

Distinct mechanisms control contrast adaptation over different timescales

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Changes to the visual environment can happen at many timescales, from very transient to semi-permanent. To adapt optimally, the visual system also adjusts at different timescales, with longer-lasting environmental changes producing longer-lasting effects, but how the visual system adapts in this way remains unknown. Here, we show that contrast adaptation—the most-studied form of visual adaptation—has multiple controllers, each operating over a different time scale. In a series of experiments, subjects completed either a contrast matching, contrast detection, or tilt adjustment task, while adapting to contrast at one orientation. Following a relatively longer period (5 min) of adaptation to high contrast, subjects were “deadadapted” for a shorter period (e.g., 40 s) to a lower contrast. Deadadaptation eliminated perceptual aftereffects of adaptation, but continued testing in a neutral environment revealed their striking recovery. These results suggest the following account: Adaptation was controlled by at least two mechanisms, with initial adaptation affecting a longer-term one and deadadaptation affecting a shorter-term one in the opposite direction. Immediately following deadadaptation, the effects of the two mechanisms cancelled each other, but the short-term effects rapidly decayed, revealing ongoing longer-term adaptation. A single controlling mechanism cannot account for the observed recovery of effects, since once deadadaptation cancels the initial longer-term adaptation, no trace of it remains. Combined with previous results at very long adaptation durations, the present results suggest that contrast adaptation is possibly controlled by a continuum of mechanisms acting over a large range of timescales.

Introduction

Adaptation allows the visual system to continuously adjust to the environment, in order to improve its processing. For example, prolonged viewing of a high contrast stimulus reduces both perceptual and neural sensitivity to subsequent stimuli of similar pattern, a phenomenon referred to as contrast adaptation (e.g., Blakemore & Campbell, 1969; Fang, Murray, Kersten, & He, 2005; Ohzawa, Sclar, & Freeman, 1985; Sclar, Lennie, & DePriest, 1989). The lowering of response, from near-ceiling levels produced by the adapter, may allow neurons in early visual cortex to transmit more information about the relatively small changes in contrast likely to arise in the environment (Kohn, 2007; Wark, Lundstrom, & Fairhall, 2007). Recent studies have also found that adaptation to reductions in contrast increase perceptual and neural contrast sensitivity (Kwon, Legge, Fang, Cheong, & He, 2009; Zhang, Bao, Kwon, He, & Engel, 2009).

Effects of contrast adaptation get stronger and longer lasting as the adapting duration lengthens, an effect we term the “duration scaling” law (Bao & Engel, 2012; Greenlee, Georgeson, Magnussen, & Harris, 1991; Magnussen & Greenlee, 1985; Wark, Fairhall, & Rieke, 2009). This pattern might occur because, over time, either a single mechanism controlling adaptation gains strength, or additional mechanisms operating over longer timescales become active (Grzymacz & de Juan, 2003; Kording, Tenenbaum, & Shadmehr, 2007;

Citation: Bao, M., Fast, E., Mesik, J., & Engel, S. (2013). Distinct mechanisms control contrast adaptation over different timescales. *Journal of Vision*, 13(10):14, 1–11, <http://www.journalofvision.org/content/13/10/14>, doi:10.1167/13.10.14

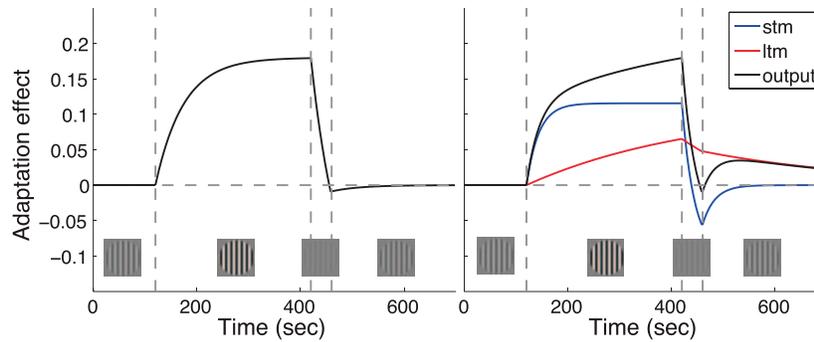


Figure 1. Time courses of adaptation effects predicted by two theories of contrast adaptation. Vertical dashed lines mark the onsets of adaptation (5 min), deadadaptation (40 s), and a posttest, respectively. Adapting contrasts for the four stages are 25%, 80%, 6.25%, and 25% respectively, depicted by the gratings in each panel. If adaptation is controlled by a single neural mechanism, aftereffects will remain around the baseline level following deadadaptation, which rapidly eliminates the effect of the longer adaptation (left panel). However, if adaptation is controlled by two mechanisms with different time constants, adaptation followed by rapid deadadaptation may cause opposing signals from the two mechanisms. Decay in the posttest will affect the short-term mechanism more strongly, leading to spontaneous recovery of adaptation due to the long-term mechanism. Black curves (“output”) represent the time courses of a behavioral aftereffect that reflects the output signal of neural mechanism(s) adjusting the responsiveness, or gain, of neurons. In the two-mechanism model, this quantity is equal to the sum of two components produced by the long-term (“ltm”) and short-term (“stm”) mechanisms.

Vul, Krizay, & MacLeod, 2008; Wark et al., 2009). It remains unknown which of these theories best explains visual contrast adaptation.

To distinguish between them, we borrowed a paradigm from the recent motor adaptation literature, involving a “deadadaptation” procedure, in which subjects are exposed to an environment that causes changes that counteract initial adaptation (Smith, Ghazizadeh, & Shadmehr, 2006). Below, for example, we follow a longer period of exposure to high contrast patterns, which lowers sensitivity, with a shorter period of exposure to low contrast patterns, which raises it (Figure 1).

