

Four Days of Visual Contrast Deprivation Reveals Limits of Neuronal Adaptation

Koen V. Haak,^{1,*} Elizabeth Fast,² Min Bao,³ Michael Lee,⁴ and Stephen A. Engel^{2,*}

¹Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Kapittelweg 29, 6525 EN Nijmegen, the Netherlands

²Department of Psychology, University of Minnesota, 75 East River Road, Minneapolis, MN 55455, USA

³Institute for Psychology, Chinese Academy of Sciences, 16 Lincui Road, Chaoyang District, Beijing 100101, China

⁴Department of Ophthalmology and Visual Neurosciences, University of Minnesota, 420 Delaware Street South East, Minneapolis, MN 55455, USA

Summary

Sensory systems continuously adjust their function to match changes in the environment. Such adaptation produces large perceptual effects, and its pervasiveness makes it a key part of understanding cortical function generally [1–3]. In visual contrast adaptation, for example, brief exposure to vertical stripes can dramatically alter the apparent orientation and intensity of similarly oriented patterns (e.g., [4–7]). However, many environmental changes are long lasting. How does the visual system adjust to such challenges? Most past work on contrast adaptation has adapted subjects for just a few minutes. Only a few studies have examined durations greater than 1 hr [8–12], and none have exceeded 1 day. Here, we measured perceptual effects of adaptation in humans who viewed a world lacking vertical information for 4 days continuously. As expected, adaptation increased in magnitude during the first day, but it then showed a drop in strength. The decrease in adaptation is surprising because the adapting environment remained constant, and in short-term work, adaptation always strengthens or at least is maintained under such conditions. It indicates that the classical effects of contrast adaptation, which arise largely in primary visual cortex [13–18], are not maintained after approximately 1 day. Results from day 2 through day 4 further showed that slower adaptive processes can overcome this limit. Because adaptation is generally beneficial overall, its limits argue that the brain is sensitive to costs that arise when the neural code changes [19, 20]. These costs may determine when and how cortex can alter its function.

Results and Discussion

We tested the limits of visual contrast adaptation by measuring effects of 4 days of continuous exposure to an altered visual environment. Subjects were deprived of visual input at a specified range of orientations. They wore a video camera and viewed its feed on a head-mounted display after filtering in real time [10, 12] to remove 85% of vertical energy (Figure 1A). Reducing energy at an orientation produces a form of contrast adaptation, where weak input causes

neurons in visual cortex to increase their responsiveness [9, 10, 12, 15].

We measured adaptation with two tasks used in past work. In a contrast appearance judgment [5, 14, 21, 22], observers adjusted the contrast of a horizontal pattern to match the apparent contrast of a weak vertical one (of 5% contrast, Figure 1B), and we measured the amount of adjustment required. Following deprivation, this value increased, indicating that the neural response to vertical contrast strengthened. In an orientation judgment (Figure 1C), subjects adjusted the relative tilts of two superimposed 45° diagonal patterns, whose intersections normally appear square. Adaptation tilted the perceived orientation of the individual patterns [23], which caused the checks to appear rectangular [24]. Such tilt again indicates that deprivation altered the strength of a neural signal for the deprived orientation. Subjects adjusted the patterns' orientations to make the checks reappear square.

Each task was tested twice daily in 2.5 min sessions, during which time subjects made many settings. Within a given session, adaptation was strongest at the beginning and then decayed to a nonzero level near the session's end. We separately estimated the amplitudes of each session's peak and ending level in order to quantify both adaptation's strength and its durability. Detailed methods and associated references are available in the [Supplemental Experimental Procedures](#). The experiments were approved by the University of Minnesota Institutional Review Board.

In a group of five pilot subjects, tested using only the contrast appearance measure, adaptation showed a local maximum on the first day (Figure 1D; warmer colors show stronger adaptation). Total adaptation during the first session on day 1 was greater than it was during surrounding sessions ($t_4 = 3.7$, $p < 0.02$; $t_4 = 2.5$, $p < 0.07$ for peak). The local maximum on the first day is surprising because in past reports, short-term adaptation has never decreased in strength over time. Across subsequent sessions, there were trends for both the peak level and the ending level to grow stronger (both $t_4 > 2.3$, $p < 0.08$).

