

Effects of Orientation-Specific Visual Deprivation Induced with Altered Reality

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Summary

What happens to neurons in visual cortex when they are deprived of their preferred stimuli? Long-term deprivation during development, spanning weeks, reduces the number of neurons selective for the deprived orientation [1–4]. In contrast, short-term deprivation in adults, for periods of seconds, can increase neural sensitivity relative to a stimulated baseline [5]. Effects over intermediate timescales remain largely unexplored, however. Here we introduce a new method for manipulating the visual environment of adult humans and report effects of four hours of orientation-specific deprivation. Subjects wore a head-mounted video camera that fed into a laptop computer that drove a head-mounted display. Software filtered the video stream in real time, allowing subjects to interact with the world while being deprived of visual input at a specified orientation. Four hours in this environment increased sensitivity to the deprived orientation, which likely reflected an increase in responsiveness of neurons in early visual cortex. Our results help distinguish between two theories of neural adaptation: the response increase optimized the responses of individual neurons, rather than increasing the efficiency of the population code. Our method should be able to produce a wide range of environmental manipulations useful for studying many topics in perception.

Results and Discussion

A Method for Manipulating the Visual Environment

To deprive subjects of information at a specified orientation while leaving information at other orientations intact, we developed a novel display device. The system is comprised of a digital video camera housed on a battery-powered, portable, head-mounted display (HMD; see Figure 1A). The camera connects to a high-end graphics laptop computer that runs image-processing algorithms on the video feed and displays the results on the HMD. To remove information at one orientation, we filtered incoming video frames in the Fourier domain in real time prior to their display (Figures 1B–1D; filtered video was displayed at 30 frames per second).

Subjects wore this “altered reality” system for 4 hr, during which time they took walks, played games, ate, and watched movies, among other activities. The system is housed on a cart that draws power from either a wall outlet or a battery pack. A long cable allows subjects to walk away from the cart, and they push the cart when taking longer walks. For

details of methods, see [Experimental Procedures](#), below, and [Supplemental Experimental Procedures](#) available online.

Orientation-Specific Deprivation

Subjects tolerated the altered reality system well and reported a noticeable difference in the visual world during deprivation, finding it “blurry” and “weird.” Everyday tasks were more difficult during deprivation, and most subjects reported adapting to the environment, noting that tasks got easier over time.

To measure these effects quantitatively, we gathered detection thresholds for sinusoidal patterns of light and dark before and after deprivation. Detection thresholds represent the weakest stimuli that subjects can reliably distinguish from a uniform screen.

Subjects were deprived of either vertical or horizontal information, and deprivation lowered thresholds at the deprived orientation compared to the orthogonal orientation. Figure 2A plots thresholds averaged across subjects and the two deprived and control orientations. Immediately following deprivation, thresholds for the deprived orientation were reliably lower than thresholds for the control orientation ($t(7) = 3.71$, $p < 0.01$ for vertical deprivation; $t(7) = 2.90$, $p < 0.03$ for horizontal deprivation). This difference was reduced at the second posttest ($t(7) = 2.47$, $p < 0.05$; $t(7) = 1.01$, $p > 0.3$) and disappeared 24 hr later ($p > 0.1$ for both conditions).

These results suggest that deprivation increased the relative sensitivity of perceptual mechanisms that respond to the deprived orientation. Note, however, that absolute thresholds to both orientations rose following deprivation. The most likely explanation for this pattern is that wearing the goggles fatigued subjects, which led to an overall rise in thresholds in the first two posttests. This rise was visible in the control orientation but was cancelled out by a decrease in thresholds in the deprived orientation. Supporting such an interpretation is the fact that deprived orientation thresholds rose between the first and second posttests, whereas control thresholds stayed constant. This suggests that the sensitivity increase to the deprived orientation was lost as subjects were exposed to it during testing, whereas the fatigue effect, as expected, did not recover rapidly. Also consistent is the further drop of thresholds at the 24 hr posttests, by which time fatigue effects should have disappeared.

