

Orientation-Tuned fMRI Adaptation in Human Visual Cortex

Fang Fang,¹ Scott O. Murray,² Daniel Kersten,¹ and Sheng He¹

¹*Department of Psychology, University of Minnesota, Minneapolis, Minnesota; and* ²*Department of Psychology, University of Washington, Seattle, Washington*

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Fang, Fang, Scott O. Murray, Daniel Kersten, and Sheng He.

Orientation-tuned fMRI adaptation in human visual cortex. *J Neurophysiol* 94: 4188–4195, 2005. First published August 24, 2005; doi:10.1152/jn.00378.2005. Adaptation is a general property of almost all neural systems and has been a longstanding tool of psychophysics because of its power to isolate and temporarily reduce the contribution of specific neural populations. Recently, adaptation designs have been extensively applied in functional MRI (fMRI) studies to infer neural selectivity in specific cortical areas. However, there has been considerable variability in the duration of adaptation used in these experiments. In particular, although long-term adaptation has been solidly established in psychophysical and neurophysiological

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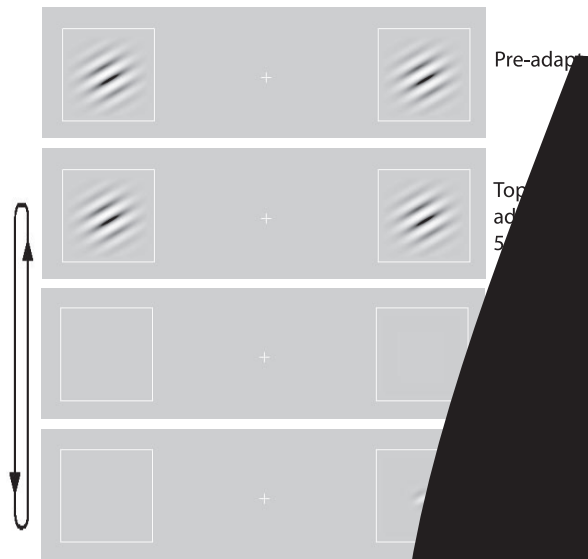
METHODS

Subjects

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were randomized at the beginning of the study to minimize psychophysical short-term contrast adaptation. Prior to the fMRI experiments, adaptation time was 20 s. All other parameters were equivalent to the long-term adaptation scan, that there was no 20-s preadaptation in the test experiment. The stimuli were presented on a Sanyo Colorscan G420 19-in monitor, with a spatial resolution of 1024 × 768 and refresh rate of 100 Hz. The viewing distance was 57 cm, background luminance was 43 cd/m², and luminance of the monitor ranged from 0 to 86 cd/m².

fMRI data acquisition

In the scanner, the stimuli were back-projected using a video projector (60 Hz) onto a translucent screen placed inside the scanner bore. Subjects viewed the stimuli through a mirror located above their eyes. fMRI data were collected using a 3-T Siemens Trio scanner with a high-resolution eight-channel head array coil. Blood oxygen level-dependent (BOLD) signals were measured with an echo-planar imaging (EPI) sequence (TE: 30 ms, TR: 1,000 ms, FOV: 22 × 22 cm², matrix: 64 × 64, flip angle: 60°, slice thickness: 5 mm, number of slices: 14, slice orientation: axial). The bottom slice was positioned at the bottom of 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 × 1 × 1-mm³ 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.