The pilot results were confirmed with an independent sample of seven subjects (Figures 2A and 2B), who performed both the appearance and orientation tasks. For appearance, peak adaptation again showed an early local maximum ($t_6 = 2.4$, $p < 0.05$), although during the second session of day 1 rather than during the first session. On subsequent days, both peak and late adaptation grew steadily across sessions ($t_6 = 4.7$, $p < 0.01$; $t_6 = 2.5$, $p < 0.05$).

Adaptation's effects on orientation also showed an early local maximum in peak strength during day 1 ($t_6 = 3.4$, $p < 0.02$). However, following that, adaptation rose to maximum strength and then fell over the last three or four sessions, producing an inverted U-shaped function, reliably for the ending level ($t_6 = 3.6$, $p < 0.02$). This pattern during the later sessions differed from adaptation's effects on appearance (Figures 2C and 2D; $F_{9,54} = 3.4$, $p < 0.01$).

Adaptation's early peak arose in the second session for the appearance test in our main experiment, but in the first session of the main experiment's orientation task, as well as for the pilot experiment's appearance test. This difference occurred

*Correspondence: k.haak@donders.ru.nl (K.V.H.), engel@umn.edu (S.A.E.)

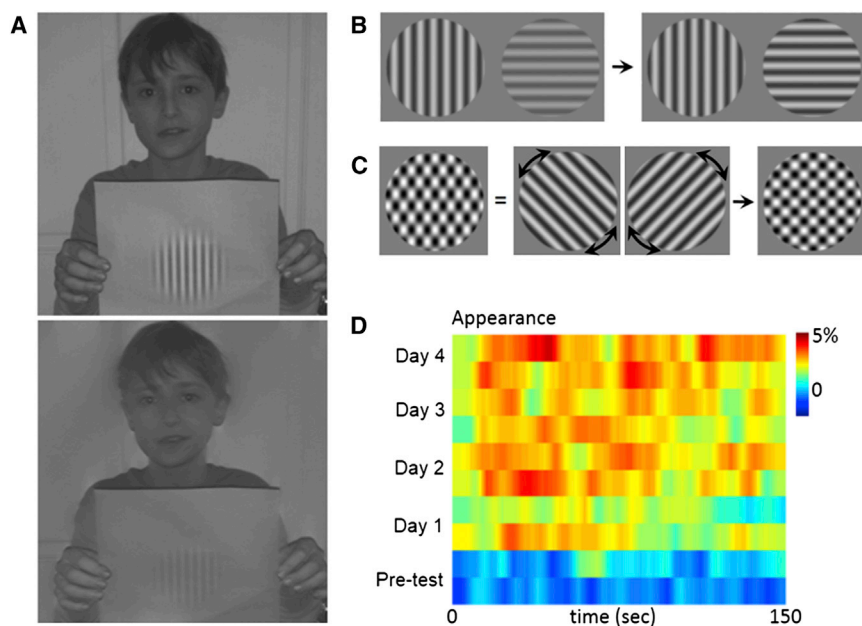


Figure 1. Effects of Filtering, Tasks, and Adaptation in the Pilot Experiment

(A) An intact image (top) and the same image with 85% of vertical energy removed (bottom).

(B) Appearance task. Subjects adjusted a horizontal grating patch to match the appearance of a vertical patch. Contrast has been raised for clarity.

(C) Orientation task. Subjects viewed a plaid pattern comprised of two diagonal gratings and adjusted the orientations of the diagonals to make the plaid's checks appear square.

