Depth-dependent contrast gain-control

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Abstract

Contrast adaptation that was limited to a small region of the peripheral retina was induced as observers viewed a multiple depth-plane textured surface. The small region undergoing contrast adaptation was present only in one depth-plane to determine whether contrast gain-control is depth-dependent. After adaptation, observers performed a contrast-matching task in both the adapted and a non-adapted depth-plane to measure the magnitude and spatial specificity of contrast adaptation. Results indicated that contrast adaptation was depth-dependent under full-cue (disparity, linear perspective, texture gradient) conditions; there was a highly significant change in contrast gain in the depth-plane of adaptation and no significant gain change in the unadapted depth-plane. A second experiment showed that under some monocular viewing conditions a similar change in contrast gain was present in the adapted depth-plane despite the absence of disparity information for depth. Two control experiments with no-depth displays showed that contrast adaptation can also be texture- and location-dependent, but the magnitude of these effects was significantly smaller than the depth-dependent effect. These results demonstrate that mechanisms of contrast adaptation are conditioned by 3-D and 2-D viewing contexts.
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1. Introduction

The human visual system has evolved a variety of mechanisms that render a unique interpretation from the highly variable stimulation that impinges on the two retinas. These mechanisms fall under the rubric of perceptual constancies, and they function in a variety of domains such as color, contrast, depth, direction, lightness, orientation, shape, size, and speed. While some of these constancy mechanisms may require little or no postnatal perceptual experience to function effectively, all of them must be under adaptive control. That is, there must be a perceptual-learning component that adjusts the weights for different sources of information so that the resultant integrated signal correctly matches the distal environment. Without such an adaptive mechanism, any change in bias or sensitivity of the underlying sensors (e.g., proprioceptors in the case of size constancy or spatial summation areas in the case of lightness constancy) would lead to non-veridical interpretations of the external world.

Perhaps the most fundamental problem facing any perceptual constancy mechanism is sensor inhomogeneity. Consider the case of variations in spatial resolution across the retinal surface. The greater packing density of cones in the fovea, and the falloff in density with retinal eccentricity, results in a monotonic degradation in visual acuity and contrast sensitivity from the central to the peripheral visual field. Thus, at near-threshold levels of stimulus contrast, an object of uniform physical contrast (the distal stimulus) is not perceived veridically because of the inhomogeneity of the retinal receptor array (the proximal stimulus). However, at suprathreshold levels of stimulus contrast this inhomogeneity no longer results in a mismatch between the distal and proximal stimuli. An adaptive mechanism, termed contrast-constancy by Georgeson and Sullivan (1975), adjusts the contrast-gain across the retina so that perceived contrast does not vary with eccentricity (see also Cannon, 1985; Kulikowski, 1976). That is, in a contrast-matching task, subjects judge foveal and peripheral patches of grating of the same *physical* contrast to have the same *perceived* contrast, even though their *retinal* contrasts are different (because of optical and neural degradations with increasing retinal eccentricity).

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The mechanism subserving contrast constancy, although clearly post-retinal, has remained unclear. While there are local, retinal adaptation mechanisms, these cannot be sufficient to account for a variety of effects, including orientation-specific contrast gain-control and interocular transfer, both of which have a cortical locus (see Snowden & Hammett, 1992, 1996). Moreover, there are compelling ecological reasons why contrast adaptation should not be limited to the level of the retinal image. Consider a natural scene in which various objects are located not only at different retinal eccentricities but also at different viewing distances. While fixating one object, the *retinal* contrasts of the other objects are reduced because of the limited depth of focus of the visual system, and this contrast reduction varies monotonically with the difference in depth between the fixated object and the other objects. Yet, the *apparent* contrasts of these other objects located off the plane of fixation appear to remain invariant. This implies that contrast adaptation operates within a depth plane; that is, contrast constancy is not determined solely by the properties of the 2-D retinal images.

To examine this hypothesis, we used a paradigm developed by Li and Aslin (1992). In their study, subjects tracked a smoothly moving fixation target as it passed over a large, stationary grating of medium contrast. Located eccentric to the fixation target (i.e., 7 deg in the periphery) was a Gaussian-shaped window of contrast decrement. Thus, as the subject tracked the moving fixation target, this peripheral region of contrast decrement *moved* across the background grating. Interestingly, subjects rarely noticed the region of contrast decrement, even though the Gaussian-shaped window reduced contrast from 38% to 0%. Rather, subjects reported that the background grating appeared to be of uniform physical contrast. Importantly, in a contrast-matching task after 3 min of adaptation, subjects judged a Gabor patch presented in the region of contrast decrement to be of *higher* perceived contrast than an identical Gabor patch presented at an unadapted location. Thus, a local contrast gain-control mechanism adjusted the sensitivity of the adapted region of retina.