The multiple mechanisms theory assumes that sensitivity is proportional to the sum of the outputs of multiple controllers, with each operating over its own preferred timescale. Mechanisms that prefer long timescales affect sensitivity only after exposure to an environment has reached a relatively long duration, while mechanisms that prefer short timescales affect sensitivity rapidly after an environmental change. By this account, the longer adaptation to high contrast will cause a long-term mechanism to signal for a sensitivity decrease, and the brief deadadaptation using low contrast will cause a shorter-term mechanism to signal an increase in sensitivity, cancelling the effects of long-term adaptation (Figure 1). If the system is then put into a relatively neutral environment, the short-term mechanism will quickly decay to baseline, but the long-term mechanism will continue to signal a decrease for some time, producing “spontaneous recovery” of its effects on sensitivity. A single mechanism cannot account for this recovery.

We conducted a series of experiments using this deadadaptation procedure with initial adaptation durations of 5 min. Results from contrast matching, contrast detection, and tilt aftereffect tasks, all showed clear patterns of spontaneous recovery after deadadaptation, strongly suggesting that multiple mechanisms control contrast adaptation over these timescales.

Methods

Observers

Fifteen observers, ten of whom were naïve to the experimental hypotheses, participated in the present study. Eight subjects participated in Experiment 1, which measured adaptation effects with a contrast matching task. One of these and three new subjects participated in Experiment 2, which measured effects with a detection task. Two of the subjects from Experiment 1 and three new subjects, participated in Experiment 4, which tested the tilt aftereffects following adaptation. Ten subjects, among whom five were new subjects, participated in Experiment 5. Two subjects who had participated in Experiments 4 and 5, along with three new subjects, participated in Experiment 3 (which was run after Experiments 4 and 5). All subjects had normal or corrected to normal vision. Experimental procedures were approved by the University of Minnesota Institutional Review Board.

Apparatus

Stimuli were presented binocularly on a gamma-corrected CRT monitor (1152 × 870 resolution at 75 Hz) in a dimly lit room. A Bits++ video card (Cambridge Research Systems) drove the display to obtain 14 bit rendering precision. The monitor was calibrated using a PhotoResearch PR-655 spectrophotometer. To calibrate the display, display gamma curves were measured and inverted using a look-up table.

Stimuli

Experiment 1 (Contrast matching)

Stimuli were patches of sine-wave gratings whose edges had been smoothed with a Gaussian filter. The patches subtended 4.5°, and were centered 4.1° away from fixation. The spatial frequency of the gratings was 1.5 cycle per degree.

Experiment 2 (Detection)

Stimuli were sine-wave gratings with identical parameters to those in the contrast-matching experiment, except that they were shown on the center of the screen and subtended 8° for the test and 12° for the topup.

Experiment 3 (2AFC detection)

Stimuli were identical to those used in Experiment 1, except the stimulus during topup subtended 6°.

Experiment 4 (Tilt aftereffect)

The same topup stimulus was used as in Experiment 1. The test stimulus was a plaid made from two superimposed diagonal sinusoidal gratings at 25% contrast, initially oriented $\pm 45^\circ$ from vertical (Bao & Engel, 2012; Meese & Georgeson, 1996). The plaid perceptually resembled a blurred square checkerboard.

Experiment 5 (Comparing two adapting durations)

Stimuli were identical to those used in Experiment 1.

Procedure

There were four stages in each experiment, a “baseline” period where the contrast of the adapter was 25%, an initial “adaptation” period where the contrast of the adapter was increased to 80%, a short “dead-adaptation” period where the contrast of the adapter was reduced to 6.25%, and a final “posttest” period where the adapter contrast returned to 25% (see Figures 2 and

3). Adapting to 25% contrast during the baseline period is considered a neutral environment relative to those for the adaptation and deadadaptation periods, which are higher and lower contrast than 25%. Experiment 3 used 90% contrast during adaptation and 5% contrast during deadadaptation. The duration of the adaptation period was 5 min in Experiments 1, 2, and 4, 10 min in Experiment 3, 90 s and 270 s in Experiment 5. The duration of deadadaptation was fixed (40 s) for Experiment 1, but it was set individually for each subject in Experiments 2 (40~60 sec), 4 (40~70 sec) and 5 (40~120 sec) based upon a pretest. (In the pretest, each subject adapted for 5 min to 80% contrast followed by a 2 min deadadaptation to 6.25% contrast. The average duration of deadadaptation required for each subject to return to the level measured in the baseline was computed and used in the main experiment.) The deadadaptation duration was 80 s in Experiment 3. The posttest lasted for 240 s in Experiment 1, 300 s in Experiments 2 and 4, 480 s in Experiment 3, and 120 s in Experiment 5.

Subjects completed four repetitions of all four stages of the procedure in Experiment 1. Three subjects completed eight repetitions and one subject completed six repetitions in Experiment 2. In Experiment 4, three subjects completed eight repetitions, one subject completed six repetitions and one subject completed seven repetitions. Two subjects completed 12 repetitions, and the other three subjects completed 14, 17, or 18 repetitions in Experiment 3. All subjects did four repetitions of both adaptation durations in Experiment 5. All repetitions of all experiments were separated by at least one hour.

Experiment 1 (Contrast matching)

Both the “test” gratings, used for contrast matching, and “topup” gratings, used as adapters, were oriented vertically. In each trial, four test gratings were presented simultaneously on mid-gray background (30.8 cd/m²), each in one quadrant for 200 ms (see Figure 2). The contrast of the grating varied with a Gaussian temporal profile that had a standard deviation of 50 ms. After a 200 ms blank gap, two topup gratings that drifted towards or away from each other at 4 Hz were presented for 1400 ms. Using two topup gratings drifting in this way aimed to minimize the possibility of stimulus-driven eye movements during adaptation. The adapters were centered on the two test locations in the upper visual field for half of the subjects, and in the lower visual field for half the subjects. After another 200 ms blank gap, the test stimuli for the next trial were presented.