(D) Adaptation in the pilot experiment. Color shows change in apparent contrast of a vertical test grating as a function of the time during the testing session (x axis) and the time of the testing session (y axis). The first two testing sessions were a pretest before deprivation, and their mean was subtracted from all sessions to compute changes due to adaptation. Across days, adaptation grew stronger and longer lasting. There was also evidence of a local maximum in adaptation strength on the first day of deprivation.

most likely because the appearance data in the main group were gathered earlier in the day than the other two sets of data, effectively shifting the peak to one session later. The peak timing may have also reflected the overall strength of adaptation, which differed slightly between the pilot and main experiments.

The simplest account of our results is that they arise from two distinct neural processes controlling adaptation. The striking local maximum of adaptation during the first day of deprivation likely represents the action of a “fast” process. This process relatively rapidly detected the altered environment and signaled for vertical-preferring neurons to increase their gain. However, its effects weakened in strength by the following session. A second, slower process then became evident following the early local maximum, as peak adaptation increased in strength and duration for both tasks. For neurons supporting the appearance task, this process continued to grow in strength until the end of the experiment. For orientation, it reached its maximum strength at the end of the second day and then grew weaker. A number of shorter-term studies have identified multiple processes of adaptation that operate at different timescales [12, 17, 25–27], but none has identified processes that operate over days.

To formally test this account, we fit a model containing separate rapid and slow processes to our data (Figure 3). The rapid process was constrained to peak on the first day and then decline. The slower process was constrained to grow in strength throughout the first 3 days and either was allowed to continue rising on the fourth day or was allowed to fall. The model fit well, accounting for over 70% of the data's total variance (compare Figure 2 to right column of Figure 3). It also fit reliably better than a single-mechanism model that lacked the early peak, even when taking into account its extra parameters (resampling analysis, $p < 0.01$).

Why does the fast process decline on the second day of adaptation? The data rule out two possible accounts. One account is that adaptation decayed during sleep. However, for the orientation task, the falloff was visible within the first day,

and we also measured effects only after at least 3 hr of additional deprivation every morning. Another possible account is that the very first testing session showed an exaggerated response, but this was not the case for the appearance task, and both tasks had been practiced following 30 min of deprivation the previous day.

Another possibility is that following the first day, adaptation grew relatively little in neurons tuned to vertical, whereas it grew rapidly and in the same direction in neurons tuned to horizontal. Such an increase in horizontal gain could have been caused by general deprivation of visual input from the low spatial and temporal resolution of the altered reality system. Although we cannot rule out such an account, it is unlikely for two reasons: first, we used relatively low spatial frequencies in our test stimuli in order to be in a range unaffected by the spatial resolution of our cameras and display. Second, in a prior study, we measured detection thresholds following 4 hr of adaptation, and when fatigue effects were minimized, we found no effect on orientations orthogonal to those removed by filtering [10]. This suggests that our paradigm generates little effect of general deprivation.

Current theory holds that visual adaptation improves visual processing, with aftereffects originally attributed to neural “fatigue” now taken as evidence of neurons more optimally encoding stimuli (e.g., [2, 3, 18, 28]). If adaptation in our paradigm did in fact optimize vision, then the fast process must have declined because the costs of remaining highly adapted outweighed its benefits. Many possible costs exist: for example, more rapid and more gradual environmental changes may have independent causes, making independent adaptation to each rate of change optimal [29]. Thus, for long-lasting environmental changes, it can be costly to maintain adaptation in a fast adaptive process, which could be needed to adjust to future rapid changes. A second possible cost is the “coding catastrophe,” in which adaptive changes in firing of early-stage visual neurons are misinterpreted as stimulus changes by neurons at subsequent levels in the processing hierarchy, leading to inaccurate percepts [19, 20, 30, 31].