In a follow-up experiment, Aslin and Li (1993) showed that this localized contrast gain-control mechanism is not orientation-specific and that it transfers interocularly (under some conditions). Thus, the *perception* of contrast under these simulated contrast-scotoma conditions is consistent with a post-retinal mechanism that recalibrates contrast gain. In the present study, we extended the simulated contrast-scotoma paradigm of Li and Aslin (1992) to the third dimension. Subjects tracked a smoothly moving fixation target as it traversed a large-field grating of medium contrast. The grating was rendered in 3-D using perspective and stereo information; it had the appearance of a continuous surface with a depth discontinuity in the middle of the display. Thus, half of the surface (left or right) appeared to be nearer to the subject than the other half of the surface. As in Li and Aslin, a Gaussian-shaped region of contrast decrement was located eccentric to the moving fixation target. However, this simulated contrast-scotoma was present only when the fixation target was located on either the near or the far depth surface. At issue was whether the contrast decrement under these circumstances would lead to a depth-dependent adjustment in contrast-gain. If so, this would suggest that a powerful perceptual-learning mechanism maintains contrast constancy, even in the face of sensor inhomogeneities that are tied to the depth of the display.

2. Experiment 1: contrast adaptation to displays containing multiple cues to depth

2.1. Methods

2.1.1. Participants

Eight adults (students at the University of Rochester between 19 and 23 years of age) with normal or corrected-to-normal acuity and normal stereopsis served as the participants. Four participants each were assigned to two stimulus conditions: (a) near-adapt or (b) far-adapt. Participants were paid $8/h for completion of each 30 min session and were treated in accordance with ethical guidelines established by the University's Research Subjects Review Board.

2.1.2. Stimuli and apparatus

Participants viewed a display on a 19 in Sony Trinitron monitor while wearing Crystal Eyes wireless stereoscopic glasses, which alternated video frames between the two eyes at 50 Hz. None of the participants in this or the following experiments reported that the displays flickered or that the viewing conditions prevented them from seeing the stimuli clearly. The stimuli in this experiment were generated using only the red channel of the monitor, creating a red grating on a black background. The red channel on the monitor was linearized (gamma corrected) to control luminance and contrast of the displayed gratings. Participants were seated 38.5 cm from the monitor and an average interocular separation of 6.5 cm was used to calculate retinal disparities.

The stimulus display consisted of a simulated 3-D surface. As shown in Fig. 1A, the display depicted a surface with two regions in the frontoparallel plane and a depth discontinuity between the near and the far regions. We will refer to the three surface regions as the near surface, the far surface, and the incline surface. The near surface was rendered using both perspective, texture gradient, and stereo cues to appear 32 cm from the participant and the far surface to appear 45 cm from the
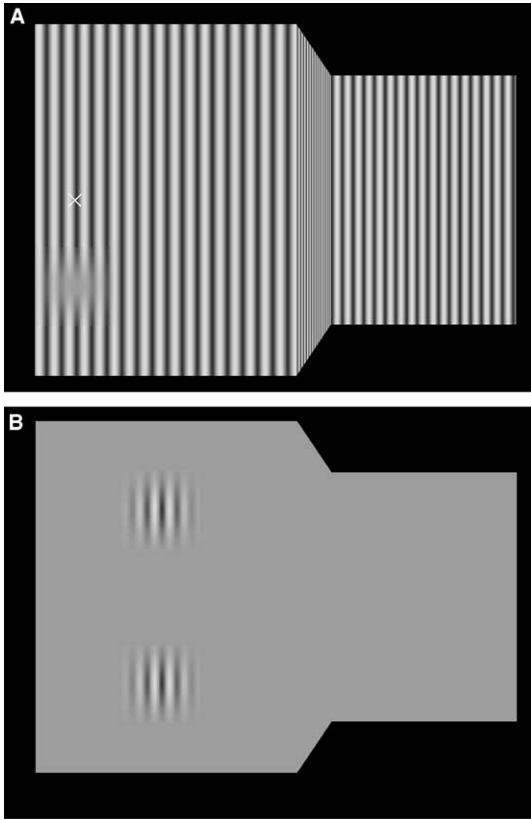
Fig. 1. Schematic of the stimulus display used during (A) adaptation and (B) test. The Gabor-shaped region of contrast decrement was located peripheral to the fixation cross, which moved smoothly (left–right–left) across the depth-rendered surface during adaptation. During test, two Gabor patches (standard-above and comparison-below) were presented for 250 ms while the background grating was replaced with an even luminance field for 750 ms. Participants judged which test patch was of higher apparent contrast. Two different sized test patches (separated by different eccentricities) were presented during testing on the non-adapted depth surface.

participant. The entire surface was overlaid with a sine-wave grating of constant spatial frequency. Thus the near-surface grating had a frequency of 1.25 c/deg and the far-surface grating had a frequency of 1.75 c/deg. The mean luminance of the grating was 2.97 cd/m^2 and the Michelson contrast was 60%.

2.1.3. Procedure

Each participant was adapted to a contrast decrement located on only one side of the display (left-near or right-far). Participants were then tested repeatedly in a 2AFC contrast-matching task, with short periods of readaptation between test trials. During the adapting phase, participants fixated a small red cross (1.04 deg) that traveled horizontally back and forth across the display of the grating surface. The fixation cross traversed the display (one complete cycle) in about 10 s. During the adapting phase, a small patch of the 60%-contrast surface grating, located in the periphery below

the fixation cross, had less than 60% contrast. This small patch had a 2-D Gabor modulation of the grating contrast, such that at its center the contrast was zero. Because this Gabor-shaped region of contrast decrement was rendered in depth, it was 4.35 cm (6.0 deg) below the fixation cross on the far surface and 6.15 cm (8.5 deg) below the fixation cross on the near surface, and its diameter also varied with the simulated surface depth (s.d. = 0.81 cm on the far surface and 1.14 cm on the near surface). Note that in each of the two adapting conditions (near or far), the Gabor-shaped region of contrast decrement was present *only* when the fixation cross was located on that depth surface. When the fixation cross moved to the non-adapting surface, there was no contrast decrement present (i.e., the surface contrast was a uniform 60%).

