Orientation-Tuned fMRI Adaptation in Human Visual Corte

Fang Fang,[1] Scott O. Murray,[2] Daniel Kersten,[1] and Sheng He[1]

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

Submitted 13 April 2005; accepted in nal form 14 August 2005

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

for detecting the test stimulus f
failed to nd orientation-tuned
a short-term adaptation paradigm
nd Finne 's (2003) nding and
nations (e.g., transient attention
ng-term fMRI adaptation effect

H O D S

cts

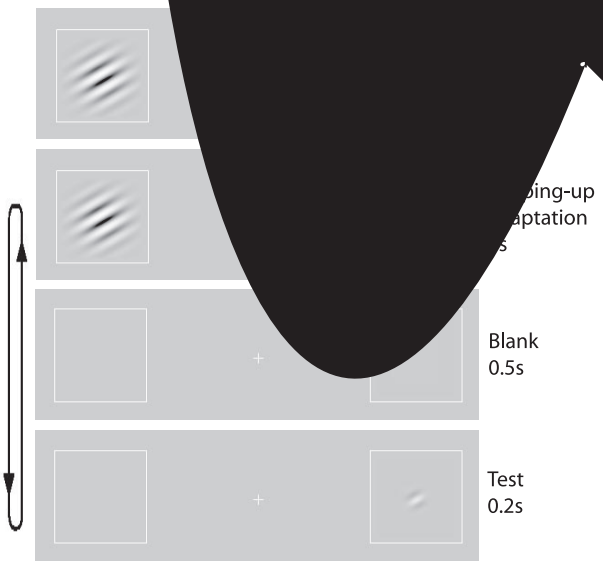
tal of ve health subjects (2 fema
M) were involved in these e perim
pated in the long-term ps choph
nents. YJ, WL, FF, and PT par
h sical and fMRI adaptation e
and ranged in age from 25 to
d-to-normal vision and gave w
nce with procedures and protoc
review committee of the Univer

periments

apting and test stimuli consisted
ranged in two concentri annul
1). Each of the eight p tches
f 1.9 (σ = 0.38) and a pati
outer annulus patches ea h
a spatial frequenc of 2.5 c cl
in the adapting stimuli wa

ed in each adaptation scan. Four test stimuli were
the adapting

ions.



were randomi ed at the beginning of the staircase. We also performed a ps choph sical short-term contrast adaptation e periment. Parallel to the fMRI e periments, adaptation time was shortened to 1 s, and all other parameters were equivalent to the long-term e periment, e cept that there was no 20-s preadaptation in the short-term adaptation e periment. The stimuli were presented on a SONY Trinitron Multiscan G420 19-in monitor, with a spatial resolution of 1280 × 1024 and refresh rate of 100 H . The viewing distance was 57 cm. The background luminance was 43 cd/m^2, and luminance level in the 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 × 22 cm^2, matri : 64 × 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 × 1 ×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 in 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

a
whic

In th
evoked B
the 30 and 9
and 7.5_test st
tation e periment,
each t pe of test stim
a 3- to 7-s latenc win
window was chosen to bi
other rapid event-related fM
scans) conducted in our laborat
fMRI adaptation effect between th
tation e periments, we subtracted the
test stimulus as baseline from those b
(Fig. 4*B*).