Subjects judged whether the test gratings in the adapted locations appeared to be higher or lower contrast than the gratings in the unadapted locations,

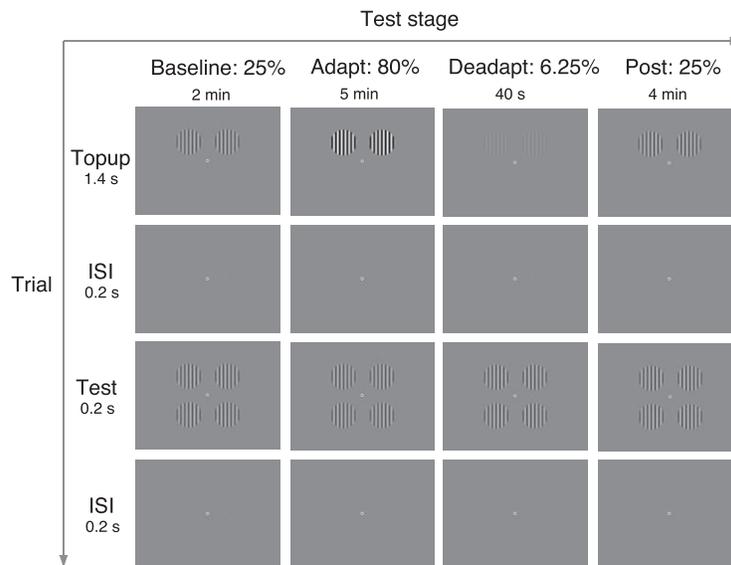


Figure 2. Schematic of methods in the contrast matching experiment (Experiment 1).

and indicated their response by pressing one of two buttons on a keyboard. The contrast of testing gratings in the unadapted locations was held constant at 25%. The test contrast in the adapted locations began at 25%, and was continuously adjusted through a one-down-one-up staircase procedure. The initial contrast step size was 0.1 (10% contrast). After three reversals, the step size was reduced to 0.06, and to 0.02 after another three reversals, where it remained for the rest of the staircase.

Experiment 2 (Detection)

Stimulus timing was the same as in Experiment 1, except that the blank gap was increased to 250 ms and

the topup duration was reduced to 1300 ms (see Figure 2). The adapting grating was static, but randomly changed its phase every 100 ms. The orientation of testing gratings alternated between vertical and horizontal across trials, allowing us to sample the time courses of threshold for both orientations evenly in time. The adapter was oriented vertically for two subjects and horizontally for two others.

Subjects were instructed to press one button if they saw the testing grating and press the other if they did not, a “yes/no” procedure. The contrast of testing grating started from 2%, and varied following an independent one-down-one-up staircase procedure for each testing orientation. The contrast steps decreased logarithmically from 0.02 (2% contrast) to 0.0005 in

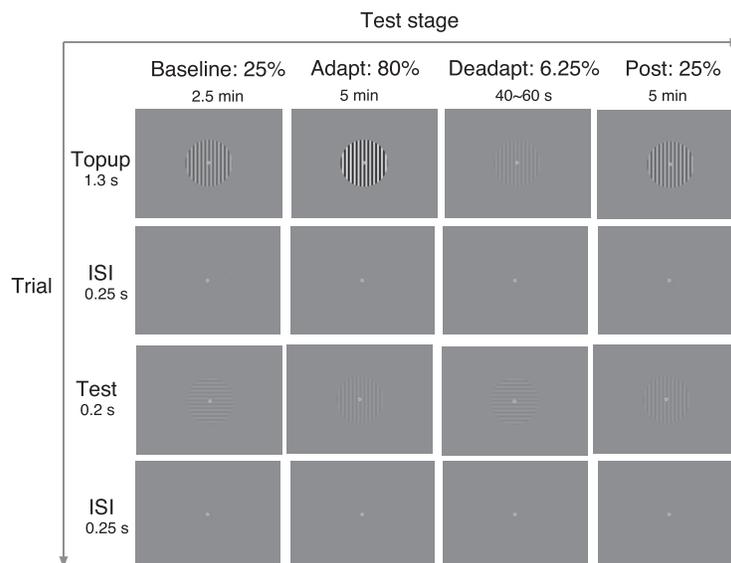


Figure 3. Schematic of methods in the contrast detection experiment (Experiment 2).

49 levels. The staircase initially moved in increments of three of these steps. After three reversals, this increment was reduced to two steps, and after another three reversals, it was set to one step, where it remained for the rest of the staircase. Before the baseline measurement, thresholds for both orientations were also measured without any adapter present (a 0 contrast topup pattern), which we termed absolute baseline. For this stage only, a brief beep cued the start of each trial.

Experiment 3 (2AFC detection)

Timing of the stimuli was the same as Experiment 1. Topup gratings were always oriented vertically and drifted as in Experiment 1, but test gratings were either vertical or horizontal within a session and were static. Three subjects were tested with gratings in the upper visual field, and two with the gratings in the lower visual field. Test contrast was tailored to approximately 75% correct threshold contrast through a staircase procedure at the beginning of each repetition. Test contrast was then fixed at this level throughout the remainder of the session. A single test grating was presented on each trial in the adapted field, either to the left or right of fixation. Participants responded whether the grating appeared in the left or right location.

Experiment 4 (Tilt aftereffect)

Timing of adapter and test presentations were identical to those in Experiment 2. The plaid made from two 45° gratings perceptually resembled a blurred square checkerboard. A tilt aftereffect (TAE) from adaptation to vertical causes the component gratings to appear symmetrically tilted relative to 45°, which in turn causes the checks to appear rectangular. The physical tilt, relative to 45°, required to cause the checks to appear square was recorded as our measure of the TAE.

Subjects were instructed to adjust the tilt of the components to make the checks at the adapted location appear square. The difference angle between the tilt of the components and 45° reflected the size of the tilt aftereffect. A one-down-one-up staircase procedure was used to control the orientation of the two component gratings, and so track subject's subjective 45° point. The initial orientation step size used in the staircase was 2°. After three reversals, the step size was reduced to 1.125°, and was further reduced to 0.25° after another three reversals. Before the baseline measurement, subjects viewed a blank mean-field background for 1 min, in order to reduce light adaptation in the beginning of the test.