During the initial adaptation phase, participants viewed 15 left–right–left excursions of the fixation cross before any testing was performed. After this initial 2.5 min of adaptation, a test trial was presented. Each test trial was followed by 1.5 cycles of movement of the fixation cross during a readaptation phase, followed by another test trial. This pattern of readaptation and test was repeated until the testing requirements (see below) were met.

The test phase consisted of the fixation cross (and nearby Gabor scotoma) pausing for 750 ms in the center of either the near or far surface (alternating on each test trial) while the entire grating surface was replaced by a mean luminance (zero contrast) pattern (see Fig. 1B). While the background grating was reduced in contrast from 60% to 0%, two Gabor test-patches were presented above and below the fixation cross for 250 ms. After the 250 ms presentation of the two test Gabors, the entire surface remained at zero contrast until the participant made a 2AFC judgment as to which Gabor was higher in apparent contrast. The Gabor above the fixation cross (the standard) always had a contrast of 60%, which matched the surface grating during the adaptation phase. The Gabor below the fixation cross (the comparison) had a contrast that varied across test trials according to a 1-up, 1-down staircase algorithm. The participant's task was to decide on each trial whether the above or below Gabor had greater contrast. The staircase began with the comparison Gabor at 5% or 90% contrast and used a step size of 20% contrast until the first reversal, with a step size of 10% contrast thereafter. The test phase ended after eight reversals of the pattern of responding in the staircase, but only the last six reversals were used to estimate the point of subjective contrast-matching between the two Gabors.

Although the adapting surface was rendered in depth, the contrast gain-control mechanism could be based solely on which regions of the retina had been presented with the contrast decrement. According to this retinally based hypothesis, the appropriate size of the Gabor

test-patches would be whatever size (in retinal angle) was used during adaptation (either near- or far-surface). Alternatively, if the contrast gain-control mechanism was depth-specific, then the appropriate size of the Gabor test-patches would be larger (in retinal angle) when presented on the near surface than on the far surface. To examine these two hypotheses, we used two types of test trials on the non-adapted depth surface: (a) Gabor test-patches with a size that was depth-scaled and (b) Gabor test-patches that were the same retinal size as on the adapted depth surface. Specifically, paired Gabor test-patches on the near depth surface in the near-adapt condition were large in diameter (s.d. = 1.14 cm) and 6.15 cm from the fixation cross. Paired Gabor test-patches on the far (non-adapted) depth surface in the near-adapt condition were either identical in retinal size and location (s.d. = 1.14 cm; 6.15 cm from fixation) or depth-rendered (s.d. = 0.81 cm; 4.35 cm from fixation). Analogously, paired Gabor test-patches on the far depth surface in the far-adapt condition were small in diameter (s.d. = 0.81 cm) and 4.35 cm from the fixation cross. Paired Gabor test-patches on the near (non-adapted) depth surface in the far-adapt condition were either identical in retinal size and location (s.d. = 0.81 cm; 4.35 cm from fixation) or depth-rendered (s.d. = 1.14 cm; 6.15 cm from fixation). Contrast matches for the two sizes of Gabor test-patches on the non-adapted depth surfaces and the adapted size on the adapted depth surface were assessed using three randomly interleaved 1-up, 1-down staircases.

2.2. Results and discussion

The final six reversals from the staircase used to measure contrast matching were averaged for each participant in each of the four test conditions. Fig. 2A shows the mean contrast matches for each of the four participants in the near-adapt condition. If the effect of the Gabor-shaped contrast decrement on the near surface was to induce an *increase* in contrast gain, then participants should judge the contrast of the Gabor test-patch (which was the same size and in the same retinal location as the adapting contrast-decrement) to be higher than the 60% contrast of the background grating. As a result, they should *decrease* the physical contrast of this comparison Gabor-patch to obtain a match to the 60% standard Gabor-patch. All four participants had contrast matches that were significantly less than 60% ($M = 39.6\%$; $t(3) = -4.19$, $p < .025$). Thus, the near-adapt condition was successful in increasing contrast gain in the adapted retinal location.

