed on inflated and flattened cortices. In addition, for each experiment described above, another retinotopic localizer scan was performed using a flickering annulus that occupied the same portion of the visual field (3–7°) as that occupied by the stimulus elements. We restricted our analysis to this portion of retinotopic cortex.

RESULTS

Experiment 1: part 1

Experiment 1 tested whether there were spatially dependent repetition effects and included single stimulus, same position, and different position trials. The average time-course representing the summed response (stimulus 1, ISI, and stimulus 2) is shown in Fig. 2. The single-stimulus condition (i.e., only stimulus 1—no ISI or stimulus 2) had the smallest response, and the different-position condition (the elements changed position by 1.0°) had the largest response—slightly less than doubling the single-stimulus response. The same-position condition, however, was significantly lower than the different-position condition, showing a strong, spatially dependent repetition effect.

Experiment 1: part 2

Part 2 examined whether the repetition effect is spatially tuned and dependent on the length of the ISI (100 and 800 ms). Three different spatial changes were used: 0.0, 0.5, and 1.0°. To manipulate attention, one of two tasks was performed— either a demanding luminance change task at fixation (elements unattended) or reporting whether the elements were in the same or different positions (elements attended).

The data are summarized in Fig. 3, where the response for each condition was converted to a single value (the peak response) and normalized with respect to the 1.0° separation condition to characterize the magnitude of the repetition effect. For example, the response in V1 for the identical (0°) condition is ~80% of the response for 1.0° separation condition. The *top row* summarizes the results for the two ISI conditions, and the
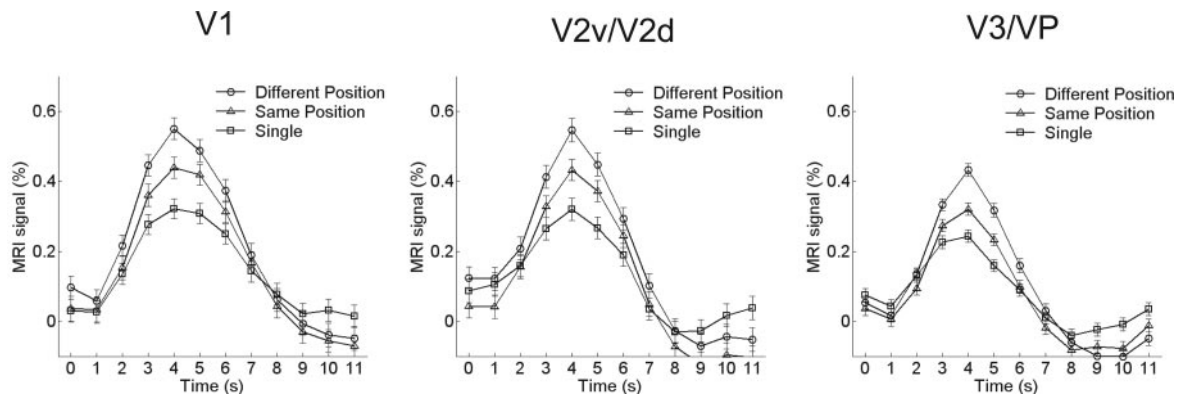
FIG. 2. Results from *experiment 1*. Event-related averages representing the summed response to *1*) a single presentation of a stimulus array, "single," *2*) presentation of 2 arrays with elements in the same position, "same position," and *3*) presentation of 2 arrays with elements shifted by 1.0° to different positions, "different position." Summed response is significantly less for same-position condition compared with different-position condition in all of examined visual areas.

bottom row summarizes the two attention conditions. As is clearly evident from visual inspection of Fig. 3, a repeated-measures ANOVA of the normalized values revealed a significant main effect of the degree of spatial shift of the array elements for all of the analyzed visual areas. In other words, as the amount of spatial separation decreases (i.e., the elements in successive presentations get closer), the magnitude of the repetition effect (suppression) gets larger. No area showed a significant effect of ISI duration, attention, or an interaction.