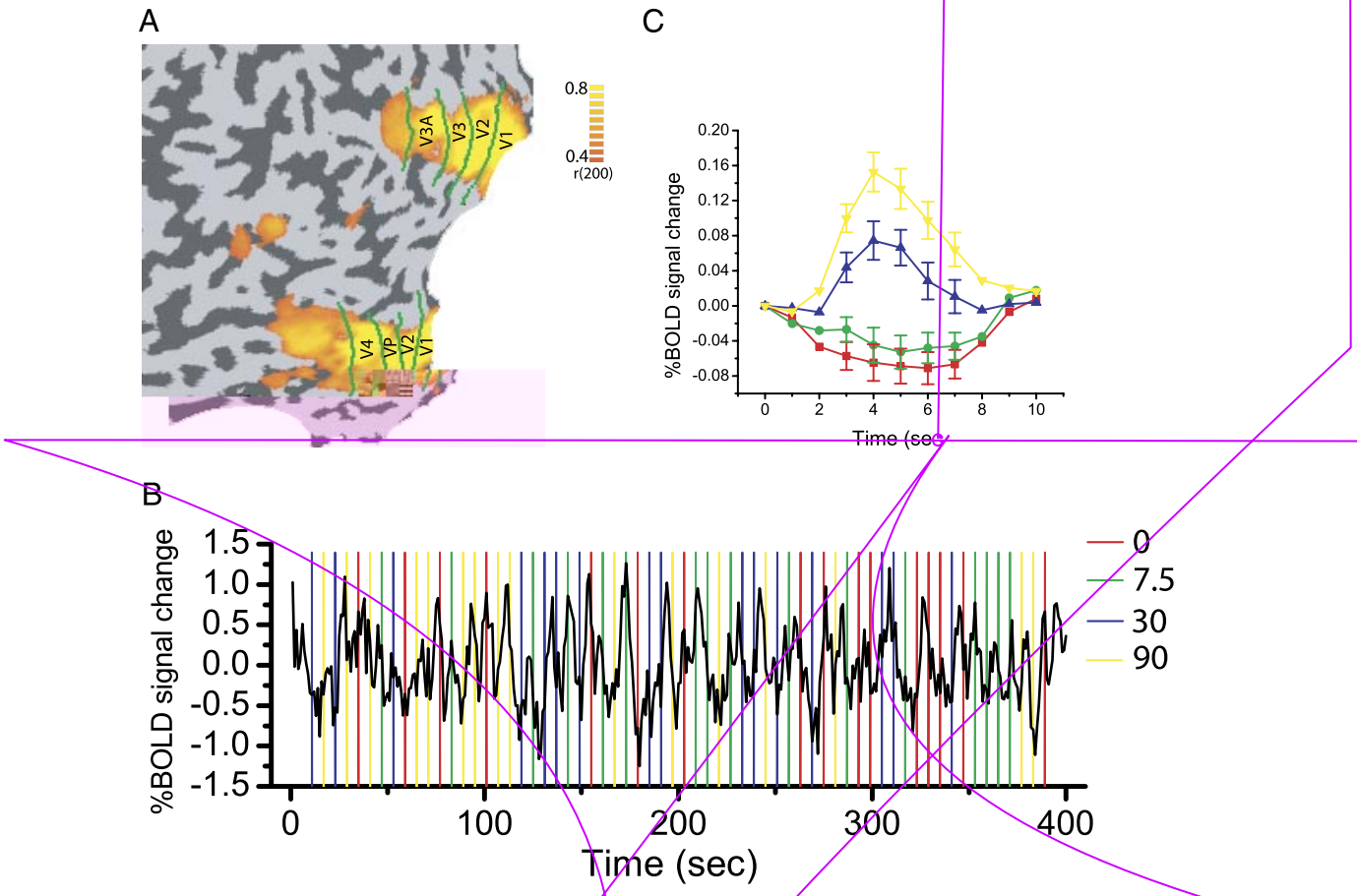
RESULTS

Behavioral responses to fixation tasks

In both short-term and long-term fMRI adaptatio
ments, we categori ed reaction time (RT) and correct rat
for the ation task into ve groups (test 0, test 7.5, test 30,
90, and adaptation), dependent on whether there was tempora
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 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: $y = 0.11007 - 0.29666x$,

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.

ACKNOWLEDGMENTS

We thank B. Tjan, Y. Jiang, J. Liu, and three anon mous reviewers for helpful comments.

GRANTS

This research was supported b the National Geospatial-Intelligence Agenc (NGA HM1582-05-C-0003), the James S. McDonnell Foundation, and National Institutes of Health Grants R01 EY-015261-01 and NCRR P41 RR-008079. F. Fang was also supported b the Eva O. Miller Fellowship from the Universit of Minnesota.

REFERENCES

Alonso J and Martinez LM. Functional connectivit between simple cells and comple cells in cat striate corte . *Nat Neurosci* 1: 395 403, 1998.

Blakemore C, Muncey JP, and Ridley RM. Stimulus speci cit in the human visual s stem. *Vision Res* 13: 1915 1931, 1973.

Blakemore C and Nachmias J. The orientation speci cit of two visual after-effects. *J Physiol* 213: 157 174, 1971.

Boynton G and Finney E. Orientation-speci c adaptation in human visual corte . *J Neurosci* 23: 8781 8787, 2003.

Brefczynski JA and DeYoe EA. A ph siological correlate of the 'spotlight' of visual attention. *Nat Neurosci* 2: 370 374, 1999.