Fig. 2A also shows that the near-adapt condition was depth-specific. If the effect had been retinally based, then it would be evident on both the left (near) and right (far) surfaces. Neither the larger-sized Gabor test-patches, which were the same retinal size and in the same retinal
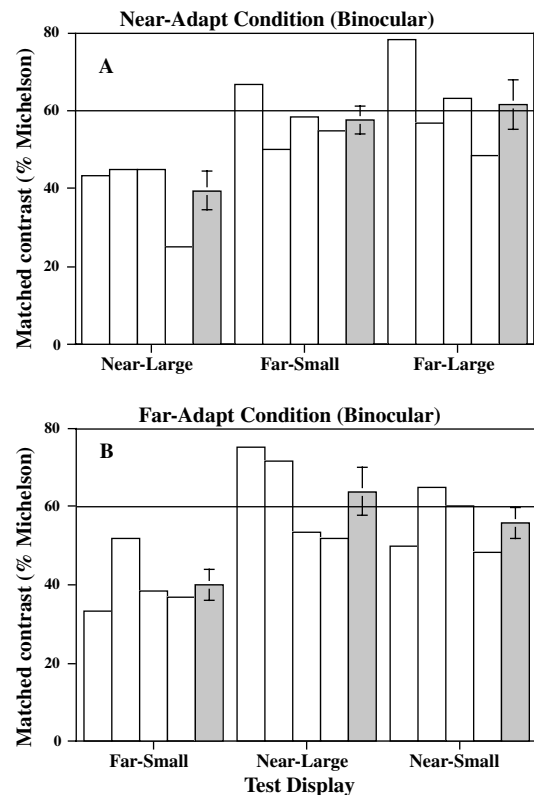

Fig. 2. Contrast matching data from each participant in (A) the near-adapt condition and (B) the far-adapt condition of Experiment 1. Values are the mean of the final six reversals in the staircase procedure that generated a contrast match between the comparison (the adapted region) and the standard (an unadapted region). Open bars = individual participant means; filled bars = group means ± 1 s.e.m.

location as the adapting Gabor-shaped contrast decrement, nor the smaller-sized Gabor test-patches, which were adjusted in size to conform to the projected size and location of the depth-rendered display, showed mean contrast matches that were different from the 60% standard (large $M = 61.7\%$; small $M = 57.5\%$). Thus, contrast gain was adjusted only for the near (adapted) surface and did not generalize to the far (unadapted) surface.

Fig. 2B shows the comparable contrast-matching data for the far-adapt condition. The pattern of results is identical to that of the near-adapt condition. Participants showed evidence of contrast adaptation, as evidenced by significantly lower contrast matches, only in the far-adapt (small Gabor test-patch) condition ($M = 40.0\%$; $t(3) = -4.95$, $p < .02$). In the other two test conditions, contrast matches did not differ significantly from the 60% standard ($M = 63.7\%$ in the near-large condition; $M = 55.8\%$ in the near-small condition). Thus, as in the case of the near-adapt condition, participants showed clear evidence of depth-dependent contrast gain-control.

A more direct test of differential adaptation as a function of depth is shown in Fig. 3 (leftmost bar).
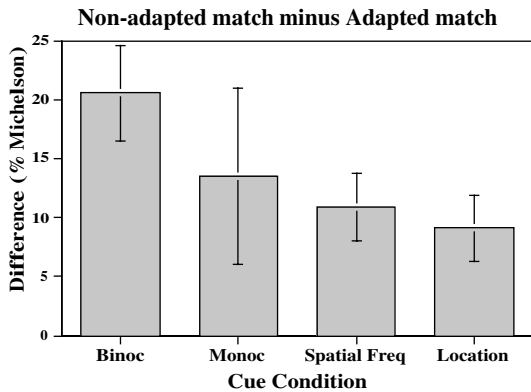
Fig. 3. Differences in contrast matching between the non-adapted side of the display and the adapted side of the display, obtained from each participant and averaged across participants in each of the four experiments. Positive values indicate that contrast gain was higher on the adapted than on the non-adapted side. Error bars = ±1 s.e.m.

Each participant's mean contrast threshold at the near and far test surfaces was expressed as a difference score (non-adapted minus adapted). Positive scores indicate a greater amount of contrast adaptation at the adapted than at the non-adapted depth surface. As shown in Fig. 3, the magnitude of the depth-dependent contrast adaptation was substantial ($M = 20.5\%$) and was significantly different from zero ($t(7) = 5.10$, $p < .002$).

The results of Experiment 1 provide clear evidence of depth-dependent contrast adaptation. A localized region of contrast decrement caused an increase in contrast gain. But this localized region of contrast adaptation, when limited to one depth-plane of a multi-plane surface, was present only for that adapted depth plane. This suggests that the type of contrast adaptation studied here is conditioned by the depth plane within which it is induced. However, because multiple cues to depth were present in the display, it is not clear if the depth-dependent effect reported here is specific to retinal disparity or to non-binocular information for depth (linear perspective or texture gradient). The goal of Experiment 2 was to determine whether retinal disparity information in the stereoscopic display was necessary for the depth-dependent contrast adaptation effect.

3. Experiment 2: contrast adaptation to displays without disparity as a cue to depth

3.1. Methods

3.1.1. Participants

Eight participants (students at the University of Rochester between 19 and 23 years of age) were tested in Experiment 2, none of whom served in Experiment 1.

3.1.2. Stimuli and apparatus

The stimulus display was identical to the one used in Experiment 1 except that retinal disparity was set to zero and the participants viewed the display monocularly (using an eye-patch). Thus, there was linear perspective information from the outline shape of the display and texture gradient information from the variation in spatial frequency of the grating across the surface of the display, but there was no retinal disparity information to support stereopsis.

3.1.3. Procedure

The procedure was identical to Experiment 1, with half of the participants in the near-adapt condition and half in the far-adapt condition.