Experiment 5 (Comparing two adapting durations)

Stimuli and procedure were identical to those in Experiment 1 with the following exceptions: The adaptation period was 90 s in four sessions and 270 s in four other sessions (one subject did six sessions for each condition). Adaptation was always induced in the upper visual field, and the adapter was always oriented vertically. The length of the deadadaptation period was variable, terminating whenever the effect of adaptation was detected to return to the baseline or the duration of deadadaptation reached 120 s.

Analysis

Experiment 1 (Contrast matching)

Test contrasts for the last 15 reversals of the baseline measurement were averaged to obtain an estimate of baseline adaptation for each repetition of each subject. This estimate was subtracted from subsequent contrast values from the staircase forming a time series of the change in test contrast due to adaptation. The time series was then nearest-neighbor interpolated to a 2 s sample interval and averaged across repetitions and subjects. The average time series for each subject was then entered into a subsequent point-by-point t test against zero to examine the adaptation effect in each experimental stage. A linear trend analysis was also performed on the beginning of the posttest to test for the presence of spontaneous recovery.

Experiment 2 (Detection)

The last ten staircase reversals in the absolute baseline stage were averaged to serve as a measure of absolute baseline. The time series during other stages were normalized separately by dividing by the absolute baseline for the respective orientation in that session. These normalized time series were nearest-neighbor interpolated to 2 s sample interval. Time series from different periods were then entered into a subsequent point-by-point t test against the baseline values to examine the adaptation effect.

Experiment 3 (2AFC Detection)

Proportion correct was calculated for both orientations for each subject. To give more stable estimates, accuracy was computed within bins of 10 successive trials, and then plotted as a function of time. To keep a comparable timeframe with the other experiments, linear trend analysis was completed for the first 240 s of the posttest period for both vertical and horizontal test orientations.

Experiment 4 (Tilt aftereffect)

Tilt values from the staircase were concatenated to construct a time series of the physical orientation that appeared to be 45°. For each session, the time series were nearest-neighbor interpolated to a 2 s sample interval. A point-by-point t test against the corresponding baseline value was then performed to show the tilt aftereffect in different experimental stages.

Experiment 5 (Comparing two adapting durations)

Analysis was identical to that used in Experiment 1, except that average timecourses for deadaptation could not be constructed because the deadaptation duration varied across sessions and subjects. A linear trend analysis was performed on the first 20 s of the posttest to examine the spontaneous recovery. To examine overall strength of recovered aftereffects, the sum of the timeseries was computed (an “area under the curve” measure).

Results

Experiment 1 used a contrast-matching measure to test whether adaptation to contrast showed spontaneous recovery, a result which would suggest that multiple mechanisms with differing timescales control the effect. Subjects adjusted the contrast of test gratings in adapted locations in the visual field to match the appearance of constant contrast presented at unadapted locations. Adaptation strength was reflected by the increased physical contrast required to produce an appearance match.

Our results show clear evidence of the spontaneous recovery of contrast adaptation. Exposure to the high contrast adapter lowered the apparent contrast of the test stimulus, and subjects raised its contrast significantly, $t(7) = 3.94$, $p < 0.01$, to match a constant 25% contrast unadapted stimulus (Figure 4). At asymptote, the increase above the baseline was around 16% contrast. During the deadaptation stage, the test contrast was reduced rapidly to a level comparable to the baseline, $t(7) = 1.45$, $p > 0.19$. But strikingly, during the posttest the adaptation effect recovered over time (linear trend 0–38 s, $t(7) = 3.86$, $p < 0.01$), and then stayed reliably higher than baseline ($p < 0.05$ for 98 out of 100 time points). These results lend support to the view that contrast adaptation is controlled by at least two separate mechanisms with differing timescales, following the logic shown in Figure 1.

Experiment 2 investigated the dynamics of adaptation at threshold levels, using a similar procedure to the first experiment, but with a contrast detection task. During adaptation, all subjects reliably showed in-

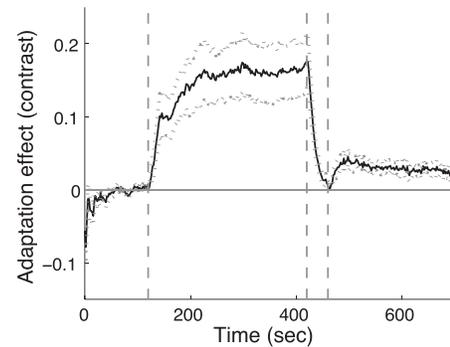


Figure 4. Grand average time course from the contrast matching experiment. The average match contrast from the baseline period was subtracted from each match value to yield a measure of adaptation. The three vertical dashed lines mark the onsets of the adaptation, deadaptation, and posttest periods, respectively. The dotted lines indicate \pm one standard error of the mean across subjects.

creased detection thresholds for the adapted orientation ($t > 3.85$, $p < 0.01$, Figure 5). This adaptation effect was stronger for the adapted orientation than for the orthogonal control orientation. Deadaptation effectively eliminated adaptation ($p > 0.19$). Again, we observed the spontaneous recovery of the adaptation effect during the posttest (all subjects $t > 3.17$, $p < 0.05$). These results also support the multiple mechanisms account of contrast adaptation.

Experiment 3 offered a more objective measure of contrast detection that used a 2AFC procedure, and confirmed that spontaneous recovery in the previous experiment was not a result of bias. When participants were adapted and tested on vertical, there was clear evidence of spontaneous recovery. Accuracy decreased during adaptation and increased back to baseline during deadaptation. Accuracy then decreased again, instead of remaining at baseline, when subjects returned to 25% contrast adapter (see Figure 6, black line). A linear trend analysis of the posttest found this decrease to be significant, $t(4) = 5.08$, $p < 0.01$. This trend represents spontaneous recovery of the effects of the high contrast adaptation, providing further evidence for the multiple mechanisms account.