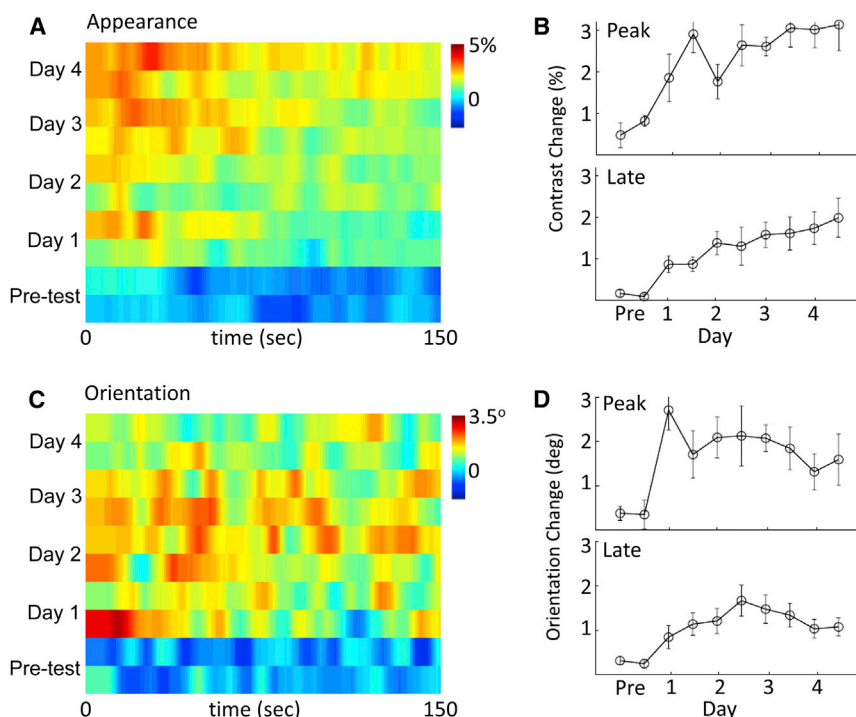


Figure 2. Effects of 4 Days of Adaptation

(A) Contrast appearance as a function of testing session and time during the session. Conventions are as in Figure 1D.

(B) Strength of peak (top) and late adaptation (bottom) as a function of testing session for the appearance task. All error bars represent ± 1 SEM.

(C) Orientation judgments as a function of testing session and time during the session.

(D) Strength of peak (top) and late adaptation (bottom) as a function of testing session for the orientation task.

Distinguishing among these and other possible costs is an important step for future work. One prior study using gratings as adapters found tilt aftereffects that asymptoted in size after about 1 hr [8]. The decline observed here could indicate that costs are higher when adapting to more natural stimuli, where coding changes would have greater effects.

The slow process grew steadily in strength for the appearance task but followed an inverted U-shaped function for the orientation task. The appearance results are consistent with Bayesian theories of visual adaptation, which predict that longer experience in an environment produces greater confidence in the observed structure of the world; this in turn produces stronger and longer-lasting effects of adaptation [32, 33]. Several theoretical accounts may explain the different pattern of results for the orientation task. The orientation judgments were performed using central vision, whereas the appearance task was slightly toward the periphery. The costs of the slower adaptation could be greater in foveal vision, leading to a reduction of effects on day 4. The two tasks also differ functionally. Effects of adaptation in the orientation task are illusory aftereffects, in which the world is seen nonveridically, with, for example, 45° gratings perceived as being 43° . Such errors are likely due to the coding catastrophe [19, 20], and the visual system may have begun to correct them.

The fast process evident in our paradigm likely depends on the same rapid neural mechanisms of contrast adaptation that have been investigated in dozens of short-term laboratory studies [1–13]. The neural bases of these fast processes include gain and tuning changes in neurons in primary visual cortex (e.g., [7–13]). Our results predict that such changes, as measured with either unit recording or imaging, should decline markedly in strength after about 1 day of continuous adaptation to filtered images. If this decline is caused by costs (like the coding catastrophe) that arise later in processing, then it will depend upon feedback and should therefore be absent in preparations in which such signals are disrupted. In

addition, some costs of adaptation arise only when the stimulus changes (for example, the tilt aftereffect is absent for test patterns at the same orientation as the adapter). Hence, adaptation to a uniform stimulus, such as a grating, may be less costly, so it would be predicted to show less decline after long adapting durations [8].

