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


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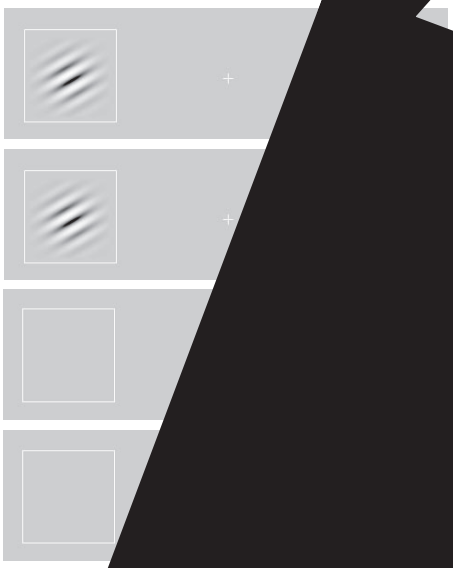

were ran so performed
a ps ch ment. Parallel
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R: 1,000 ms, FOV: 22 × 22 cm^2,
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. The bottom slice was positioned at
T2-weighted structural images at the
gh-resolution three-dimensional (3-D)
AGE; 1 × 1 ×1-mm^3 resolution) were
before the functional runs. The scans for
run in a different session in the same

olumes were transformed into a brain space that
ll subjects (Talairach and Tournou 1988) and
nVo ager 2000. Functional volumes for each sub-
ere pr cessed, which included 3-D motion correction using
slice scan time correction linear trend removal and high-

ROI s for the annulus than the
centra signals were discarded to
n effects. For the scans with the
he original BOLD signals from the
rcent signal changes, and event-related
to the t pe of test stimuli. Finall , the
s were baseline-corrected to the time-point at
uli occurred.

term adaptation e periment, the peak values of the
signals were de ned as the positive peak response for
and 90__test stimuli and the negative peak response for the 0
7.5__test stimuli, respectivel (Fig. 5*A*). In the short-term adap-
ion e periment, the univariate BOLD amplitude was computed for
ach t pe of test stimulus b averaging the evoked BOLD signal over
a 3- to 7-s latenc window (Fig. 5*B*) (Ress and Heeger 2003). The window was chosen to bracket the peak response determined from other rapid event-related fMRI e periments (hemod namic reference scans) conducted in our laborator for each subject. To compare the fMRI adaptation effect between the long-term and short-term adaptation e periments, we subtracted the BOLD signal evoked b the 0__ test stimulus as baseline from those b 7.5, 30, and 90__test stimuli (Fig. 4*B*).