An alternative explanation of the results of Experiment 3 is that the decrease in accuracy during the baseline period could be the result of fatigue, rather than a spontaneous recovery of the decrease in sensitivity. To rule out this account, we tested the linear trend of the posttest when participants were adapted to vertical and tested on horizontal. Participants were not adapted to horizontal, and therefore any decrease could not be explained as a spontaneous recovery; but if fatigue was a factor, it should nevertheless be present. We found no evidence of a trend in the posttest for this unadapted orientation; see Figure 6, gray line, $t(4) =$

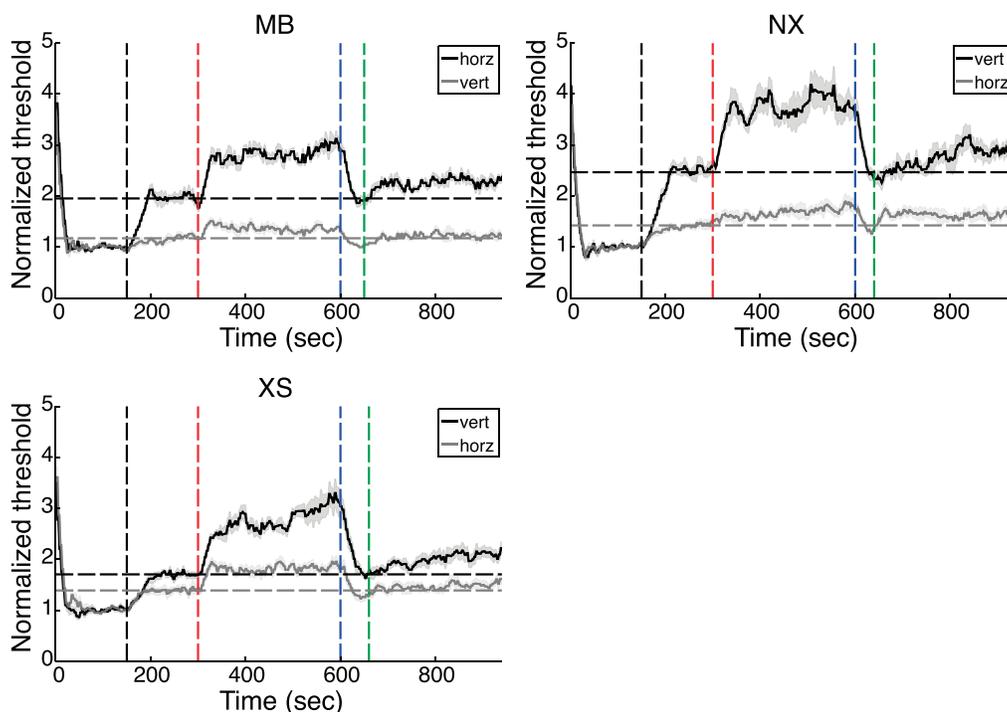


Figure 5. Average time courses for individual subjects in the contrast detection experiment. Black curves show the time courses for test patterns of the adapting orientation, and the gray curves for those of the perpendicular control orientation (the adapter was vertical). Thresholds were normalized by dividing by the threshold measured in each session with a zero contrast (mean field) adapter. The horizontal dashed lines show the normalized thresholds for the adapted vertical (dark gray) and horizontal control (light gray) orientation measured with adaptation to 25% contrast in the baseline period. The four vertical dashed lines mark the time onsets for the baseline, adaptation, deadadaptation, and posttest periods, respectively.

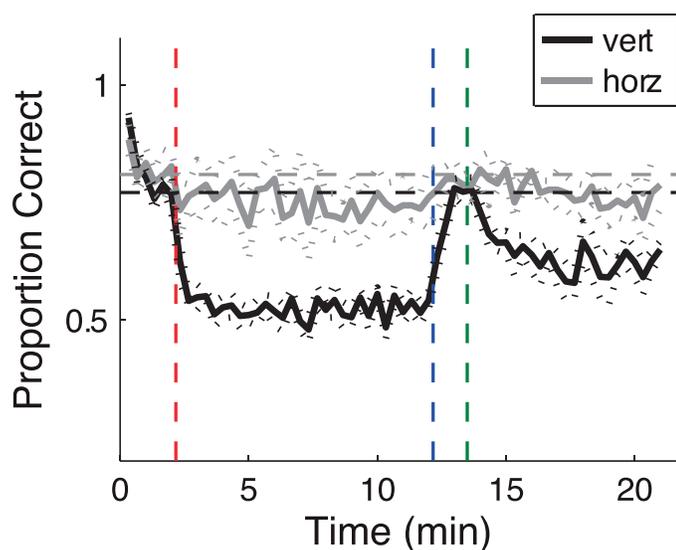


Figure 6. Grand average time course from the 2AFC detection experiment. The black horizontal dashed line indicates average performance for vertical measured in the baseline period, and the horizontal gray dashed line is the baseline average for horizontal. The three vertical dashed lines mark the onsets of the adaptation, deadadaptation, and posttest periods, respectively. The dotted lines indicate \pm one standard error of the mean across subjects.

1.16, $p > 0.3$, and the strength of trends for vertical and horizontal test orientations differed significantly from each other, $t(4) = 9.24$, $p < 0.001$.

Experiment 4 tested for spontaneous recovery of the tilt aftereffect. Subjects adapted to high contrast vertical gratings, and all showed reliable increases in the tilt aftereffect (all $t > 2.47$, $p < 0.05$, Figure 7). A linear trend analysis found spontaneous recovery of the tilt aftereffect during the posttests (for three subjects, $t > 2.82$, $p < 0.05$; in one subject the effect was only marginally significant, $t = 2.03$, $p < 0.08$). For one subject in Experiment 2, and one in Experiment 4, deadadaptation was not strong enough to return effects to the baseline level (data shown in the Supplementary Materials), and although these subjects showed some recovery of effects following deadadaptation, their results were not analyzed further, since they do not definitively test theories of adaptation.