Nevertheless, the data from experiment 1 do not completely rule out an alternative interpretation. It could be that wearing the goggles simply decreased sensitivity to the control orientation through well-known adaptation mechanisms: exposure to high-contrast oriented stimuli reduces sensitivity to that orientation compared to unadapted control orientations (for reviews, see [6, 7]). Although our deprivation did not explicitly increase the stimulus contrast at the control orientation, removing the deprived orientations could have increased effective contrast of remaining orientations, for example by removing energy from the pool of neurons thought to normalize neural responses by divisive inhibition [8, 9]. Filtering vertical left subjects viewing predominantly the horizontals, which may have had increased effective contrast compared to before deprivation, leading to a decrease in sensitivity to horizontal.

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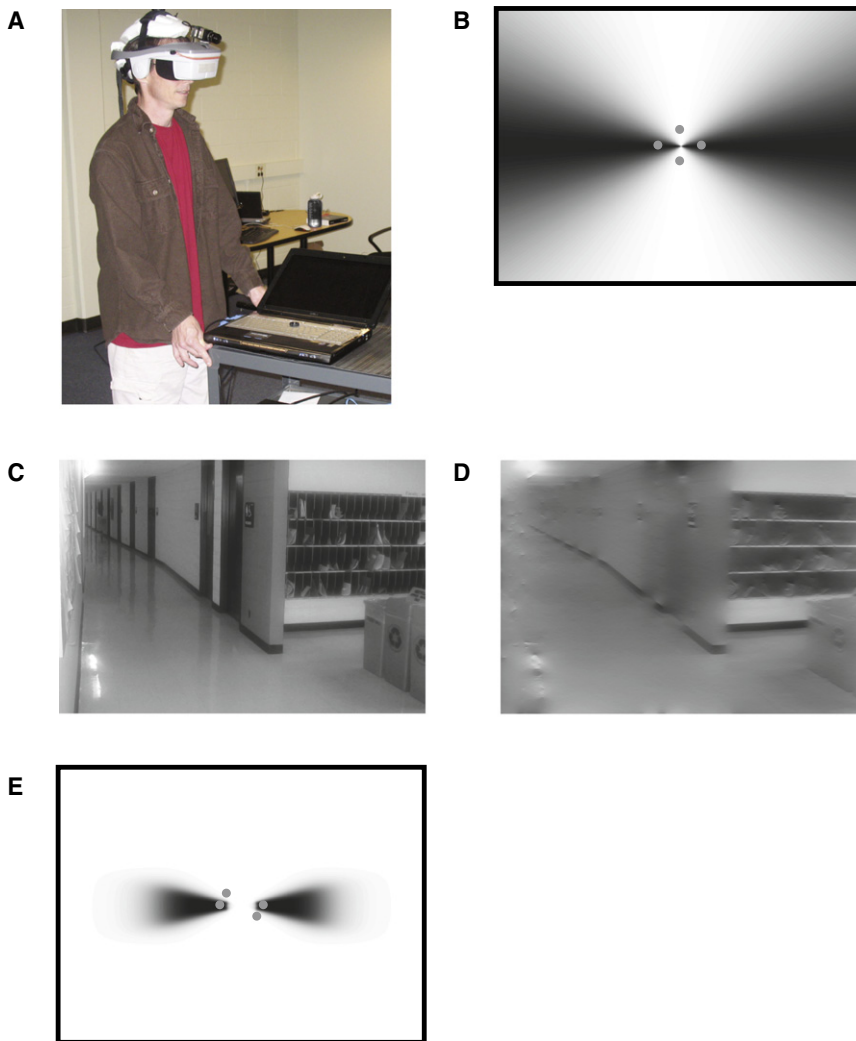


Figure 1. Experimental Methods

(A) Subjects wore a head-mounted display (HMD) and a video camera. The camera streamed video to a laptop computer where the images were filtered and displayed on the HMD.

(B) The filter used in experiment 1 is shown in the Fourier domain. Black colors indicate where the filter passed zero energy and are centered on vertical orientations (along the x axis by convention). Dots indicate the frequency and orientation of the test stimuli used in experiment 1.

(C and D) Sample intact and filtered images. Note the preservation of horizontal structure in the filtered image.

(E) The filter and stimuli used in experiment 2.

1 ($t(20) = 0.42, p > 0.68$). The data replicated our findings from experiment 1, and suggest that adaptation to the control orientation was not a major cause of the effects we observed.

The results of experiment 2 also confirmed effects of fatigue in experiment 1. Because of the more limited filtering, subjects reported that experiment 2 was less fatiguing. As expected, then, when fatigue was reduced, the rise of absolute thresholds for the nondeprived orientation seen in experiment 1 disappeared, and thresholds for the deprived orientation decreased, rather than holding level. Discussion of other possible effects that could be present in our data can be found in the [Supplemental Discussion](#).