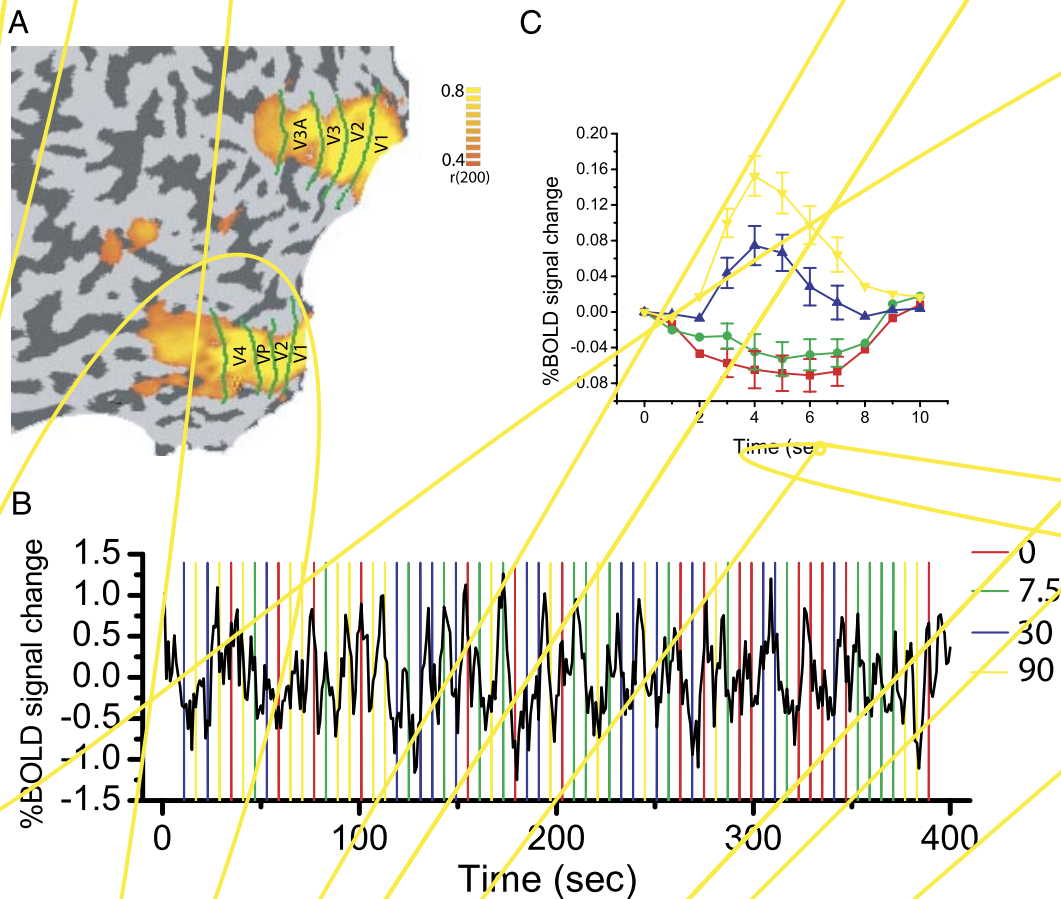
fMRI data analysis

The anatomical volumes were transformed into a brain space that was common for all subjects (Talairach and Tournoux 1988) and registered using BrainVoyager 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 Hz) filtering using BrainVoyager 2000. Correlation analysis was performed on the localizer data to define the

501 (0.03) and 90° (0.03) and 0° (0.03) and 45° (0.03) and 90° (0.03) and 135° (0.03) and 180° (0.03) adaptation experiments. The subjects' general attentional state did not differ between different test conditions.

fMRI results

Figure 3B shows a time-course of BOLD signal in V1 from a long-term adaptation scan. Figure 3C shows event-related averages in V1 evoked by 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 consistently observed in all four subjects. A one-way ANOVA shows a significant main effect of the test-adapt angular difference in V1 [$F(3,15) = 28.252, P < 0.001$]. It is interesting to note that only the 30 and 90° test stimuli elicited a significant positive peak at a latency of 4 s. The BOLD signals evoked by the 0 and 7.5° test stimuli



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

We also examined the evoked BOLD signals in extrastriate areas (V2, V3/VP, V3A, and V4). As shown in Fig. 5A, extrastriate areas also consistently exhibited a monotonic increase in signal from the 0 to 90° test conditions, which was confirmed by 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 hierarchy of visual retinotopic areas from V1 to V4.

Figures 4B and 5B show the results from the short-term adaptation experiment. To compare the fMRI adaptation effect between the long-term and short-term adaptation experiments, the BOLD signal evoked by the 0° test stimulus served as baseline and was subtracted from those evoked by the 7.5, 30, and 90° test stimuli (Fig. 4B). The BOLD signals from the short-term adaptation experiment in V1, unlike the long-term one, did not show a monotonic increase from 0 to 90° test conditions, which indicates no (or very weak) short-term adaptation effects in V1. However, as shown in Fig. 5B, extrastriate areas gradually exhibited an adaptation effect, and the

main ANOVA effect of angular difference reached significance 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 widely used to show orientation-selective adaptation in the visual system. Here, we measured the minimum Michelson contrast required to detect the presence of a Gabor patch at the adapted location after 5-s top-down adaptation and 1-s short-term adaptation.

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



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suggesting that subjects' attention was evenly distributed throughout the adaptation scans. Third, although sustained attention is very effective in modulating V1 BOLD signal, there is little evidence supporting that BOLD signals in V1 can be affected by transient attention (Liu et al. 2005) and apparent motion (Clayton et al. 2003; Liu et al. 2004). Fourth and most importantly, the short- and long-term fMRI adaptation experiments were identical except for the duration of adaptation. If transient attention and/or apparent motion were the source of the effect in the long-term experiment, we should have also observed a monotonic increase from the 0 to 90 test conditions in the short-term experiment. However, we did not observe any differences between orientation conditions with short adaptation durations. Similar evidence against transient attention and apparent motion explanation can also be found in the long-term adaptation study of Engel (2005).

