Orientation-Tuned fMRI Adaptation in Human Visual Corte

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Fang, Fang, Scott O. Murray, Daniel Kersten, and Sheng He. Orientation-tuned fMRI adaptation in human visual corte . *J Neurophysiol* 94: 4188 4195, 2005. First published August 24, 2005; doi:10.1152/jn.00378.2005. Adaptation is a general propert of almost all neural s stems and has been a longstanding tool of ps choph sics because of its power to isolate and temporaril reduce the contribution of speci c neural populations. Recentl , adaptation designs have been e tensivel applied in functional MRI (fMRI) studies to infer neural selectivit in speci c cortical areas. However, there has been considerable variabilit in the duration of adaptation used in these e periments. In particular, although long-term adaptation has been solidl established in ps choph sical and neuroph siological

ties for detecting the test stimulus following adaptation. We also failed to nd orientation-tuned fMRI adaptation in V1 with a short-term adaptation paradigm, which replicated Bo n-ton and Finne 's (2003) nding and ruled out other potential e planations (e.g., transient attention and apparent motion) of the long-term fMRI adaptation effect.

METHODS

Subjects

A total of ve health subjects (2 female, 3 male; YJ, WL, PT, FF, and SM) were involved in these e periments. YJ, WL, FF, and SM participated in the long-term ps choph sical and fMRI adaptation e periments. YJ, WL, FF, and PT participated in the short-term ps choph sical and fMRI adaptation e periments. All were right handed and ranged in age from 25 to 33 r. The had normal corrected-to-normal vision and gave written, informed cons accordance with procedures and protocols approved b th subjects review committee of the Universit of Minneso

fMRI experiments

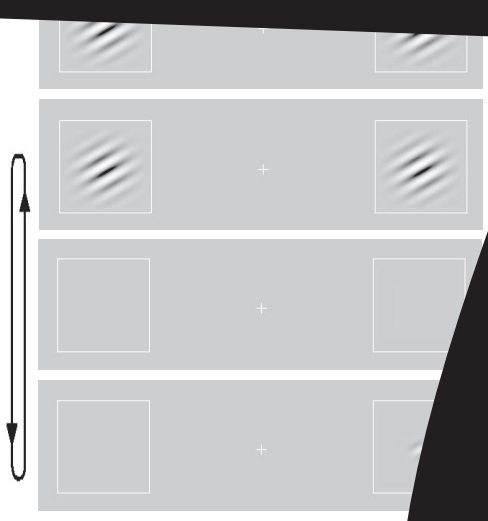
The adapting and test stimuli consisted of 16 patches arranged in two concentric annuli, wi 4.5 (Fig. 1). Each of the eight patches i diameter of 1.9 (σ = 0.38) and a spa The eight outer annulus patches eac 0.70) and a spatial frequenc of 2 Gabor patch in the adapting stim

stimuli were ed in each adapta generated b rotating the indivi stimulus b ±0, ±7.5, ±30, Gabor patch was randoml counterclockwise.

For the long-term a scan (total of 8) co of preadaptation of four test sti the Gabor p performe press o decr l

Psychophysical experiments

Ps choph sical contrast adaptation e periments were performed outside the scanner under adaptation conditions designed to match those in the fMRI e periments. Two adapting Gabor patches (diameter: 2.8 ; spatial frequenc : 2.5 c cles/ ; mean radii: 4.5 ; σ: 0.70 ; 1-H counterphase ickering), which were the same as those in the outer annulus in the fMRI e periments, were presented on opposite sides of the ation point. Like the long-term fMRI adaptation e periments, 20 s of preadaptation was also used. Then, after 5-s topping-up adaptation and a 0.5-s blank gap, a low-contrast, 1.5-c cle Gabor patch whose center and spatial frequenc were identical to the adapting stimuli was presented for 200 ms on either the left or right side. A 250-ms auditor beep preceding each test stimulus b 250 ms alerted the subject to the ensuing presentation of the test stimulus. Subjects were asked to press a button to make a two-alternative forced-choice (2-AFC) to indicate the location of the test stimulus (left or right of ation, Fig. 2). Contrast thresholds of test stimuli (82% correct rate to judge their location) after adaptation were estimated b Quest staircases (Watson and Pelli 1983), four times for each subject and test stimulus t pe. Each staircase consisted of 50 trials, with ed orientations of adapting and test Gabor patches that