Short-Term Effects of Deprivation

A final experiment examined the time course of effects of deprivation. Sub-

jects' self-reports indicated a relatively gradual change in perception, but to formally test whether deprivation effects accrued slowly, experiment 3 repeated experiment 2 with only 1 hr of exposure. After 1 hr of deprivation, subjects showed no reliable change in threshold (Figure 2C; $n = 14$; $t(12) = 1.07, p > 0.3$). Changes in threshold in experiment 3 were reliably smaller than in experiments 1 and 2 ($t(34) = 2.32, p < 0.03$).

Adaptation in the Visual System

In summary, we found that 4 hr of orientation-selective deprivation increased sensitivity to the deprived orientation. Thresholds dropped by approximately 15%. Detection of simple oriented patterns, such as the ones used here, is closely linked to responses of neurons in early visual cortex [10–12]. Deprivation likely increased the responsiveness of such neurons.

In developing animals, deprivation causes a loss of neurons tuned to the deprived orientations (e.g., [1–3]). Our work was inspired by these studies, but this first series of experiments deprived adult subjects for much shorter durations than those used in developmental work. Perhaps not surprisingly, then, the pattern of results we observed did not parallel what has been reported in developmental studies. It may also be that for human orientation deprivation, developmental

Deprivation of a Narrow Range of Orientations and Spatial Frequencies

To rule out this alternative explanation, we conducted experiment 2, in which the filter had much more limited extent in both orientation and spatial frequency (Figure 1E; filter cutoffs were $2/3$ cycles per degree [cpd] to 4 cpd and 70° to 110°). Accordingly, the remaining energy in the image was much more broadly distributed than in the first experiment. The restricted filtering should produce smaller changes in contrast normalization mechanisms, and so effective contrast at control orientations should be relatively unaffected, reducing the possibility of selective adaptation at those orientations. We also used a 45° pattern as the control in experiment 2. This diagonal orientation contained lower energy during the deprivation period than the horizontal and vertical control orientations used in experiment 1, which should reduce the possibility of traditional adaptation effects even further. Thus, if adaptation to the control orientation was driving the effects seen in experiment 1, then experiment 2 should show much smaller effects of deprivation.

Thresholds measured in experiment 2 showed effects of deprivation that were the same size as in experiment 1. At the first posttest, thresholds for the deprived orientation were approximately 15% lower than the diagonal control orientation (Figure 2B). This difference was reliable ($t(5) = 3.86, p < 0.02$) and did not differ in magnitude from that seen in experiment