An alternative explanation of our results is that following an increase in adapter contrast, as occurred at the end of the deadadaptation period, the perceived contrast of a test grating simply always decreases, regardless of prior adaptation history. We termed this the “bounce” hypothesis, since it suggests that measures will automatically rebound after hitting the floor of baseline during deadadaptation. This effect should be

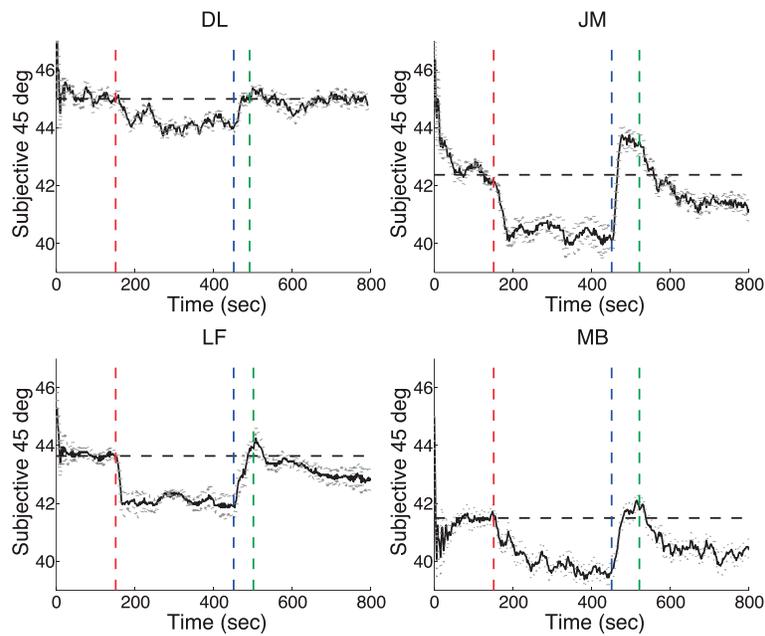


Figure 7. Average time courses of individual subjects in the tilt aftereffect experiment. Dotted lines represent \pm one standard error across sessions. The horizontal dashed line marks the average of values measured during the baseline period before the 5 min adaptation to high contrast. The three vertical lines mark the time onsets for adaptation, deadaptation, and posttest.

insensitive to the length of the duration of initial induction, however. Hence, to exclude this alternative, Experiment 5 examined the time courses of contrast adaptation with two different adapting durations, 90s and 270 s.

The results of Experiment 5 showed that spontaneous recovery was in fact sensitive to the duration of prior adaptation. A linear trend analysis showed reliable spontaneous recovery in the time courses in both conditions, 90 sec: $t(9) = 6.26$, $p < 0.001$, 270 s: $t(9) = 6.70$, $p < 0.001$. However, the area under the curve in the posttest was significantly larger for the 270 s condition than for the 90 s condition, ($t(9) = 2.53$ $p <$

0.05, see Figure 8), indicating a stronger recovery of aftereffects for the longer initial induction period.

Discussion

In five experiments, adaptation to high contrast was eliminated by rapid adaptation to low contrast, but recovered during continued testing. We measured this spontaneous recovery using three different behavioral paradigms: contrast matching, contrast detection, and tilt adjustment. The spontaneously recovered adapta-

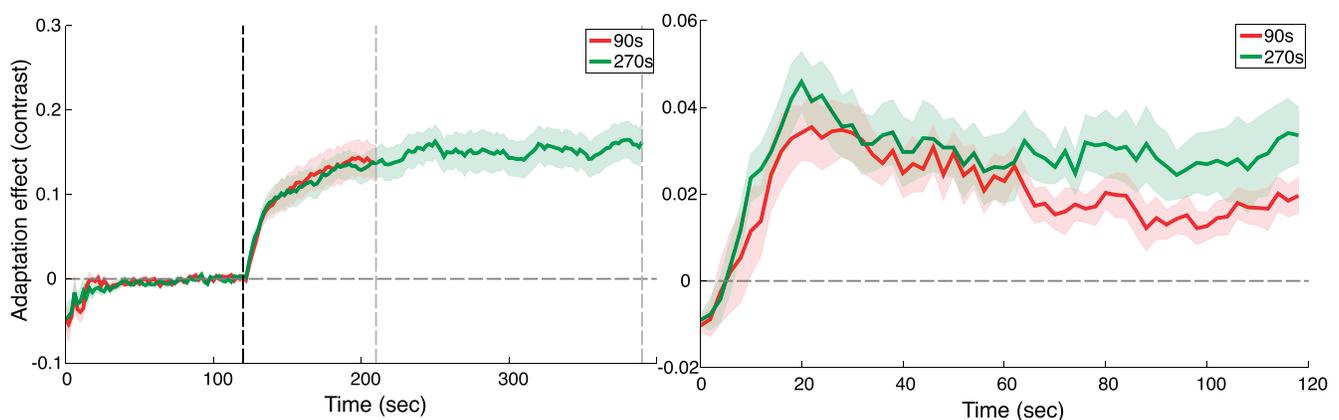


Figure 8. Grand average time courses before (left panel) and after (right panel) deadaptation in Experiment 5. Plotting conventions are as in Figure 4, except that the vertical lines in the left panel represent the onsets for adaptation and deadaptation for the 90 s condition, and deadaptation for the 270 s condition, from left to right.

tion also decayed more slowly following longer initial adaptation, indicating that it is a result of stimulus history and not an inevitable consequence of rapid deadaptation.