were randomi ed at the beginning of the sta
a ps choph sical short-term contrast adapta
to the fMRI e periments, adaptation time wa
other parameters were equivalent to the long-
that there was no 20-s preadaptation in the
e periment. The stimuli were presented on a S
scan G420 19-in monitor, with a spatial resoluti
and refresh rate of 100 H . The viewing distance
background luminance was 43 cd/m^2, and luminan
monitor ranged from 0 to 86 cd/m^2 .

fMRI data acquisition

In the scanner, the stimuli were back-projected using a video projector (60 H) onto a translucent screen placed inside the scanner bore. Subjects viewed the stimuli through a mirror located above their e es. fMRI data were collected using a 3-T Siemens Trio scanner with a high-resolution eight-channel head arra coil. Blood o gen level-dependent (BOLD) signals were measured with an echo-planar imaging (EPI) sequence (TE: 30 ms, TR: 1,000 ms, FOV: 22 $\times$ 22 cm^2, matri : 64 $\times$ 64, ip angle: 60, slice thickness: 5 mm, number of slices: 14, slice orientation: a ial). The bottom slice was positioned at the bottom the temporal lobes. T2-weighted structural images at the same slice locations and a high-resolution three-dimensional (3-D) structural data set (3D MPRAGE; 1 $\times$ 1 $\times$1-mm^3 resolution) were collected in the same session before the functional runs. The scans for retinotopic mapping were run in a different session in the same scanner.