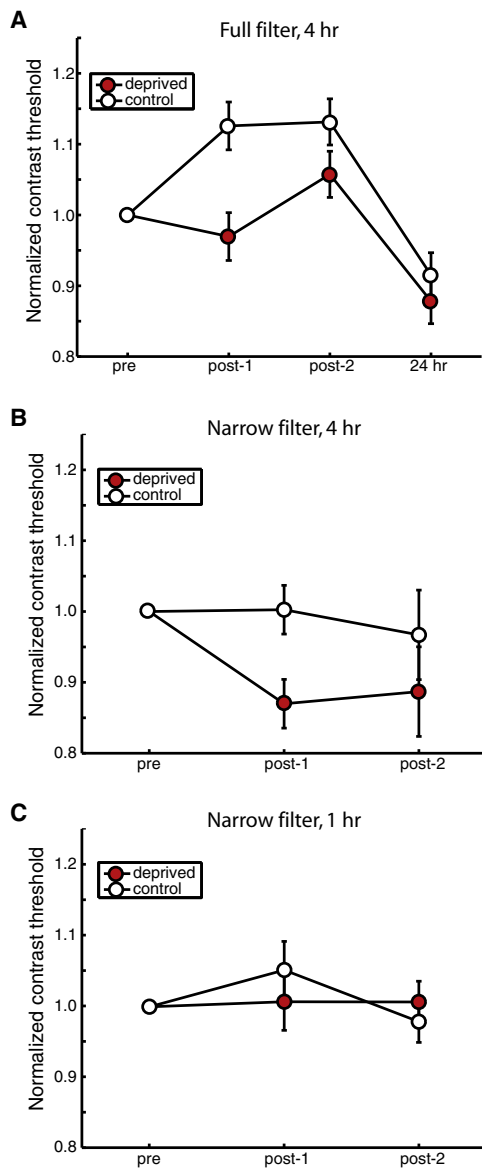


Figure 2. Results

(A) Experiment 1. Mean contrast detection thresholds are plotted as a function of testing session. The two halves of the 40 min testing session following deprivation were analyzed separately and are labeled “post-1” and “post-2,” and another testing session, labeled “24 hr,” was conducted a day later. Thresholds were normalized separately for each condition by dividing by the pretest threshold, which set the pretest scores to unity. Relative threshold for the deprived orientation is lower than the control orientation at the first posttest following deprivation.

(B) Experiment 2. The difference of threshold at the first posttest was observed even when a more limited filtering was performed.

(C) Experiment 3. No differences were observed following only 1 hr of deprivation.

All error bars represent \pm one standard error of the mean.

mechanisms of plasticity are no longer active after the end of a critical period.

Our results are more consistent with classical effects of short-term adaptation to contrast, in which exposure to a high-contrast pattern reduces sensitivity (for reviews, see [6, 7]). Psychophysically, short-term contrast adaptation is selective for both orientation and spatial frequency, and

physiological work has shown that it decreases the responsiveness of neurons tuned to the adapting stimulus. Our data are essentially the inverse of these experiments: deprivation removed adapting contrast normally present in the environment, which in turn released adaptation and increased sensitivity. Under this interpretation, our results illustrate how vision is always in some state of adaptation to the environment and that even baseline measures of contrast sensitivity, such as those made during our pretest, are not absolute measures of function (see [5] for a similar argument made about neural thresholds; see [Supplemental Results](#) and [Supplemental Discussion](#) for additional discussion of these and other topics).

Our results are also generally consistent with prior work examining longer-term adaptation in adults. For example, aging gradually changes the color of light reaching the eye. The visual system adapts to these changes in a way that keeps perceived colors relatively constant [13]. Similarly, wearing colored lenses for many hours per day across many days can induce changes in perception that neutralize the effects of the lenses [14], and long-term adaptation may serve to maintain color constancy despite changes in neural sensitivity across the visual field [15]. Additionally, 4 hr of exposure to a global reduction in visual contrast induces compensatory visual system plasticity [16]. Collectively, these results suggest that one function of adaptation is to keep perception constant despite environmental changes. Our results fit well within this interpretation; the sensitivity increases we observed could have been the visual system’s (unsuccessful) attempt to compensate for the decrease in contrast at the deprived orientation.

Effects that can be considered contrast adaptation have time courses of acquisition and decay that span several orders of magnitude. For example, responses in cat visual cortex can be altered by as little as 50 ms of adaptation [17], whereas classical perceptual contrast adaptation takes seconds or minutes to arise (e.g., [18]). Our effects appear to accumulate even more slowly, requiring hours. However, a single mechanism of adaptation, operating over multiple timescales, might account for both our results and traditional contrast adaptation. The strength and duration of contrast adaptation generally scales with the strength and length of the adaptation period (e.g., [18]). Thus, it is possible that effects of deprivation were present after 1 hr (or even sooner) but decayed too quickly to be measured, whereas 4 hr of adaptation allowed them to be detected. It nevertheless remains possible that the mechanisms of adaptation that account for our more slowly accruing effects are different than those that account for contrast adaptation. The methods introduced here provide an opportunity to test in future work whether the same adaptation mechanisms operate over the short, medium, and long term.

Functional Role of Sensitivity Changes

Why should deprivation produce a sensitivity increase? Most theories hypothesize that adaptation increases the efficiency of visual cortex in some way. One focuses on individual cells. Neurons may adjust sensitivity to keep their most useful operating range (the steepest part of their contrast response function) centered on current stimulus contrast [5, 19]. Such adaptation increases a measure of efficiency, the amount of information about the current stimulus that a given neuron is able to transmit, by increasing the accuracy with which signals around current levels of stimulation are represented. Our

results are consistent with this account: cells selective for the deprived orientation may have increased their sensitivity in order to be able to respond well to small changes to the unusually low levels of input they received during deprivation. Prior psychophysical evidence for adaptation improving visual sensitivity (reviewed in [20]) is mixed, leaving the question of the functional role of adaptation an open one [7]. Our results present a clear case of adaptation improving visual sensitivity in a manner that could be expected to benefit the observer.