3.2. Results and discussion

Fig. 4A shows the mean contrast matches for each of the four participants in the near-adapt condition. All four participants had contrast matches that were significantly less than 60% for the adapted depth plane
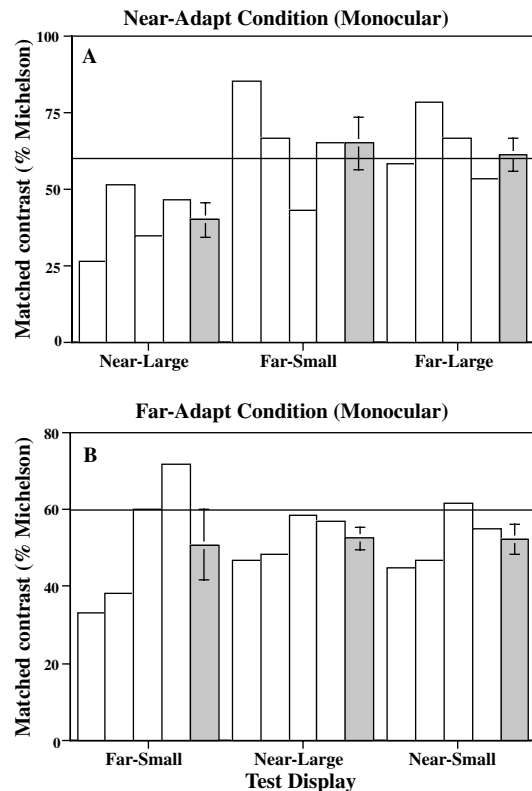

Fig. 4. Contrast matching data from each participant in the (A) near-adapt and the (B) far-adapt, no-disparity (monocular) conditions of Experiment 2. Values are the mean of the final six reversals in the staircase procedure that generated a contrast match between the comparison (the adapted region) and the standard (an unadapted region). Open bars = individual participant means; filled bars = group means ± 1 s.e.m.

($M = 40.0\%$; $t(3) = -3.53$, $p < .02$). Thus, the near-adapt condition under monocular viewing conditions was successful in increasing contrast gain in the adapted retinal location. Fig. 4A also shows that the near-adapt condition was depth-specific. If the effect had been retinally based, then it would be evident on both the left (near) and right (far) surfaces. Neither the larger-sized Gabor test-patches, which were the same retinal size and in the same retinal location as the adapting Gabor-shaped contrast decrement, nor the smaller-sized Gabor test-patches, which were adjusted in size to conform to the projected size and location of the depth-rendered display, showed mean contrast matches that were different from the 60% standard (large $M = 61.1\%$; small $M = 65.0\%$). Thus, contrast gain was adjusted only for the near (adapted) surface and did not generalize to the far (unadapted) surface.

Fig. 4B shows the mean contrast matches for each of the four participants in the far-adapt condition. Two of the four participants showed contrast matches to the far surface that were less than the 60% standard. While this group mean was numerically below 60% ($M = 50.8\%$), it was not significantly below 60% ($t(3) = 1.01$, $p = $ n.s.). The mean contrast matches to the near (unadapted) surface also did not differ from 60% (52.5% for the large test patches; 52.1% for the small test patches). Thus, there was no evidence of a depth-dependent contrast adaptation effect in the far-adapt condition.

As in Experiment 1, the data were pooled across the near- and far-adapt conditions and expressed as a difference score (non-adapted minus adapted). As shown in the second bar of Fig. 3, the mean magnitude of depth-dependent contrast adaptation was greater than zero ($M = 13.4\%$), but because of the high between-subject variance, this difference was not significant ($t(7) = 1.80$, $p = .11$). However, we noted that one participant in this sample (from the far-adapt condition) showed a depth-dependent contrast match that was quite large (15%) but in the opposite direction (more adaptation to the un-adapted surface). When this participant was dropped from the sample, the remaining seven participants showed a depth-dependent contrast adaptation effect that was marginally significant ($M = 17.5\%$; $t(6) = 2.43$, $p = .052$).

The results of Experiment 2 from the near-adapt condition provide evidence that depth from disparity is not essential for observing a depth-dependent contrast adaptation effect. However, there was considerably more between-subject variance in the contrast adaptation effect under monocular than under binocular viewing conditions. To further examine the specificity of this effect, and to ensure that it was linked to depth and not to other non-depth cues in the displays (right–left location or a high–low spatial frequency difference), we conducted two control conditions in Experiments 3 and 4 with displays containing no cues to depth.

4. Experiment 3: spatial-frequency (texture) control in a non-depth display

4.1. Methods

4.1.1. Participants
Eight participants (students at the University of Rochester between 19 and 23 years of age) were tested in Experiment 3, none of whom served in Experiments 1 or 2.

4.1.2. Stimuli and apparatus
The stimulus display was identical to the one used in Experiment 2 except that texture gradient and linear perspective information were eliminated. Two rectangular panels of the same size as the larger side of the display in Experiments 1 and 2 were placed side by side, with a small vertical strip of uniform mean luminance separating the two sides of the display. The spatial frequencies on the left and right sides of the display were identical to those used in Experiments 1 and 2. The Gabor-shaped region of contrast decrement was also identical to Experiment 1 and 2, including its variation in diameter depending on spatial frequency. That is, the Gabor-shaped region was larger on the left side of the display where the spatial frequency was lower, simulating the depth-rendering used in Experiments 1 and 2. Participants viewed the display binocularly, as in Experiment 1, but both sides of the display had zero disparity, simulating two surfaces at the same depth.