Experiment 2

Thus far, the results have shown that repetition effects in retinotopic cortex strongly depend on the spatial position of the elements in the stimulus array. *Experiment 2* tested whether the results could be extended to pattern repetitions. In other words, the repetition effects seem to depend on the same area of cortex being stimulated; do they also depend on whether the same visual pattern is used?
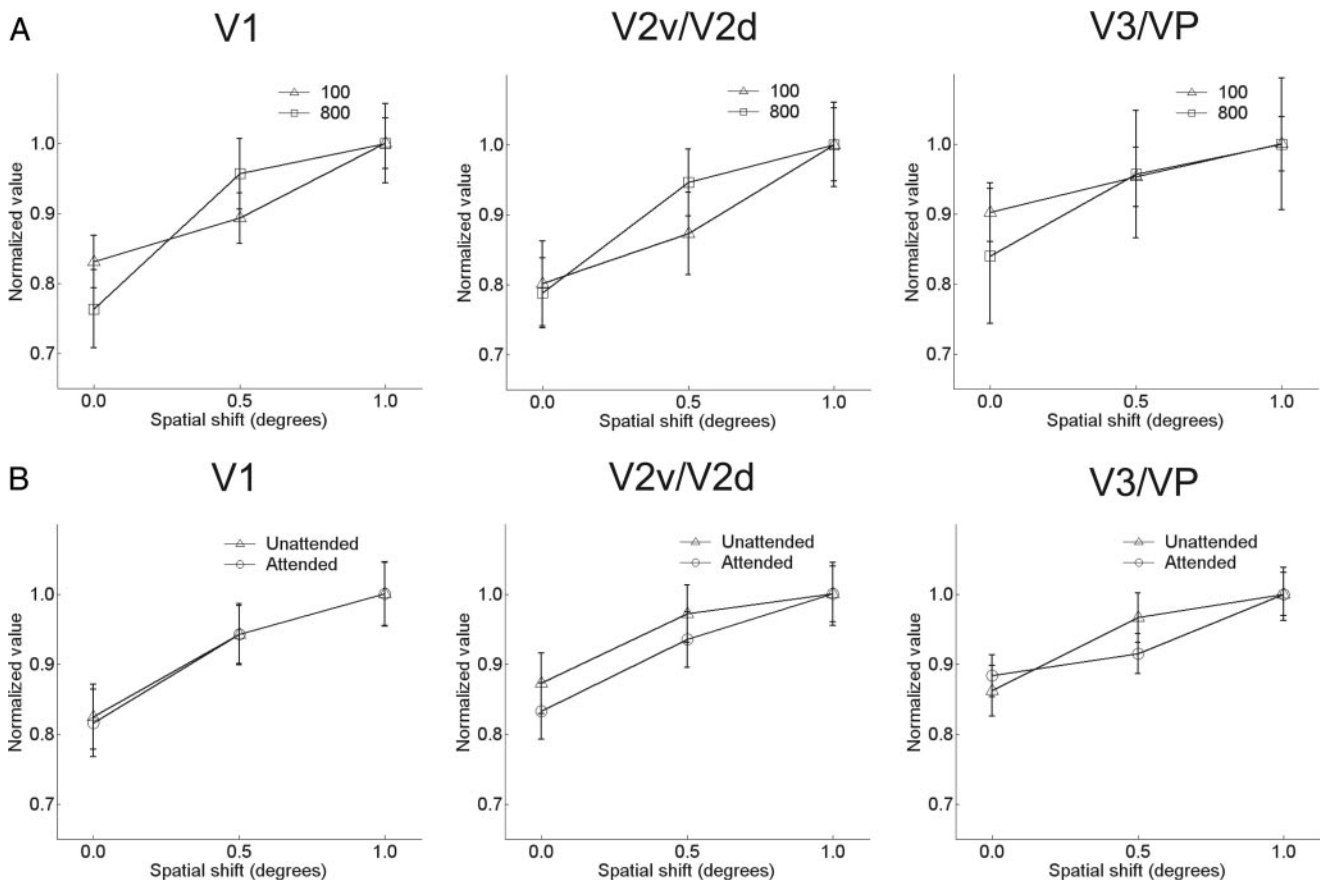

FIG. 3. Results from *experiment 1*. *A*: effect sizes were calculated by normalizing peak responses to peak in the 1.0° shift condition and represent magnitude of repetition effect. No differences were observed between the 2 ISI conditions. *B*: plot is similar to *A* but collapses across ISI conditions. No differences were observed between the 2 attention conditions.

The average results are shown in Fig. 4. The time-courses for the three different rotation conditions are nearly identical in V1—there are no significant differences or trends observed as a function of the orientation difference between the first and second stimulus, consistent with Boynton and Finney (2003). Also, consistent with Boynton and Finney (2003), we observed a significant increase in extrastriate retinotopic areas for the 90° rotation condition. Although no area showed statistically significant "tuning" (a progressive increase as a function of orientation change), V2v/V2d had a trend in that direction.