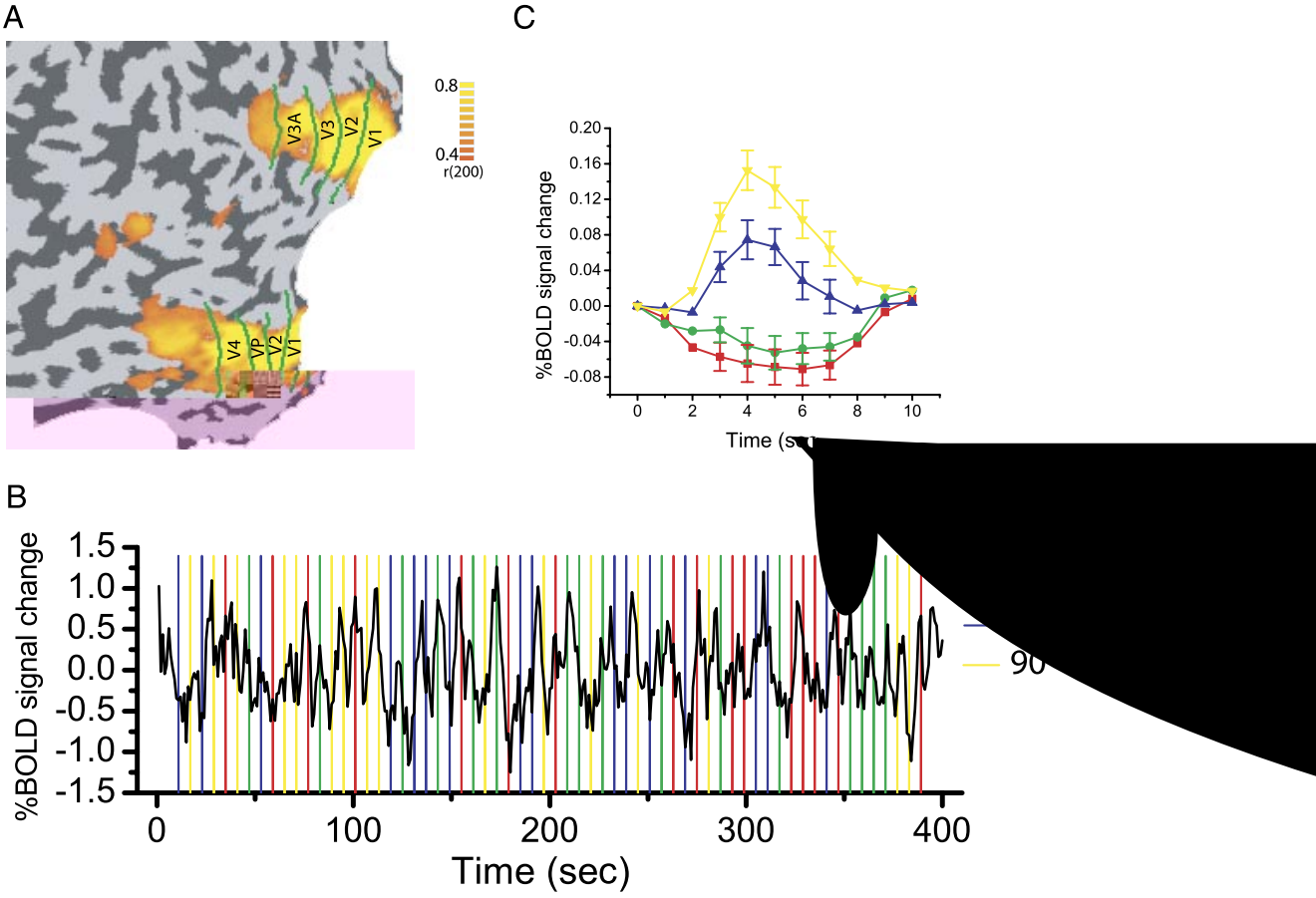
fMRI data analysis

The anatomical volumes were transformed into a brain space that was common for all subjects (Talairach and Tournou 1988) and i ated using BrainVo ager 2000. Functional volumes for each subject were preprocessed, which included 3-D motion correction using SPM99, slice scan time correction, linear trend removal, and high-pass (0.015 H) (Smith et al. 1999) ltering using BrainVo ager 2000. Correlation anal sis was performed on the locali er data to de ne the

0.03) and
491 $\pm$ 28 ms, 0.
test 90: 495 $\pm$ 15 ms,
0.80 $\pm$ 0.03) adaptation e per
subjects' general attentional state did
different test conditions.

fMRI results

Figure 3*B* shows a time-course of BOLD signal in V1 from a long-term adaptation scan. Figure 3*C* shows event-related averages in V1 evoked b the four test stimuli (0, 7.5, 30, and 90 angular difference from the adaptor) averaged across four subjects. Test stimuli were presented at *time 0*. The fMRI signals show a monotonic increase from 0 to 90 test conditions. This response pattern was consistentl observed in all four subjects. A one-wa ANOVA shows a signi cant main effect of the test-adapt angular difference in V1 [$F(3,15) = 28.252$, $P < 0.001$]. It is interesting to note that onl the 30 and 90 test stimuli elicited a signi cant positive peak at a latenc of 4 s. The BOLD signals evoked b the 0 and 7.5 test stimuli



are negative and kept decreasing until time-points 5 and 6. This ma be attributed to the overlapping neural populations tuned to 0 and 7.5 . The fMRI signals evoked b the 0 and 7.5 test stimuli began to increase after time-point 6 because of the presentation of the ne t test stimulus.