4.1.3. Procedure
The procedure was identical to Experiments 1 and 2, with half the participants in the left-adapt condition (low spatial frequency) and half in the right-adapt condition (high spatial frequency).

4.2. Results and discussion

Fig. 5A shows the mean contrast matches for each of the four participants in the left-adapt (low SF) condition. Two of the four participants had contrast matches that were less than 60%, but the group mean was not significant ($M = 43.7\%$; $t(3) = -1.98$, $p = .14$). Thus, the low spatial frequency condition was only partially successful in increasing contrast gain in the adapted retinal location. However, Fig. 5A also shows that there was less adaptation on the right (high SF) side of the display. If the effect had been retinally based, then it would be evident on both the left (low SF) and right (high SF) surfaces. Neither the larger-sized Gabor test-patches, which were the same retinal size and in the same retinal location as the adapting Gabor-shaped contrast decrement, nor the smaller-sized Gabor test-patches, which were adjusted in size to conform to the projected size and location of the depth-rendered display used in
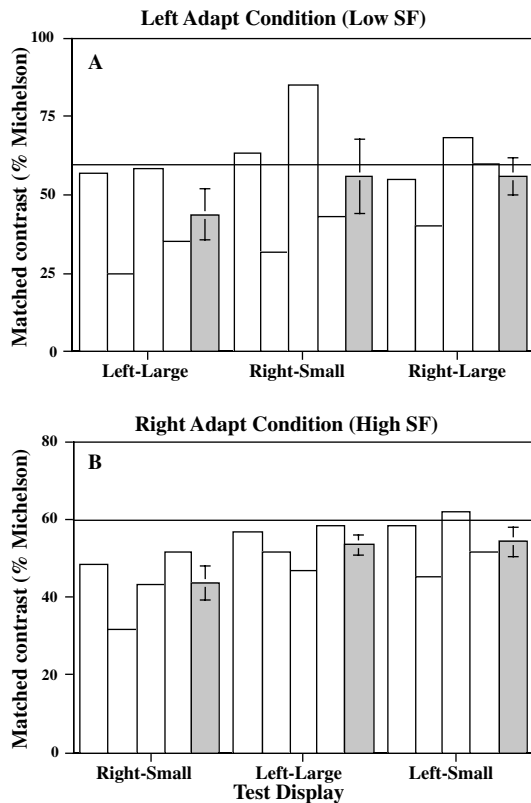
Fig. 5. Contrast matching data from each participant in the (A) left-adapt and the (B) right-adapt, spatial frequency control conditions of Experiment 3. Values are the mean of the final six reversals in the staircase procedure that generated a contrast match between the comparison (the adapted region) and the standard (an unadapted region). Open bars = individual participant means; filled bars = group means ± 1 s.e.m.

Experiment 1, showed mean contrast matches that were different from the 60% standard (large $M = 55.8\%$; small $M = 55.8\%$). Thus, there was some evidence that contrast gain was adjusted only for the low spatial frequency (adapted) surface and did not generalize to the high spatial frequency (unadapted) surface.

Fig. 5B shows the mean contrast matches for each of the four participants in the right-adapt (high SF) condition. All four of the participants showed contrast matches to the high spatial frequency surface that were less than the 60% standard ($M = 43.7\%$, $t(3) = -3.72$, $p < .04$). The mean contrast matches to the low spatial frequency (unadapted) surface did not differ from 60% (53.3% for the large test patches; 54.2% for the small test patches). Thus, there was evidence of a spatial frequency-dependent contrast adaptation effect in the right (high SF) adaptation condition.

As in Experiments 1 and 2, the data were pooled across the low and high spatial frequency adaptation conditions and expressed as a difference score (non-adapted minus adapted). As shown in the third bar of Fig. 3, the mean magnitude of spatial frequency-dependent contrast adaptation was significantly greater

than zero ($M = 10.8\%$; $t(7) = 3.98$, $p < .001$). Thus, across all participants in this spatial frequency control condition, there was clear evidence that contrast adaptation did not transfer fully from one side of the display to the other when the spatial frequency (texture) of the two sides of the display differed. Thus, at least some of the effect of depth-dependent contrast adaptation observed in Experiment 1 can be attributed to location (right–left) and texture (spatial frequency) cues. However, Fig. 3 shows that the magnitude of the effect in the full-cue (disparity, linear perspective, texture, and location) display of Experiment 1 was greater than in the partial-cue (texture and location) display of the present experiment ($M = 20.5\%$ vs. 10.8%; $t(14) = -1.97$, $p < .04$ one-tailed).

To further examine this difference between full-cue and partial-cue displays, we conducted a final control experiment in which only location (right–left) was correlated with the presence of a contrast decrement.

5. Experiment 4: location (right–left) control in a non-depth display

5.1. Methods

5.1.1. Participants

Eight participants (students at the University of Rochester between 19 and 23 years of age) were tested in Experiment 4, none of whom served in Experiments 1–3.