The slow process observed here likely depends on the same neural mechanisms that underlie observed effects in the few other multiday adaptation

reports in the literature [11, 34–37]. These slow mechanisms may also produce the perceptual learning that gradually improves performance through training of specific visual tasks (e.g., [38]). In our experiment, the deprived visual system may have learned to see better in the altered environment by altering neural codes in later visual areas to correctly represent orientation despite adaptation in earlier areas. Such learning would overcome the coding catastrophe. This account predicts that subjects may be able to learn to reduce the tilt aftereffect, given enough training in an orientation task following short-term adaptation. It further predicts that long-term adaptation might show a different pattern for conditions in which perceptual learning is difficult. For example, one could vary the global distribution of filtered orientations and spatial frequencies over time, while ensuring that a small subset is always present. This sort of “roving” manipulation has been shown to make perceptual learning more difficult [39], although low-level adaptation to the unchanging subset should be maintained.

To our knowledge, this study is the first to explore the effects of multiday deprivation at a specific range of orientations in adult humans. Previous work on long-term deprivation of this kind was limited to animal studies and did not find a non-monotonic time course of adaptation strength (e.g., [40–43]). However, most of those animal studies were performed in juveniles, before the end of the critical period, so the mechanisms of neural plasticity that they probed were likely quite different from those serving adaptation in adults. Additionally, some of the work took place in rodents. Because these animals do not rely on vision as much as humans do, the costs of adaptation could be lower for them.

In sum, our results demonstrate that visual contrast adaptation peaks and then declines after about 1 day, despite the sustained presence of the adapting environment. This limit, which was observed across tasks and in two independent experiments, strongly argues that cortex is sensitive to costs that

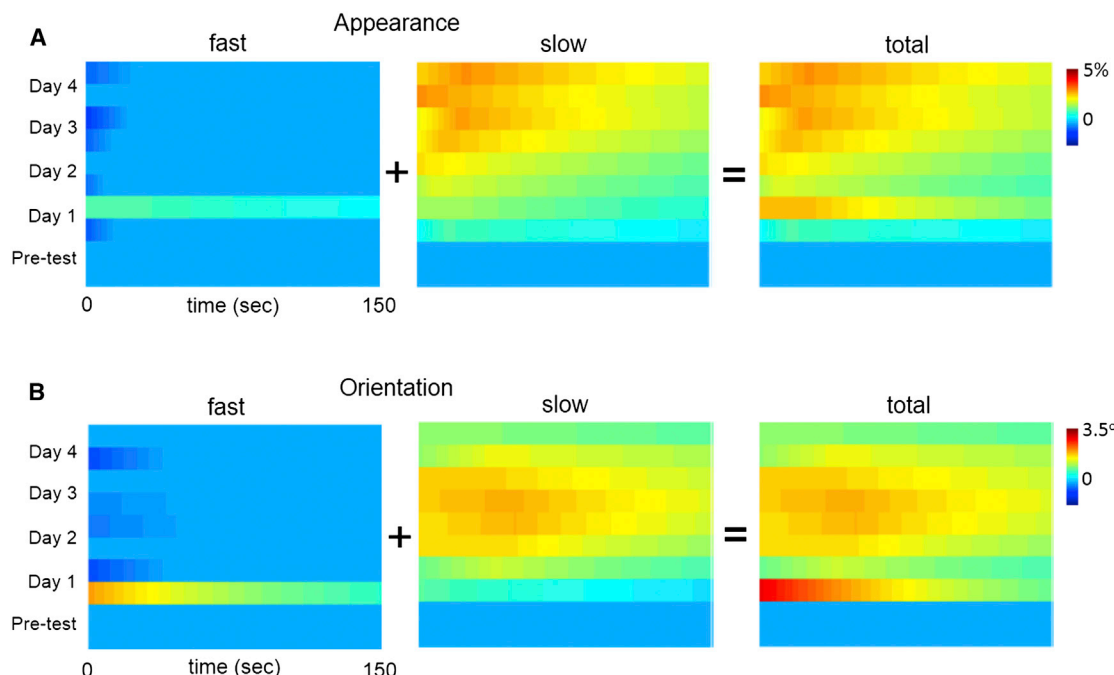


Figure 3. Fit of Model of Long-Term Adaptation Effects

(A and B) Adaptation is assumed to be the sum of a fast and slow process. The fast process rises and falls on the first day, and the slow process rises beginning on the first day and optionally falls on a later day. The model accounts for over 70% of the variance in the data.