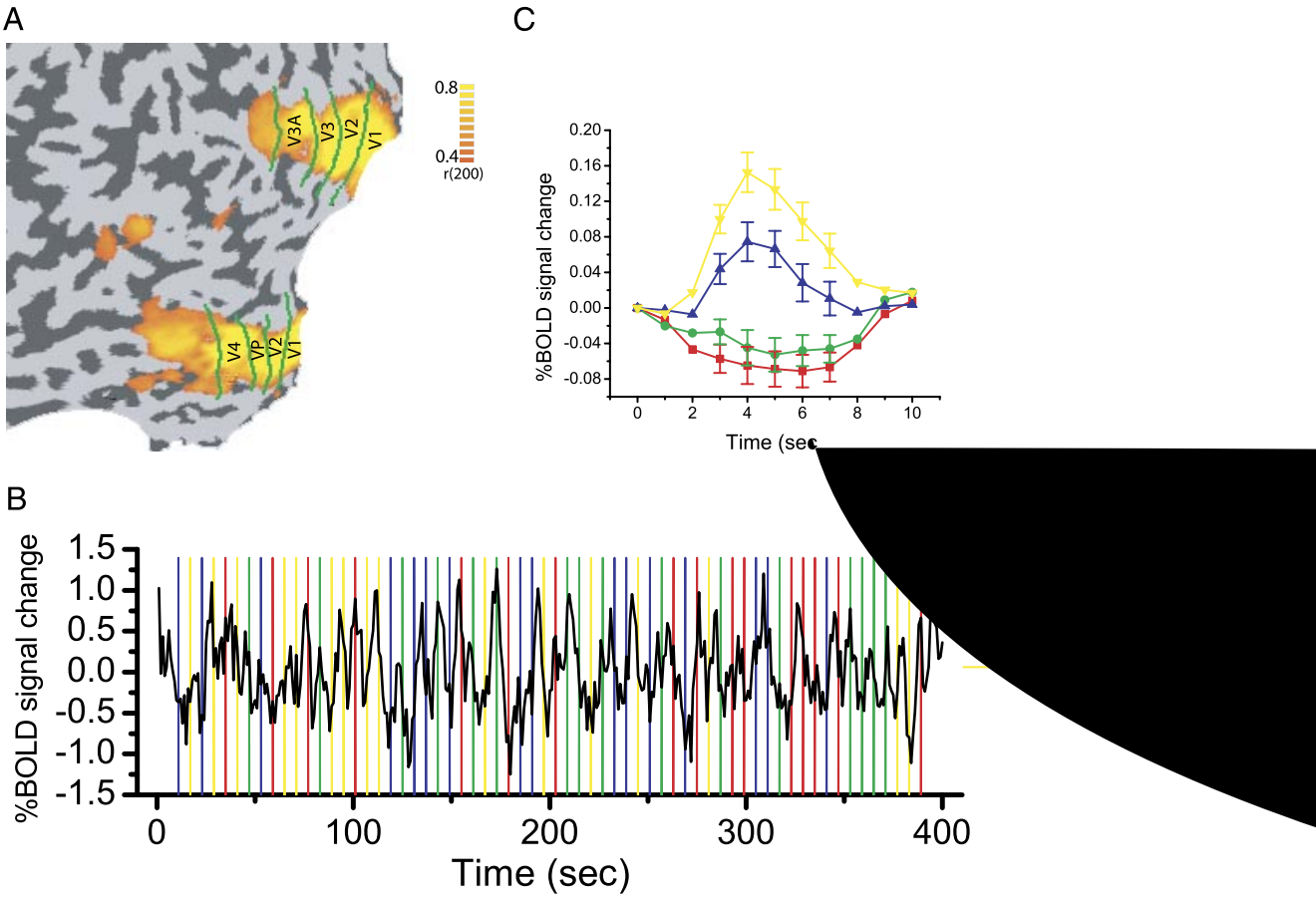
RESULTS

Behavioral responses to fixation tasks

In both short-term and long-term fMRI adaptation e periments, we categori ed reaction time (RT) and correct rate (CR) for the ation task into ve groups (test 0, test 7.5, test 30, test 90, and adaptation), dependent on whether there was temporal overlap between the luminance change of ation and a test stimulus. For e ample, if subjects made a response to a ation luminance change, which temporall overlapped with a 7.5__ test stimulus, this response was categori ed as belonging to the test 7.5 group. If the ation luminance change didn't overlap with an test stimulus, the response was categori ed as belonging to the adaptation group. The temporal variations of subjects' responses were ver small, and there was no signi cant behavioral difference between an pair of groups in both short-term (test 0: 501 ± 27 ms, 0.81 ± 0.02; test 7.5: 490 ± 34 ms, 0.79 ± 0.02; test 30: 495 ± 33 ms, 0.79 ± 0.06; test 90: 501 ± 14 ms, 0.77 ± 0.04; adaptation: 505 ± 18 ms, 0.81 ± 0.03) and long-term (test 0: 501 ± 25 ms, 0.79 ± 0.03; test 7.5: 491 ± 28 ms, 0.81 ± 0.03; test 30: 501 ± 32 ms, 0.81 ± 0.02; test 90: 495 ± 15 ms, 0.80 ± 0.04; adaptation: 523 ± 23 ms, 0.80 ± 0.03) adaptation e periments. This result suggests that subjects' general attentional state did not differ across the 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



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: $y = 0.11007 - 0.29666x$,

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shown that orientation adaptation is largel 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 e periment is not caused b 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 e planations. First, in our stud , both the adapting and test stimuli comprised multiple Gabor patches with randomi ed orientations as opposed to a large, single grating (Bo nton and Finne 2003; Tootell et al. 1998b). Having locali ed, distributed peripheral stimuli with a wide distribution of orientations helped to avoid sudden attention shifts from the ation task during the presentation of the test stimuli. In fact, most subjects reported that the were unaware when orientation changes occurred during the e periment. Second, if the presentation of test stimuli had induced transient attention shifts, we would have e pected to observe poorer behavioral performance of the ation task during test presentation. However, subjects performed equall well at all stages of the trial, 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 seems to be the duration of adaptation. The use of tens of seconds of preadaptation and topping-up adaptation is prevalent in ps choph sical and neuroph siological adaptation studies. The duration of adaptation in uences nearl 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 recover 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-speci c adaptation in V1 in the stud of Bo nton and Finne (2003) and ours with short-term adaptation ma simpl be attributed to V1 neurons not being suf - cientl adapted to be detected with fMRI. Our ps choph sical results, which show much larger elevations in contrast detection threshold after long-term adaptation, also support this possibilit . In addition, the validit of long-term fMRI adap-

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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