5.1.2. Stimuli and apparatus

The stimulus display was identical to the one used in Experiment 3 except that texture gradient information was eliminated by using a uniform spatial frequency (1.9 c/deg) across the entire display. As in Experiment 3, linear perspective was eliminated by using a simple rectangular shape (dimensions were the same as the larger half-surface used in Experiments 1 and 2). Because there was no rendering of depth in this adaptation display, the Gabor-shaped region of contrast decrement and the size of the Gabor test-patches was intermediate between the large and small regions in the near-adapt and far-adapt conditions (s.d. = 0.98 cm; 5.25 cm from fixation). To eliminate all cues to the presence of the contrast decrement except location, participants viewed the display monocularly, as in Experiment 2.

5.1.3. Procedure

The procedure was identical to Experiments 1–3, with half the participants in the left-adapt condition and half in the right-adapt condition. In contrast to Experiments 1–3, the size of the Gabor test-patch was the same size in all conditions.

5.2. Results and discussion

Fig. 6A shows the contrast-matching data for the left-adapt condition. Note that the magnitude of adaptation (the decrease from the 60% standard) was not significant when tested on the left (adapted) side of the display ($M = 47.9\%$; $t(3) = -2.36$, $p = $ n.s.), or when tested on the right (unadapted) side ($M = 55.6\%$; $t(3) = -0.93$, $p = $ n.s.). Fig. 6B shows the comparable data for the right-adapt condition. Here the magnitude of adaptation from 60% was significant when tested on the right (adapted) side ($M = 41.2\%$; $t(3) = -5.94$, $p < .01$), but not when tested on the left (unadapted) side ($M = 51.7\%$; $t(3) = -1.63$, $p = $ n.s.).

These results appear to provide only weak evidence of a location-specific effect in the uniform spatial frequency display used during adaptation in Experiment 4. However, as in Experiments 1–3, we expressed each participant's contrast adaptation effect as the difference in contrast matching between the adapted and the non-adapted sides of the display. Fig. 3 (rightmost bar) shows that the location-specific effect from Experiment 4
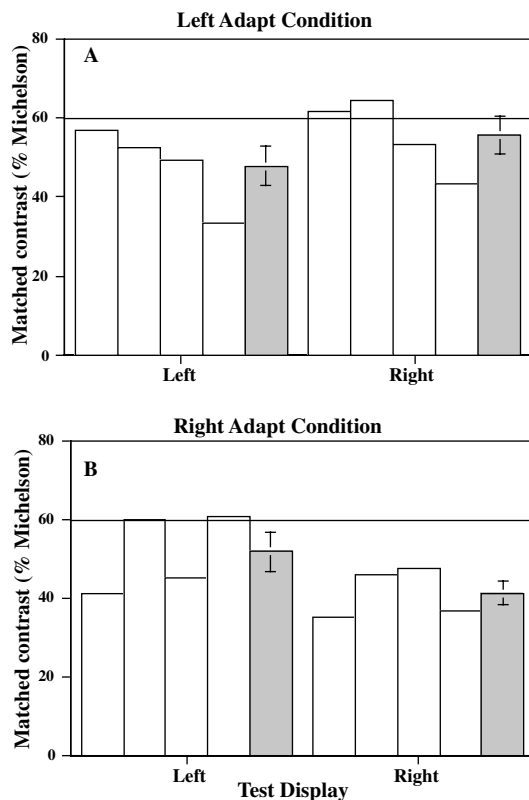

Fig. 6. Contrast matching data from each participant in the (A) left-adapt and the (B) right-adapt, location-control conditions of Experiment 4. Values are the mean of the final six reversals in the staircase procedure that generated a contrast match between the comparison (the adapted region) and the standard (an unadapted region). Open bars = individual participant means; filled bars = group means ± 1 s.e.m.

is significant ($M = 9.1\%$; $t(7) = 3.23$, $p < .015$). However, as in the partial-cue condition of Experiment 3, there is a clear reduction in the magnitude of the effect from the binocular depth displays in Experiment 1. The magnitude of the effect (non-adapted minus adapted) in Experiment 1 is significantly larger than in Experiment 4 ($M = 20.5\%$ vs. 9.1%; $t(14) = 2.33$, $p < .02$ one-tailed).

6. General discussion

The results of our experiments provide compelling evidence for a mechanism of contrast adaptation that is specific to the depth of the adapting surface. Although the strongest effect was obtained in Experiment 1, in which multiple depth cues including retinal disparity were present in the displays, depth information need not be specified by binocular cues, as shown by the significant depth-specific effect obtained in the near-adapt condition of Experiment 2 when only monocular cues were present. Importantly, the depth-specific effects obtained in Experiments 1 and 2 cannot be accounted for solely by the correlated cues of location or spatial frequency (texture) learned during adaptation. While there were significant effects of spatial-frequency and location (Experiment 3) and location alone (Experiment 4), the magnitudes of these effects were significantly less than the effect in the full-cue condition of Experiment 1 (see Fig. 3).