DISCUSSION

We observed a significant fMRI repetition effect (reduced signal) in V1 when localized stimulus elements were repeated in identical locations compared with slightly different locations. Our results indicate that early visual areas are sensitive to small changes in spatial position—a result entirely consistent with the known retinotopic organization of early visual cortex. It seems that the repetition method is an ideal tool for analyzing fine-scale spatial sensitivity. Based on our results, we were able to infer sensitivity to a spatial change of 0.5°—a resolution that exceeds the 3-mm³ voxel size that is typically used in fMRI. However, it should be emphasized that with larger spatial position changes (or with greater spatial resolution afforded by higher magnetic field strengths), it may be more appropriate to directly measure the subtle changes in the spatial pattern of response across voxels that would occur as a result of new voxels being activated.

The design and results of our experiments seem to be similar to rapid repetition experiments performed in higher visual areas: the summed fMRI response to an identical stimulus pair is compared with the repetition of stimuli that have been changed along a dimension (in this case, retinotopic position), and a larger signal is measured for the different compared with identical pair. The increased signal is used to infer neural sensitivity to the changed dimension. The mechanism underlying such short-term repetition effects has typically been attributed to neural adaptation—the logic being that in the identical condition, the second stimulus of the image pair is activating a recently used (adapted) neural population, leading to a reduced signal (Grill-Spector and Malach 2001; Tolias et al. 2002).

Although neural adaptation seems to be a possible explanation for the position results, why are orientation-specific repetition effects difficult to observe in V1? V1 is clearly sensitive

to repetition effects—it had a consistently large effect in the position experiment. In addition, similar to Boynton and Finney (2003), extrastriate retinotopic areas were sensitive to orientation changes, showing that the experimental design has sufficient power to measure orientation-dependent signals. Furthermore, electrophysiological studies have shown rapid, pattern-specific adaptation of neurons in V1 (Müller et al. 1999). Finally, our laboratory has convincingly showed orientation-specific tuning in V1 using long-term (tens of seconds) adaptation (Fang et al. 2005), showing that V1 neurons in humans are orientation tuned and that this tuning is measurable with fMRI.

We feel that one of the most important implications of our findings is that they underscore the need for caution when interpreting null effects in repetition experiments. Although null effects are always difficult to interpret, they are frequently used in repetition experiments to make claims about invariance—that is, the stimulus dimensions to which a cortical area does not respond (Altmann et al. 2004; Epstein et al. 2003; Grill-Spector et al. 1999; James et al. 2002; Kourtzi and Kanwisher 2000, 2001; Kourtzi et al. 2003a; Neri et al. 2004; Self and Zeki 2005; Vuilleumier et al. 2002) and about relative sensitivities between different cortical areas. However, consider the conclusions that would be drawn about V1 from our data assuming that we had little a priori knowledge about V1 organization (which is the case for many of the higher visual areas that are studied with repetition effects). First, based on the primary positive result from our study, we would have concluded that V1 is sensitive to spatial position. This is important to emphasize—our positive results arrive at an appropriate conclusion about the organization of V1. However, based on our null effects, we would have also concluded that V1 is insensitive ("invariant") to stimulus orientation. This conclusion is almost certainly wrong and motivates us to consider other possible mechanisms underlying our observed repetition effects.

One alternative mechanism to adaptation is that short-term repetition effects are completely vascular with the nonlinearity present in the hemodynamic—and not neural—response. The explanation is similar to adaptation but, instead of thinking about an adapted neural population, the effect is dependent on an "adapted" vascular response. Applying this to the position experiments, when the positions of the array elements are moved to a new location, they stimulate a new population of neurons recruiting a new vascular supply. Thus the slightly repositioned stimuli avoid an already saturated vascular re-
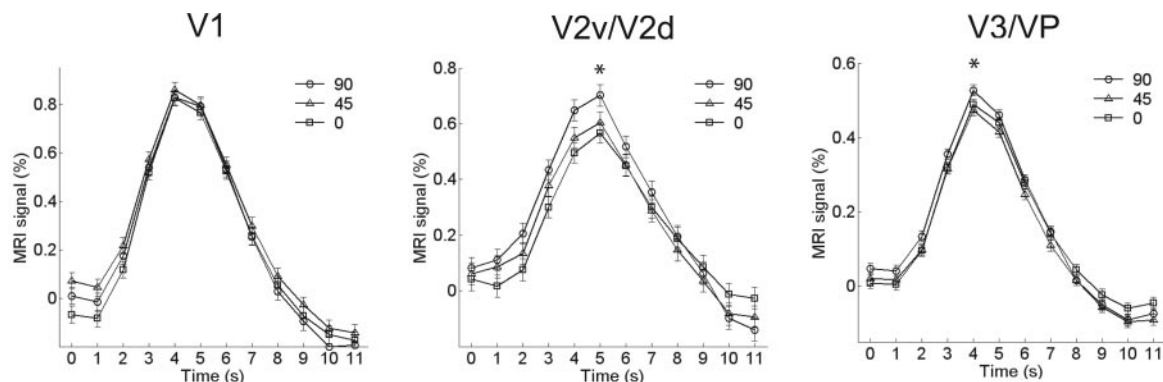