Our results are less consistent with a different notion of neural efficiency. Neurons may adjust their responsiveness to maximize information transmitted about the stimulus measured over the entire set of visual neurons, given constraints such as a finite number of neurons or overall metabolic cost of spiking [21–23]. Such models predict a reduction in neural sensitivity to the deprived orientation. To understand this, note that increasing the sensitivity of neurons tuned to the deprived orientation will only amplify noise in the neural population because no stimulus energy is in fact present for that subset of neurons to represent. Thus, it would be more optimal to devote fewer neurons and/or spikes to the deprived orientation [23], which could be implemented by either reducing the neurons' gain or shifting their tuning toward more informative orientations.

Additional constraints could, however, make our observed effects optimal for the population code. It could be, for example, that decreasing sensitivity after 4 hr of deprivation is inefficient because of the likelihood that the environment will revert to normal [24], or that relevant neural mechanisms are only active during a critical period of development or after longer periods of deprivation. Testing whether long-term deprivation can decrease sensitivity to the deprived orientation is one direction for future research. Our method for manipulating the visual environment over the medium and long term should also have applicability in many other domains.

Experimental Procedures

Image Filtering

In experiment 1, the filter was a wedge in the Fourier domain, centered on the filtered orientation with a Gaussian profile (standard deviation, 30°). This filter removed all energy at the specified orientation across all spatial frequencies while leaving the orthogonal orientations unaffected. In experiment 2, the filter was a second-order Butterworth filter centered at 1 cpd. The filter cutoffs were 2/3 cpd to 4 cpd in spatial frequency and 70° to 110° in orientation; filter strength fell to below 2% of maximum outside of this range. Description of the hardware and other methodological details can be found in the [Supplemental Experimental Procedures](#).

Subjects

Seven observers took part in both the vertical and horizontal deprivation conditions of experiment 1. Two others only participated in one condition each. Six observers participated in experiment 2, and thirteen participated in experiment 3. All subjects had normal or corrected-to-normal vision.

Detection Stimuli

Stimuli were patches of sine-wave gratings whose edges were smoothed with a Gaussian filter. In experiment 1, patches were oriented either vertically or horizontally. In experiments 2 and 3, patches were oriented either vertically or at a 45° angle. The patches subtended 6° of visual angle and were centered 8° away from fixation, in the center of one of the four quadrants of the display. The stimulus quadrant used was counterbalanced across subjects. The spatial frequency of the gratings was 1 cpd.

Subjects were tested either on the head-mounted display (HMD) or on an external cathode ray tube (CRT) display. Both displays were driven by a Bits++ 14-bit video card (Cambridge Research Systems) and were calibrated with a Photo Research PR-655 spectrophotometer. To calibrate the displays, we measured luminance gamma curves and inverted them

with a look-up table. We conducted testing within a circular aperture in order to limit exposure to horizontal and vertical edges.

Detection Task

Subjects performed a two-interval forced-choice contrast detection task. Trials consisted of two 200 ms intervals separated by 200 ms. During each trial, subjects indicated which of the two intervals contained a stimulus whose contrast varied under the control of a staircase procedure. Each subject completed six staircases of each orientation in a testing session; orientation order was counterbalanced across subjects.

Subjects participated in four testing sessions in experiment 1 and three testing sessions in experiments 2 and 3; the first session was held immediately before the adaptation period. Subjects were tested again immediately following adaptation. To give a better sense of the duration of adaptation effects, we divided these trials into two sets, containing the first three and last three staircases of each orientation (labeled "post-1" and "post-2"). In experiment 1, a final session was held 24 hr following the adaptation period.

Analysis

To measure detection thresholds, we fit Weibull functions to the data pooled across all staircases in a given condition and session. Threshold was defined as the contrast at which the best-fitting function estimated performance to be 82% correct.

Supplemental Data

Supplemental data include Supplemental Results, Supplemental Discussion, Supplemental Experimental Procedures, and one figure and can be found online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01837-5](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01837-5).