Unlike our finding of orientation-tuned adaptation in V1 with the long-term adaptation paradigm, Boynton and Finney (2003) did not observe orientation-dependent adaptation in V1 despite showing elevated orientation-specific contrast detection thresholds. Their study used short (1 s) adaptation durations and examined responses to 1-s parallel and orthogonal test stimuli. Our results with short-term adaptation replicated Boynton and Finney's (2003) failure to observe orientation-dependent adaptation in V1. The critical factor for observing orientation-tuned adaptation effects in V1 measured with fMRI seems to be the duration of adaptation. The use of tens of seconds of preadaptation and topping-up adaptation is prevalent in psychophysical and neurophysiological adaptation studies. The duration of adaptation influences nearly all dependent measures including the perceptual consequence (Fang and He 2004; Leopold et al. 2002), the strength of the aftereffect (Fang and He 2005; Greenlee et al. 1991; Mather et al. 1998), the length of recovery time (Greenlee et al. 1991), the proportion of adapted neurons in studied neurons (Movshon and Lennie 1979; Nelson 1991), and the shift magnitude of tuning curves (Dragoi et al. 2000; Muller et al. 1999). The failure to detect orientation-specific adaptation in V1 in the study of Boynton and Finney (2003) and ours with short-term adaptation may simply be attributed to V1 neurons not being sufficiently adapted to be detected with fMRI. Our psychophysical results, which show much larger elevations in contrast detection threshold after long-term adaptation, also support this possibility. In addition, the validity of long-term fMRI adap-

shown that orientation adaptation is largely independent of attention and awareness of the stimulus (He and MacLeod 2001; He et al. 1996; Moradi et al. 2005).

Even with such an attention control task, it could still be argued that the observed monotonic increase of BOLD signals in the long-term adaptation experiment is not caused by adaptation but to transient attention shifts to the test stimuli and/or apparent motion between the adapting and test stimuli. However, there are a number of reasons that argue against these potential explanations. First, in our study, both the adapting and test stimuli comprised multiple Gabor patches with randomized orientations as opposed to a large, single grating (Boynton and Finney 2003; Tootell et al. 1998b). Having localized, distributed peripheral stimuli with a wide distribution of orientations helped to avoid sudden attention shifts from the fixation task during the presentation of the test stimuli. In fact, most subjects reported that they were unaware when orientation changes occurred during the experiment. Second, if the presentation of test stimuli had induced transient attention shifts, we would have expected to observe poorer behavioral performance of the fixation task during test presentation. However, subjects performed equally well at all stages of the trial,

Given that fMRI is an indirect measure of neural activity, it is important to consider the potential source of our signals. Logothetis et al. (2001) suggested that the BOLD signal reflects the input and intracortical processing of a given area rather than its spiking output. The majority of input to V1 is from the lateral geniculate nucleus (LGN) and neurons in LGN are known to have little or no orientation selectivity (Hubel and Wiesel 1961). We can therefore speculate that one source of the orientation-specific signal we observed is from intracortical processing in V1, possibly from orientation-specific synaptic activity between simple and complex cells (Alonso and Martinez 1998). One reason to attribute our results in V1 partially to simple cell activity is that previous neurophysiological studies have shown that complex cells exhibit stronger orientation-specific 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 by test-stimulus contrast (Movshon and Lennie 1979; Sclar et al. 1989). Other sources could be horizontal connections linking neurons within V1 (Callaway 1998) and feedback from high-level cortical areas (Lamme et al. 1998). Certainly, more studies are needed to better understand the complex relationship between BOLD signals (released from adaptation) and neuronal activities.

Because the effects of long-term adaptation are known to be relatively 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 study, subjects had at minimum 1-min break between adaptation scans. Previous studies (e.g., Greenlee et al. 1991) have shown that adaptation recovery time is approximately equal to the duration of adaptation (20-s preadaptation and 5-s topping-up adaptation in our studies), suggesting that lingering adaptation likely had very small effects on our results. However, it could be possible that larger adaptation effects would have been found if we had not randomized adapting orientations in each adaptation scan.

We observed orientation-specific 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 only by luminance defined stimuli, but also by illusory contours (Paradiso et al. 1989), equiluminous and colored stimuli (Elsner 1978), and random dot stereograms (Tyler 1975). It has been shown that neurons in V2, V4, and V3A are sensitive to these visual properties (Tsao et al. 2003; von der Heydt and Peterhans 1989; Zeki and Marini 1998). Our finding of orientation adaptation across multiple levels of the early visual hierarchy supports the notion that orientation processing is ubiquitous in early areas of the visual system. Future application of our experimental design to other stimulus dimensions and other cortical areas will help understand neural coding at multiple stages of the human visual system.

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