(A) Fits of each process and their sum for the main experiment appearance task, displayed as in Figure 1D.

(B) Model fits for the orientation task.

arise as a consequence of neural adaptation. Slower processes engaged by long-term adaptation appear to be able to overcome these costs. In visual cortex, the balance between the costs and the known benefits of adaptation likely determines the amount, type, and location of neuroplasticity. This principle may apply throughout the brain.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.09.027>.

Acknowledgments

This research was supported by National Science Foundation grant BCS1028584. The authors thank Peter Griswold, Shane Hernandez, and the many other research assistants who helped with the study. We also thank three anonymous reviewers.

Received: June 5, 2014

Revised: August 11, 2014

Accepted: September 9, 2014

Published: October 23, 2014

References

- Clifford, C.W., Webster, M.A., Stanley, G.B., Stocker, A.A., Kohn, A., Sharpee, T.O., and Schwartz, O. (2007). Visual adaptation: neural, psychological and computational aspects. *Vision Res.* 47, 3125–3131.
- Kohn, A. (2007). Visual adaptation: physiology, mechanisms, and functional benefits. *J. Neurophysiol.* 97, 3155–3164.
- Webster, M.A. (2011). Adaptation and visual coding. *J. Vis.* 11.
- Blakemore, C., and Campbell, F.W. (1969). Adaptation to spatial stimuli. *J. Physiol.* 200, 11P–13P.
- Ross, J.R., and Speed, H.D. (1996). Perceived contrast following adaptation to gratings of different orientations. *Vision Res.* 36, 1811–1818.
- 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.
- Graham, N.V.S. (1989). *Visual Pattern Analyzers* (New York: Oxford University Press).
- Magnussen, S., and Greenlee, M.W. (1985). Marathon adaptation to spatial contrast: saturation in sight. *Vision Res.* 25, 1409–1411.
- 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.
- Zhang, P., Bao, M., Kwon, M., He, S., and Engel, S.A. (2009). Effects of orientation-specific visual deprivation induced with altered reality. *Curr. Biol.* 19, 1956–1960.
- Yehezkel, O., Sagi, D., Sterkin, A., Belkin, M., and Polat, U. (2010). Learning to adapt: dynamics of readaptation to geometrical distortions. *Vision Res.* 50, 1550–1558.
- Bao, M., and Engel, S.A. (2012). Distinct mechanism for long-term contrast adaptation. *Proc. Natl. Acad. Sci. USA* 109, 5898–5903.
- Maffei, L., Fiorentini, A., and Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science* 182, 1036–1038.
- Movshon, J.A., and Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature* 278, 850–852.
- Ohzawa, I., Sclar, G., and Freeman, R.D. (1985). Contrast gain control in the cat's visual system. *J. Neurophysiol.* 54, 651–667.
- Dragoi, V., Sharma, J., and Sur, M. (2000). Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron* 28, 287–298.
- Patterson, C.A., Wissig, S.C., and Kohn, A. (2013). Distinct effects of brief and prolonged adaptation on orientation tuning in primary visual cortex. *J. Neurosci.* 33, 532–543.
- Benucci, A., Saleem, A.B., and Carandini, M. (2013). Adaptation maintains population homeostasis in primary visual cortex. *Nat. Neurosci.* 16, 724–729.
- Schwartz, O., Hsu, A., and Dayan, P. (2007). Space and time in visual context. *Nat. Rev. Neurosci.* 8, 522–535.
- Seriès, P., Stocker, A.A., and Simoncelli, E.P. (2009). Is the homunculus “aware” of sensory adaptation? *Neural Comput.* 21, 3271–3304.