Acknowledgments

The authors thank G. Legge and P. Schrater for helpful discussions and L. Shams, M. Falconbridge, and A. Yuille for initial inspiration to build the system. This work was funded by a Digital Technology Initiative grant from the University of Minnesota Digital Technology Center and a grant from the Keck Foundation to the University of California, Los Angeles Center for Image and Vision Science.

Received: June 2, 2009

Revised: October 2, 2009

Accepted: October 5, 2009

Published online: November 5, 2009

References

1. Blakemore, C., and Cooper, G.F. (1970). Development of the brain depends on the visual environment. *Nature* 228, 477–478.
2. Hirsch, H.V., and Spinelli, D.N. (1970). Visual experience modifies distribution of horizontally and vertically oriented receptive fields in cats. *Science* 168, 869–871.
3. Sengpiel, F., Stawinski, P., and Bonhoeffer, T. (1999). Influence of experience on orientation maps in cat visual cortex. *Nat. Neurosci.* 2, 727–732.
4. Tanaka, S., Ribot, J., Imamura, K., and Tani, T. (2006). Orientation-restricted continuous visual exposure induces marked reorganization of orientation maps in early life. *Neuroimage* 30, 462–477.
5. Ohzawa, I., Sclar, G., and Freeman, R.D. (1985). Contrast gain control in the cat's visual system. *J. Neurophysiol.* 54, 651–667.
6. Graham, N. (1989). *Visual Pattern Analyzers* (Oxford: Oxford University Press).
7. Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *J. Neurophysiol.* 97, 3155–3164.
8. Albrecht, D.G., and Geisler, W.S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual cortex. *Vis. Neurosci.* 7, 531–546.
9. Heeger, D.J. (1992). Normalization of cell responses in cat striate cortex. *Vis. Neurosci.* 9, 181–197.
10. Hawken, M.J., and Parker, A.J. (1990). Detection and discrimination mechanisms in the striate cortex of the old-world monkey. In *Vision: Coding and Efficiency*, C. Blakemore, ed. (Cambridge: Cambridge University Press), pp. 103–116.

11. Ress, D., and Heeger, D.J. (2003). Neuronal correlates of perception in early visual cortex. *Nat. Neurosci.* 6, 414–420.
12. Tolhurst, D.J., Movshon, J., and Dean, A. (1983). The statistical reliability of signals in single neurons in cat and monkey visual cortex. *Vision Res.* 23, 775–785.
13. Delahunt, P.B., Webster, M.A., Ma, L., and Werner, J.S. (2004). Long-term renormalization of chromatic mechanisms following cataract surgery. *Vis. Neurosci.* 21, 301–307.
14. Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M., and Williams, D.R. (2002). Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron* 35, 783–792.
15. Webster, M.A., and Leonard, D. (2008). Adaptation and perceptual norms in color vision. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* 25, 2817–2825.
16. Kwon, M., Legge, G.E., Fang, F., Cheong, A.M.Y., and He, S. (2009). Adaptive changes in visual cortex following prolonged contrast reduction. *J. Vis.* 9, 1–16.
17. Bonds, A.B. (1991). Temporal dynamics of contrast gain in single cells of the cat striate cortex. *Vis. Neurosci.* 6, 239–255.
18. Greenlee, M.W., Georgeson, M.A., Magnussen, S., and Harris, J.P. (1991). The time course of adaptation to spatial contrast. *Vision Res.* 31, 223–236.
19. Albrecht, D.G., Farrar, S.B., and Hamilton, D.B. (1984). Spatial contrast adaptation characteristics of neurones recorded in the cat's visual cortex. *J. Physiol.* 347, 713–739.
20. Abbonizio, G., Langley, K., and Clifford, C.W. (2002). Contrast adaptation may enhance contrast discrimination. *Spat. Vis.* 16, 45–58.
21. Atick, J.J., and Redlich, A.N. (1992). What does the retina know about natural scenes? *Neural Comput.* 4, 196–210.
22. Sharpee, T.O., Sugihara, H., Kurgansky, A.V., Rebrik, S.P., Stryker, M.P., and Miller, K.D. (2006). Adaptive filtering enhances information transmission in visual cortex. *Nature* 439, 936–942.
23. Wainwright, M.J. (1999). Visual adaptation as optimal information transmission. *Vision Res.* 39, 3960–3974.
24. Wark, B., Fairhall, A., and Rieke, F. (2009). Timescales of inference in visual adaptation. *Neuron* 61, 750–761.