The simplest account of these results is that contrast adaptation is controlled by multiple distinct mechanisms, each tuned to a different timescale. In the multiple mechanisms account, rapid deadaptation causes a short-term mechanism to signal for a sensitivity increase, cancelling ongoing signals from long-term ones. However, once deadaptation ends, the short-term mechanism rapidly returns to baseline, and the slowly decaying effects in the long-term mechanisms reemerge. Spontaneous recovery cannot be explained by a model of contrast adaptation with only a single mechanism, because once deadaptation cancels the original effects, there is no memory of their original strength.

Together with our prior work, the current findings suggest that a continuum of mechanisms might control contrast adaptation. We previously observed spontaneous recovery over timescales two orders of magnitudes longer than those used here (initial adaptation was 240 min, Bao & Engel, 2012). The findings in that work suggested that a mechanism controlling especially long-term adaptation was distinct from those controlling shorter-term adaptation. However, this long-term mechanism may have been unique. It remained possible that one mechanism in the visual system could have controlled adaptation for durations longer than a few hours, while another controlled all shorter-term contrast adaptation. Our observation of spontaneous recovery over relatively short timescales strongly suggests that this is not the case, and that at least two distinct controlling mechanisms act over shorter timescales. Although the ultimate number of distinct mechanisms could yet turn out to be some small number, it seems more likely to us that adaptation time constants are continuously distributed, like the constants defining tuning for other visual attributes, such as orientation or spatial frequency.

Our observation of spontaneous recovery depend upon comparing effects of a 25% adapter in the initial baseline period to effects of a 25% adapter measured later in the posttest period, with stronger effects arising in the posttest. It is possible, in theory, that effects of the 25% adaptation simply accumulated over time, with stronger adaptation being produced later in the experiment (e.g., Hammett, Snowden, & Smith, 1994), and that this accumulated effect produced the recovery visible in the posttest. However, as can be seen in Figure 4, any effect of such “baseline adaptation” has reached asymptote by the late stage of the baseline measurement. Any remaining slight trend is dwarfed by the slope of the

“spontaneous recovery” in the posttest. There is no reason to believe that the effect of the 25% grating could strengthen over time; indeed, one would expect it to decrease, making it unable to produce the spontaneous recovery we observed. Adaptation to the 25% grating also cannot explain the downward trend we see in Figure 4 after the completion of spontaneous recovery, which we interpret as the decay of the long-term mechanism. Note also that even the slight trend for continuing effects of the 25% grating is absent for the data shown in Figure 5, and for two of the subjects in Figure 7. Therefore, it is highly unlikely that the spontaneous recovery we found is due to effects of the 25% adapter.

One prior behavioral study (Magnussen & Johnsen, 1986) has reported spontaneous recovery of a tilt aftereffect following 30 min of adaptation and 2 min of deadaptation. However, the orientation used for deadaptation in that study was not the same as that used for the initial adaptation. Therefore, the spontaneous recovery found in that study could be accounted for by two mechanisms, each tuned to a different orientation, and each controlling adaptation across all timescales. Since we kept the adapting orientation constant throughout the experiment, our results reveal distinct temporal mechanisms tuned to the same orientation. Multiple temporally tuned mechanisms of adaptation have also been proposed for the McCollough effect, face adaptation, and adaptation to motion (Kovacs, Zimmer, Harza, & Vidnyanszky, 2007; Roach & McGraw, 2009; Vul et al., 2008).

The neural loci that control contrast adaptation over differing timescales remain to be determined. Adaptation effects with different time constants have been reported in the retina, where the rapid process is an almost instantaneous contrast normalization (Baccus & Meister, 2002; Fairhall, Lewen, Bialek, & de Ruyter Van Steveninck, 2001). The orientation selectivity of the effects reported here make a cortical locus more likely, however. Within cortex, multiple timescales of adaptation could in principle arise from differing adaptation rates at different sites in the visual hierarchy, different populations within the same site (Ahmed, Anderson, Douglas, Martin, & Whitteridge, 1998), or even different cellular mechanisms within a single neuron (La Camera et al., 2006). The latter two of these possibilities have received some support from studies of primary visual cortex, where classical and extra-classical receptive fields show distinct adaptive effects (Dhruv, Tailby, Sokol, & Lennie, 2011) including, importantly, differences as a function of adaptation duration (Patterson, Wissig, & Kohn, 2013). Additionally, some forms of adaptation in V1 can continue to strengthen over periods of minutes (Dragoi, Sharma, & Sur, 2000; Sharpee et al., 2006).

Our behavioral results are also consistent with an early cortical locus. Because detection of simple patterns may depend relatively directly upon responses there (Hawken & Parker, 1990; Ress & Heeger, 2003), our finding of spontaneous recovery in the contrast detection experiment suggests that the multiple controlling mechanisms may exist as early as in V1. However distinct mechanisms that can control orientation-specific contrast adaptation over seconds versus over minutes have yet to be clearly delineated in early visual cortex.

Adapting at multiple timescales may be an optimal strategy for the brain (Kording et al., 2007). Changes in our visual environment are produced by a variety of causes that act over a variety of timescales. For example, saccades, locomotion, sun position, and eye disease can all affect contrast of the retinal image, but such changes happen over different timescales spanning many orders of magnitude. Since each cause can arise independently, an optimal observer should be capable of adjusting to each independently, and this strategy is naturally implemented by having distinct controlling mechanisms tuned to each timescale (Kording et al., 2007).

Conclusions

The present results suggest that contrast adaptation, in paradigms similar to those used in dozens, if not hundreds of prior studies, is controlled by multiple mechanisms operating over different timescales. These results, taken together with our previous findings in longer-term contrast adaptation, suggest that a continuum of mechanisms could possibly control contrast adaptation over a wide range of timescales. This organization may be optimal, allowing the visual system to operate efficiently during both transient and enduring changes in the world. Future work will further verify whether such a continuum of mechanisms exists, or whether these experiments have tapped into discrete timescales of adaptation.