21. Bryngdahl, O. (1966). Characteristics of the visual system. Psychophysical measurements of the response to spatial sine-wave stimuli in the photopic region. *J. Opt. Soc. Am.* 56, 811–821.
22. Georgeson, M.A., and Sullivan, G.D. (1975). Contrast constancy: deblurring in human vision by spatial frequency channels. *J. Physiol.* 252, 627–656.
23. Gibson, J.J., and Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. *J. Exp. Psychol.* 20, 453–467.
24. Meese, T.S., and Georgeson, M.A. (1996). The tilt aftereffect in plaids and gratings: channel codes, local signs and “patchwise” transforms. *Vision Res.* 36, 1421–1437.
25. Magnussen, S., and Greenlee, M.W. (1986). Contrast threshold elevation following continuous and interrupted adaptation. *Vision Res.* 26, 673–675.
26. Vul, E., Krizay, E., and MacLeod, D.I. (2008). The McCollough effect reflects permanent and transient adaptation in early visual cortex. *J. Vis.* 8, 1–12.
27. Bao, M., Fast, E., Mesik, J., and Engel, S.A. (2013). Distinct mechanisms control contrast adaptation over different timescales. *J. Vis.* 13.
28. Haak, K.V., Fast, E., Baek, Y., and Mesik, J. (2014). Equalization and decorrelation in primary visual cortex. *J. Neurophysiol.* 112, 501–503. <http://dx.doi.org/10.1152/jn.00521.2013>.
29. Kording, K.P., Tenenbaum, J.B., and Shadmehr, R. (2007). The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nat. Neurosci.* 10, 779–786.
30. Dhruv, N.T., and Carandini, M. (2014). Cascaded effects of spatial adaptation in the early visual system. *Neuron* 81, 529–535.
31. Patterson, C.A., Wissig, S.C., and Kohn, A. (2014). Adaptation disrupts motion integration in the primate dorsal stream. *Neuron* 81, 674–686.
32. Wark, B., Fairhall, A., and Rieke, F. (2009). Timescales of inference in visual adaptation. *Neuron* 61, 750–761.
33. Grzywacz, N.M., and de Juan, J. (2003). Sensory adaptation as Kalman filtering: theory and illustration with contrast adaptation. *Network* 14, 465–482.
34. Adams, W.J., Banks, M.S., and van Ee, R. (2001). Adaptation to three-dimensional distortions in human vision. *Nat. Neurosci.* 4, 1063–1064.
35. 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.
36. Belmore, S.C., and Shevell, S.K. (2008). Very-long-term chromatic adaptation: test of gain theory and a new method. *Vis. Neurosci.* 25, 411–414.
37. Wolpert, D.M., Miall, R.C., Cumming, B., and Boniface, S.J. (1993). Retinal adaptation of visual processing time delays. *Vision Res.* 33, 1421–1430.
38. Lu, Z.L., Yu, C., Watanabe, T., Sagi, D., and Levi, D. (2010). Perceptual learning: functions, mechanisms, and applications. *Vision Res.* 50, 365–367.
39. Sagi, D., Adini, Y., Tsodyks, M., and Wilkanski Technion, A. (2003). Context dependent learning in contrast discrimination: effects of contrast uncertainty. *J. Vis.* 3, 173a.
40. Blakemore, C., and Cooper, G.F. (1970). Development of the brain depends on the visual environment. *Nature* 228, 477–478.
41. Hirsch, H.V.B., and Spinelli, D.N. (1970). Visual experience modifies distribution of horizontally and vertically oriented receptive fields in cats. *Science* 168, 869–871.
42. Sengpiel, F., Stawinski, P., and Bonhoeffer, T. (1999). Influence of experience on orientation maps in cat visual cortex. *Nat. Neurosci.* 2, 727–732.
43. Kreile, A.K., Bonhoeffer, T., and Hübener, M. (2011). Altered visual experience induces instructive changes of orientation preference in mouse visual cortex. *J. Neurosci.* 31, 13911–13920.