In fact, there was a monotonic fall-off in the magnitude of the context-dependent contrast adaptation effect as the number of cues to the presence of the contrast decrement was reduced. In the binocular condition, there were four cues correlated with the presence of the contrast decrement: retinal disparity, linear perspective, texture (spatial frequency), and location (right–left). In the monocular condition, there were three cues (all of the above except retinal disparity). In the spatial-frequency condition there were two cues: texture and location. And in the location condition there was only a right–left cue. A trend analysis on the data shown in Fig. 4 (minus the single participant in the monocular condition who showed an anomalous judgment) revealed a significant linear trend for a decrease in the magnitude of the contrast adaptation effect as the number of cues declined from four to one ($p < .05$). Thus, the more information present in the displays that was predictive of a region of contrast decrement, the greater the magnitude of contrast adaptation, with depth information serving as a particularly robust contextual cue for this adaptation effect.

There are two important implications of these results for models of contrast adaptation and perceptual learning. First, while there is clear evidence in the literature of contrast adaptation mediated by retinal, LGN, and V1 mechanisms (Kaplan & Shapley, 1986; Sclar,

Lennie, & DePriest, 1989), the present results suggest that higher-level mechanisms of contrast adaptation are operating when contrast adaptation is limited to a single depth plane. It remains unclear whether these depth-specific contrast adaptation effects are mediated by disparity-sensitive neurons themselves, by networks of contrast-sensitive neurons that receive feedback from networks of disparity-sensitive neurons, or by higher-level (multiple depth cue) mechanisms that modulate the activity of contrast-sensitive neurons. Similar depth-specific phenomena have been reported in domains other than contrast perception (Blaser & Domini, 2002; Domini, Blaser, & Cicerone, 2000; He & Nakayama, 1992; Nawrot & Blake, 1989).

Second, the small but significant spatial frequency and location effects in Experiments 3 and 4 suggest that mechanisms of contrast adaptation are influenced by the viewing context. The spatial frequency (texture) effect indicates that contrast adaptation has a limited spatial bandwidth, a result consistent with a proximal (retinal image) based mechanism. But the location (right–left) effect indicates that contrast adaptation is also influenced by eye-position in the orbit or gaze-position in space. That is, as participants look to the right or left side of a surface, the contrast adaptation mechanism can differentially adjust contrast gain. Such a mechanism may play a role in contrast perception when the stimulus contrast of an extended object is consistently modulated by differential illumination.

Finally, it is important to note that depth-dependent contrast gain-control serves a very useful function in everyday perception. Binocular fixation of a target at a particular distance results, at least in a multiple depth-plane environment, in one object whose image is projected onto the two foveas and other objects whose images are projected onto various regions of the peripheral retina. By the geometry of binocular fixation (and retinal disparity), the objects in front of and behind the plane of binocular fixation are projected onto non-corresponding regions of the two retinas. Thus, local retinally based contrast adaptation would alter *different* regions of the two retinas despite stimulation by the *same* object. Such a retinally based adaptive mechanism would result in interocular differences in contrast gain. A depth-specific contrast adaptation mechanism, on the other hand, would block this retinally based contrast adaptation effect, thereby limiting it to corresponding retinal regions (lying on the horopter). This is precisely the mechanism one would want in order to optimize the process of normalizing contrast in a binocular visual system. In recent work, we have also shown that sensitivity to stimulus blur is depth-dependent (Battaglia, Jacobs, & Aslin, 2004), suggesting that high-level adaptation mechanisms are tuned to the 3-D context in which objects are typically viewed in the natural visual world.

References

Aslin, R. N., & Li, A. (1993). Multiple mechanisms of contrast adaptation. *Investigative Ophthalmology and Visual Science, 34*(Suppl.), 1362.

Battaglia, P. W., Jacobs, R. A., & Aslin, R. N. (2004). Depth-dependent blur adaptation. *Vision Research, 44*, 113–117.

Blaser, E., & Domini, F. (2002). The conjunction of feature and depth information. *Vision Research, 42*, 273–279.

Cannon, M. W. (1985). Perceived contrast in the fovea and periphery. *Journal of the Optical Society of America A, 2*, 1760–1768.

Domini, F., Blaser, E., & Cicerone, C. M. (2000). Color-specific depth mechanisms revealed by color-contingent depth after effect. *Vision Research, 40*, 359–364.

Georgeson, M. A., & Sullivan, G. D. (1975). Contrast constancy: Deblurring in human vision by spatial frequency channels. *Journal of Physiology, 252*, 627–656.

He, Z. J., & Nakayama, K. (1992). Surfaces versus features in visual search. *Nature, 359*, 231–233.

Kaplan, E., & Shapley, R. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Sciences, USA, 83*, 2755–2757.

Kulikowski, J. J. (1976). Effect of contrast constancy and linearity on contrast sensation. *Vision Research, 16*, 1419–1431.

Li, A., & Aslin, R. N. (1992). Contrast adaptation and perceptual filling in at specific retinal locations. *Investigative Ophthalmology and Visual Science, 33*(Suppl.), 1256.

Nawrot, M., & Blake, R. (1989). Neural integration of information specifying structure from stereopsis and motion. *Science, 244*, 716–718.

Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research, 29*, 747–755.

Snowden, R. J., & Hammett, S. T. (1992). Subtractive and divisive adaptation in the human visual system. *Nature, 355*, 248–250.

Snowden, R. J., & Hammett, S. T. (1996). Spatial frequency adaptation: Threshold elevation and perceived contrast. *Vision Research, 36*, 1797–1809.