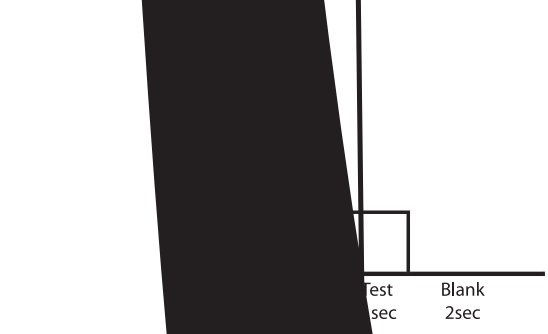
We also e amined the evoked BOLD signals in e trastriate areas (V2, V3/VP, V3A, and V4). As shown in Fig. 5*A*, e trastriate areas also consistentl e hibited a monotonic increase in signal from the 0 to 90 test conditions, which was con rmed b ANOVAs [V2: $F(3,15) = 29.768$, $P < 0.001$; V3/VP: $F(3,15) = 31.494$, $P < 0.001$; V3A: $F(3,15) = 52.41$, $P < 0.001$; V4: $F(3,15) = 81.681$, $P < 0.001$]. Also, there was a progressive increase in the magnitude of the adaptation effect through the hierarch of visual retinotopic areas from V1 to V4.

Figures 4*B* and 5*B* show the results from the short-term adaptation e periment. To compare the fMRI adaptation effect between the long-term and short-term adaptation e periments, the BOLD signal evoked b the 0 test stimulus served as baseline and was subtracted from those evoked b the 7.5, 30, and 90 test stimuli (Fig. 4*B*). The BOLD signals from the short-term adaptation e periment in V1, unlike the long-term one, did not show a monotonic increase from 0 to 90 test conditions, which indicates no (or ver weak) short-term adaptation effects in V1. However, as shown in Fig. 5*B*, e trastriate areas graduall e hibited an adaptation effect, and the main ANOVA effect of angular difference reached signi cance in V3A and V4 [V1: $F(3,15) = 0.557$, $P = 0.653$; V2: $F(3,15) = 2.112$, $P = 0.152$; V3/VP: $F(3,15) = 2.673$, $P = 0.095$; V3A: $F(3,15) = 5.976$, $P = 0.01$; V4: $F(3,15) = 6.859$, $P = 0.006$].

Psychophysical results

The elevation of contrast detection thresholds after adaptation as a function of the angular difference between adapting and test orientations has been widel used to show orientation-selective adaptation in the visual s stem. Here, we measured the minimum Michelson contrast required to detect the presence of a Gabor patch at the adapted location after 5-s topping-up adaptation and 1-s short-term adaptation.

For the long-term adaptation e periment, the ps choph sical results (Fig. 6*A*, square) clearl show that visual s stem is well adapted, and the contrast threshold is proportional to the angular difference between adapting and test orientations. However, in the short-term adaptation e periment, the magnitude of contrast threshold elevation (Fig. 6*B*, circle) is much weaker than that in the long-term one. To compare the ps choph sical and fMRI results after long-term adaptation, we plotted the contrast detection threshold against peak fMRI signal values in V1 for each subject (Fig. 6*B*). Linear functions provided a good t of the data (S1: $y = 0.11007 - 0.29666x$,



old test stimuli, and loss of perceive upra-
threshold test stimuli are both tuned to the ation
(but see also, Snowden and Hammett 1992). E both
contrast threshold elevation and fMRI adapta ectl
measured neural activities of different orient neu-
rons, and the comparison is more of a qua , we
feel it is reasonable to compare the ps ch MRI
results.

Our result of orientation-selective con-
sistent with the ndings of Tootell ver,
from the brief description of th lear
whether attention, which ma v gre
change between the adapti
ortant control because it ha
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be et al. 1995). stud not onl helped to equate attention
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on and 5-s to ing-up adapt the
the presentation of a test s ulus
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obs ed in V
thresh

suggesting that subjects' attention was evenl distributed throughout the adaptation scans. Third, although sustained attention is ver effective in modulating V1 BOLD signal, there is little evidence supporting that BOLD signals in V1 can be effected b transient attention (Liu et al. 2005) and apparent motion (Clae s et al. 2003; Liu et al. 2004). Fourth and most importantl , the short- and long-term fMRI adaptation e periments were identical e cept for the duration of adaptation. If transient attention and/or apparent motion were the source of the effect in the long-term e periment, we should have also observed a monotonic increase from the 0 to 90 test conditions in the short-term e periment. However, we did not observe an differences between orientation conditions with short adaptation durations. Similar evidence against transient attention and apparent motion e planation can also be found in the long-term adaptation stud of Engel (2005).