FIG. 4. Results from *experiment 2*: pattern repetition. Summed event-related responses (stimulus 1, ISI, stimulus 2) averaged over 2 subjects (*P < 0.01).

sponse and lead to a larger summed BOLD signal. Similarly, the lack of an orientation effect in V1 could easily be explained by the relatively close spatial distribution of neurons with different orientation sensitivities. Based on what we know about primate V1 organization, we can speculate that individual V1 orientation columns are subserved by measurably indistinguishable blood supplies.

Although our results are not able to conclusively differentiate between these two mechanisms, there seems to be nearly as much evidence in favor of a vascular mechanism as for a neural mechanism. First, we show that the position-dependent repetition effect is largely independent of the duration of the ISI (100–800 ms). A mechanism that depends on the state of a previously activated neural population (e.g., neural adaptation) would presumably depend on recovery time. For example, electrophysiological measurements in monkey MT have shown that rapid, pattern-specific adaptation is strongly dependent on interstimulus duration and is only present with short (<200 ms) ISIs (Priebe et al. 2002). Although specific values for time constants may differ between visual areas (and species), the dependence on duration is likely common across sensory neurons. Second, we show that the repetition effect is largely independent of the focus of attention. In contrast to these results, previous studies in higher visual cortex have revealed a much stronger repetition effect when attention was directed toward the stimuli (Murray and Wojciulik 2004; Yi et al. 2004), suggesting a change in the adaptability or tuning of neurons in these areas. The lack of an effect of attention does not preclude a neural mechanism, but the results are inconsistent with results in higher visual areas. Third, the timing parameters (duration of the stimuli and ISIs) that we used in the position experiments seem to have no direct behavioral correlate. For example, they are much longer than what are used for typical masking experiments (Enns and Di Lollo 2000; Macknik and Livingstone 1998) and much shorter than typical adaptation experiments. In separate behavioral experiments (not presented), we made multiple attempts to find even small behavioral differences (e.g., contrast detection) as a function of the spatial relationship of repeating stimuli and none were found. If there were a strong neural mechanism underlying the results, presumably it would manifest in an obvious behavioral effect.

Our results highlight that multiple mechanisms may underlie repetition effects and, depending on the mechanism(s) involved, not all stimulus dimensions and cortical areas are equivalent—an often implicit assumption when interpreting results from repetition experiments. The important point to emphasize is not whether orientation-specific short-term repetition effects are measurable in V1 (recent research suggests that with many subjects, effects are measurable, Kourtzi and Huberle 2005) but that there are significant inherent sensitivity differences between different stimulus dimensions and between different visual areas. The results raise important questions about how to interpret repetition effects, such as to what extent can null effects be meaningful? Can we compare results between different cortical areas? Can we compare results with different timing parameters? What implications do different underlying mechanisms have on interpretation? How important are behavioral correlates of repetition effects? More research is needed to answer these questions but, given the potential power of using repetition effects in fMRI experiments, uncovering the answers will clearly benefit future imaging research.

REFERENCES

Altmann CF, Deubelius A, and Kourtzi Z. Shape saliency modulates contextual processing in the human lateral occipital complex. *J Cogn Neurosci* 16: 794–804, 2004.

Boynton GM and Finney EM. Orientation-specific adaptation in human visual cortex. *J Neurosci* 23: 8781–8787, 2003.

Buckner RL, Goodman J, Burock M, Rotte M, Koutstaal W, Schacter D, Rosen B, and Dale AM. Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron* 20: 285–296, 1998.

Buracas GT and Boynton GM. Efficient design of event-related fMRI experiments using M-sequences. *Neuroimage* 16: 801–813, 2002.

Carandini M, Movshon JA, and Ferster D. Pattern adaptation and cross-orientation interactions in the primary visual cortex. *Neuropharmacology* 37: 501–511, 1998.

Engel SA, Glover GH, and Wandell BA. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex* 7: 181–192, 1997.

Enns JT and Di Lollo V. What's new in visual masking? *Trends Cogn Sci* 4: 345–352, 2000.

Epstein R, Graham KS, and Downing PE. Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron* 37: 865–876, 2003.

Fang F, Murray SO, Kersten D, and He S. Orientation-tuned fMRI adaptation in human visual cortex. *J Neurophysiol* 94: 4188–4195, 2005.