Buracas GT and Boynton GM. Ef cient design of event-related fMRI e periments using M-sequences. *Neuroimage* 15: 801 813, 2002.

Callaway EM. Local circuits in primar visual corte of the macaque monke . *Annu Rev Neurosci* 21: 47 74, 1998.

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

Claeys KG, IG, N T1 K2 Td Orion- 1 DTK2 TdSchut. TdEDK2 TdT1

Larsson J, Landy MS, and Heeger DJ. Orientation-selective adaptation in human V1 revealed b event-related fMRI. *Soc Neurosci* 986.8, 2004.

Leopold DA, Wilke M, Maier A, and Logothetis NK. Stable perception of visuall ambiguous patterns. *Nat Neurosci* 5: 605 609, 2002.

Liu T, Pestilli F, and Carrasco M. Transient attention enhances perceptual performance and fMRI response in human visual corte . *Neuron* 45: 469 477, 2005.

Liu T, Slotnick SD, and Yantis S. Human MT+ mediates perceptual lling-in during apparent motion. *Neuroimage* 21: 1772 1780, 2004.

Logothetis NK, Pauls J, Augath M, Trinath T, and Oeltermann A. Neuroph siological investigation of the basis of the fMRI signal. *Nature* 412: 150 157, 2001.

Mather G, Verstraten F, and Anstis S. The motion aftereffect: a modern perspective. Cambridge, MA: MIT Press, 1998.

Moradi F, Koch C, and Shimojo S. Face adaptation depends on seeing the face. *Neuron* 45: 169 175, 2005.

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

Muller JR, Metha AB, Krauskopf J, and Lennie P. Rapid adaptation in visual corte to the structure of images. *Science* 285: 1405 1408, 1999.

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

Nelson SB. Temporal interactions in the cat visual s stem. I. Orientation-selective suppression in the visual corte . *J Neurosci* 11: 344 356, 1991.

Paradiso MA, Shimojo S, and Nakayama K. Subjective contours, tilt aftereffects and visual cortical organi ation. *Vision Res* 29: 1205 1213, 1989.

Ress D and Heeger DJ. Neuronal correlates of perception in earl visual corte . *Nat Neurosci* 6: 414 420, 2003.

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

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

Smith AM, Lewis BK, Ruttimann UE, Ye FQ, Sinnwell TM, Yang Y, Duyn JH, and Frank JA. Investigation of low frequenc drift in fMRI signal. *Neuroimage* 9: 526 533, 1999.

Snowden RJ and Hammett ST. Subtractive and divisive adaptation in the human visual s stem. *Nature* 355: 248 250, 1992.

Somers DC, Dale AM, Seiffert AE, and Tootell RBH. Functional MRI reveals spatiall speci c attentional modulation in human primar visual corte . *Proc Natl Acad Sci USA* 96: 1663 1668, 1999.

Talairach J and Tournoux P. *Co-Planar Stereotaxic Atlas of the Human Brain.* New York: Thieme Medical Publishers, 1988.

Tootell RB, Hadjikhani NK, Hall EK, Marrett S, Vanduffel W, Vaughan JT, and Dale AM. The retinotop of visual spatial attention. *Neuron* 21: 1409 1422, 1998a.

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

Tsao DY, Vanduffel W, Sasaki Y, Fize D, Knutsen TA, Mandeville JB, Wald LL, Dale AM, Rosen BR, Van Essen DC, Livingstone MS, Orban GA, and Tootell RB. Stereopsis activates V3A and caudal intraparietal areas in macaques and humans. *Neuron* 39: 555 568, 2003.

Tyler CW. Stereoscopic tilt and si e aftereffects. *Perception* 4: 187 192, 1975.

von der Heydt R and Peterhans E. Mechanisms of contour perception in monke visual corte . I. Lines of pattern discontinuit . *J Neurosci* 9: 1731 1748, 1989.

Watanabe T, Harner AM, Miyauchi S, Sasaki Y, and Nielsen M. Task-dependent in uences of attention on the activation of human primar visual corte . *Proc Natl Acad Sci USA* 95: 11489 11492, 1995.

Watson AB and Pelli DG. QUEST: a ba esian adaptive ps chometric method. *Percept Psychophys* 33: 113 120, 1983.

Zeki S and Marini L. Three cortical stages of colour processing in the human brain. *Brain* 121: 1669 1685, 1998.