Keywords: adaptation, contrast, timescale, spontaneous recovery

Acknowledgments

This research was supported by grant NSF BCS-1028584 and the Key Research Program of the Chinese Academy of Sciences (KSZD-EW-TZ-003).

Commercial relationships: none.

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References

- Ahmed, B., Anderson, J. C., Douglas, R. J., Martin, K. A., & Whitteridge, D. (1998). Estimates of the net excitatory currents evoked by visual stimulation of identified neurons in cat visual cortex. *Cerebral Cortex*, 8(5), 462–476.
- Baccus, S. A., & Meister, M. (2002). Fast and slow contrast adaptation in retinal circuitry. *Neuron*, 36(5), 909–919.
- Bao, M., & Engel, S. A. (2012). Distinct mechanism for long-term contrast adaptation. *Proceedings of the National Academy of Sciences, USA*, 109(15), 5898–5903.
- Blakemore, C., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology*, 203(1), 237–260.
- Dhruv, N. T., Tailby, C., Sokol, S. H., & Lennie, P. (2011). Multiple adaptable mechanisms early in the primate visual pathway. *Journal of Neuroscience*, 31(42), 15016–15025.
- Dragoi, V., Sharma, J., & Sur, M. (2000). Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron*, 28(1), 287–298.
- Fairhall, A. L., Lewen, G. D., Bialek, W., & de Ruyter Van Steveninck, R. R. (2001). Efficiency and ambiguity in an adaptive neural code. *Nature*, 412(6849), 787–792.
- Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned fMRI adaptation in human visual cortex. *Journal of Neurophysiology*, 94(6), 4188–4195.
- Greenlee, M. W., Georgeson, M. A., Magnussen, S., & Harris, J. P. (1991). The time course of adaptation to spatial contrast. *Vision Research*, 31(2), 223–236.
- Grzymacz, N., & de Juan, J. (2003). Sensory adaptation as Kalman filtering: Theory and illustration with contrast adaptation. *Network: Computation in Neural Systems*, 14, 465–482.
- Hammett, S. T., Snowden, R. J., & Smith, A. T. (1994). Perceived contrast as a function of adaptation duration. *Vision Research*, 34(1), 31–40.
- Hawken, M., & Parker, A. (1990). Detection and discrimination mechanisms in the striate cortex of

- the old-world monkey. In C. Blakemore (Ed.), *Vision: Coding and efficiency* (pp. 103–116). Cambridge, UK: Cambridge University Press.
- Kohn, A. (2007). Visual adaptation: physiology, mechanisms, and functional benefits. *Journal of Neurophysiology*, 97(5), 3155–3164.
- Kording, K. P., Tenenbaum, J. B., & Shadmehr, R. (2007). The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience*, 10(6), 779–786.
- Kovacs, G., Zimmer, M., Harza, I., & Vidnyanszky, Z. (2007). Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Research*, 47(25), 3141–3149.
- Kwon, M., Legge, G. E., Fang, F., Cheong, A. M., & He, S. (2009). Adaptive changes in visual cortex following prolonged contrast reduction. *Journal of Vision*, 9(2):20, 1–16, <http://www.journalofvision.org/content/9/2/20>, doi:10.1167/9.2.20. [PubMed] [Article]
- La Camera, G., Rauch, A., Thurbon, D., Luscher, H. R., Senn, W., & Fusi, S. (2006). Multiple time scales of temporal response in pyramidal and fast spiking cortical neurons. *Journal of Neurophysiology*, 96(6), 3448–3464.
- Magnussen, S., & Greenlee, M. W. (1985). Marathon adaptation to spatial contrast: saturation in sight. *Vision Research*, 25(10), 1409–1411.
- Magnussen, S., & Johnsen, T. (1986). Temporal aspects of spatial adaptation. A study of the tilt aftereffect. *Vision Research*, 26(4), 661–672.
- Meese, T. S., & Georgeson, M. A. (1996). The tilt aftereffect in plaids and gratings: Channel codes, local signs, and “patchwise” transforms. *Vision Research*, 36(10), 1421–1437.
- Ohzawa, I., Sclar, G., & Freeman, R. D. (1985). Contrast gain control in the cat’s visual system. *Journal of Neurophysiology*, 54(3), 651–667.
- Patterson, C. A., Wissig, S. C., & Kohn, A. (2013). Distinct effects of brief and prolonged adaptation on orientation tuning in primary visual cortex. *Journal of Neuroscience*, 33(2), 532–543.
- Ress, D., & Heeger, D. J. (2003). Neuronal correlates of perception in early visual cortex. *Nature Neuroscience*, 6(4), 414–420.
- Roach, N. W., & McGraw, P. V. (2009). Dynamics of spatial distortions reveal multiple time scales of motion adaptation. *Journal of Neurophysiology*, 102(6), 3619–3626.
- Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, 29(7), 747–755.
- Sharpee, T. O., Sugihara, H., Kurgansky, A. V., Rebrik, S. P., Stryker, M. P., & Miller, K. D. (2006). Adaptive filtering enhances information transmission in visual cortex. *Nature*, 439(7079), 936–942.
- Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different time-scales underlie short-term motor learning. *PLoS Biology*, 4(6), e179.
- Vul, E., Krizay, E., & MacLeod, D. I. (2008). The McCollough effect reflects permanent and transient adaptation in early visual cortex. *Journal of Vision*, 8(12):4, 1–12, <http://www.journalofvision.org/content/8/12/4>, doi:10.1167/8.12.4. [PubMed] [Article]
- Wark, B., Fairhall, A., & Rieke, F. (2009). Timescales of inference in visual adaptation. *Neuron*, 61(5), 750–761.
- Wark, B., Lundstrom, B. N., & Fairhall, A. (2007). Sensory adaptation. *Current Opinion in Neurobiology*, 17(4), 423–429.
- Zhang, P., Bao, M., Kwon, M., He, S., & Engel, S. A. (2009). Effects of orientation-specific visual deprivation induced with altered reality. *Current Biology*, 19(22), 1956–1960.