Grill-Spector K and Malach R. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol (Amst)* 107: 293–321, 2001.

Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzchak Y, and Malach R. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24: 187–203, 1999.

Henson RN. Neuroimaging studies of priming. *Prog Neurobiol* 70: 53–81, 2003.

Henson RN and Rugg MD. Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia* 41: 263–270, 2003.

Huettel SA and McCarthy G. Evidence for a refractory period in the hemodynamic response to visual stimuli as measured by MRI. *Neuroimage* 11: 547–553, 2000.

Huettel SA, Obembe OO, Song AW, and Woldorff MG. The BOLD fMRI refractory effect is specific to stimulus attributes: evidence from a visual motion paradigm. *Neuroimage* 23: 402–408, 2004.

James TW, Humphrey GK, Gati JS, Menon RS, and Goodale MA. Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron* 35: 793–801, 2002.

Kourtzi Z, Erb M, Grodd W, and Bulthoff HH. Representation of the perceived 3-D object shape in the human lateral occipital complex. *Cereb Cortex* 13: 911–920, 2003a.

Kourtzi Z and Huberle E. Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fMRI adaptation. *Neuroimage* 28: 440–452, 2005.

Kourtzi Z and Kanwisher N. Cortical regions involved in perceiving object shape. *J Neurosci* 20: 3310–3318, 2000.

Kourtzi Z and Kanwisher N. Representation of perceived object shape by the human lateral occipital complex. *Science* 293: 1506–1509, 2001.

Kourtzi Z, Tolias AS, Altmann CF, Augath M, and Logothetis NK. Integration of local features into global shapes: monkey and human FMRI studies. *Neuron* 37: 333–346, 2003b.

Macknik SL and Livingstone MS. Neuronal correlates of visibility and invisibility in the primate visual system. *Nat Neurosci* 1: 144–149, 1998.

Miller EK, Li L, and Desimone R. A neural mechanism for working and recognition memory in inferior temporal cortex. *Science* 254: 1377–1379, 1991.

Movshon JA and Lennie P. Pattern-selective adaptation in visual cortical neurones. *Nature* 278: 850–852, 1979.

Müller JR, Metha AB, Krauskopf J, and Lennie P. Rapid adaptation in vusal cortex to the structure of images. *Science* 285: 1405–1408, 1999.

Murray SO and Wojciulik E. Attention increases neural selectivity in the human lateral occipital complex. *Nat Neurosci* 7: 70–74, 2004.

Naccache L and Dehaene S. The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cereb Cortex* 11: 966–974, 2001.

Neri P, Bridge H, and Heeger DJ. Stereoscopic processing of absolute and relative disparity in human visual cortex. *J Neurophysiol* 92: 1880–1891, 2004.

Priebe NJ, Churchland MM, and Lisberger SG. Constraints on the source of short-term motion adaptation in macaque area MT. I. The role of input and intrinsic mechanisms. *J Neurophysiol* 88: 354–369, 2002.

Priebe NJ and Lisberger SG. Constraints on the source of short-term motion adaptation in macaque area MT. II. Tuning of neural circuit mechanisms. *J Neurophysiol* 88: 370–382, 2002.

Schacter DL and Buckner RL. Priming and the brain. *Neuron* 20: 185–195, 1998.

Sclar G, Lennie P, and DePriest DD. Contrast adaptation in striate cortex of macaque. *Vision Res* 29: 747–755, 1989.

Self MW and Zeki S. The integration of colour and motion by the human visual brain. *Cereb Cortex* 15: 1270–1279, 2005.

Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, and Tootell RB. Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268: 889–893, 1995.

Tolias AS, Kourtzi Z, and Logothetis NK. fMRI adaptation: a technique for studying the properties of neuronal networks. In: *Exploratory Analysis and Data Modeling in Functional Neuroimaging*, edited by Sommer T and Wichert A. Cambridge, MA: MIT Press, 2002, p. 109–126.

Tootell RB, Hadjikhani NK, Vanduffel W, Liu AK, Mendola JD, Sereno MI, and Dale AM. Functional analysis of primary visual cortex (V1) in humans. *Proc Natl Acad Sci USA* 95: 811–817, 1998.

van Turennout M, Ellmore T, and Martin A. Long-lasting cortical plasticity in the object naming system. *Nat Neurosci* 3: 1329–1334, 2000.

Vuilleumier P, Henson RN, Driver J, and Dolan RJ. Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nat Neurosci* 5: 491–499, 2002.

Yi DJ, Woodman GF, Widders D, Marois R, and Chun MM. Neural fate of ignored stimuli: dissociable effects of perceptual and working memory load. *Nat Neurosci* 7: 992–996, 2004.