Unlike our nding of orientation-tuned adaptation in V1 with the long-term adaptation paradigm, Bo nton and Finne (2003) did not observe orientation-dependent adaptation in V1 despite showing elevated orientation-speci c contrast detection thresholds. Their stud used short (1 s) adaptation durations and e amined responses to 1-s parallel and orthogonal test stimuli. Our results with short-term adaptation replicated Bo nton and Finne 's (2003) failure to observe orientation-dependent adaptation in V1. The critical factor for observing orientation-tuned adaptation effects in V1 measured with fMRI aptation. The use of tens of pping-up adaptation is prev- europh siological adaptation on in uences nearl all depen- ceptual consequence (Fang and , the strength of the aftereffect et al. 1991; Mather et al. 1998), reenlee et al. 1991), the propor- studied neurons (Movshon and and the shift magnitude of tuning Muller et al. 1999). The failure to adaptation in V1 in the stud of 03) and ours with short-term adapta- buted to V1 neurons not being suf - etected with fMRI. Our ps choph sical much larger elevations in contrast detec- long-term adaptation, also support this tion, the validit of long-term fMRI adap-

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Given that fMRI is an indirect measure of neural activit , it is important to consider the potential source of our signals. Logothetis et al. (2001) suggested that the BOLD signal re ects the input and intracortical processing of a given area rather than its spiking output. The majorit of input to V1 is from the lateral geniculate nucleus (LGN) and neurons in LGN are known to have little or no orientation selectivit (Hubel and Wiesel 1961). We can therefore speculate that one source of the orientation-speci c signal we observed is from intracortical processing in V1, possibl from orientation-speci c s naptic activit between simple and comple cells (Alonso and Martine 1998). One reason to attribute our results in V1 partiall to simple cell activit is that previous neuroph siological studies have shown that comple cells e hibit stronger orientation-speci c adaptation to low-contrast than to high-contrast test stimuli (and we used a high-contrast test stimulus). Simple cells, on the other hand, are much less affected b test-stimulus contrast (Movshon and Lennie 1979; Sclar et al. 1989). Other sources could be hori ontal connections linking neurons within V1 (Callawa 1998) and feedback from high-level cortical areas (Lamme et al. 1998). Certainl , more studies are needed to better understand the comple relationship between BOLD signals (released from adaptation) and neuronal activities.

Because the effects of long-term adaptation are known to be relativel long-lasting, it is possible that some of the previous scans' adaptation is still present during the successive scan. That is, the cortical areas responsive to a given oriented patch might have reduced responses on the following scan to the orientation that was adapted at that location on the previous scan. In our stud , subjects had at minimum 1-min break between adaptation scans. Previous studies (e.g., Greenlee et al. 1991) have shown that adaptation recover time is appro - imatel equal to the duration of adaptation (20-s preadaptation and 5-s topping-up adaptation in our studies), suggesting that lingering adaptation likel had ver small effects on our results. However, it could be possible that larger adaptation effects would have been found if we had not randomi ed adapting orientations in each adaptation scan.

We observed orientation-speci c adaptation in other retinotopic areas including V2, V3/VP, V3A, and V4. One of the perceptual consequences of orientation adaptation is the tilt aftereffect, which can be induced not onl b luminance de ned stimuli, but also b illusor contours (Paradiso et al. 1989), equiluminous and colored stimuli (Elsner 1978), and random dot stereograms (T ler 1975). It has been shown that neurons in V2, V4, and V3A are sensitive to these visual properties (Tsao et al. 2003; von der He dt and Peterhans 1989; Zeki and Marini 1998). Our nding of orientation adaptation across multiple levels of the earl visual hierarch supports the notion that orientation processing is ubiquitous in earl areas of the visual s stem. Future application of our e perimental design to other stimulus dimensions and other cortical areas will help understand neural coding at multiple stages of the human visual s stem.

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