

Mechanisms of the dimming and brightening aftereffects

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Dimming and brightening aftereffects occur after exposure to a temporal luminance sawtooth stimulus: A subsequently presented steady test field appears to become progressively dimmer or brighter, depending on the polarity of the adapting sawtooth. Although described as “dimming” and “brightening,” it is plausible that a component of the aftereffects is based on contrast changes rather than on luminance changes. We conducted two experiments to reveal any contrast component. In the first we investigated whether the aftereffects result from the same mechanism that causes a polarity-selective loss in contrast sensitivity following luminance sawtooth adaptation. We manipulated test contrast: If a component of the aftereffect results from a polarity selective loss of contrast sensitivity we would expect that the aftereffects would differ in magnitude depending on the contrast polarity of the test fields. We found no effect of test-field polarity. In the second experiment we used an adapting sawtooth with a polarity consistent in contrast but alternating in luminance in order to induce a potential equivalent aftereffect of contrast. Again, we found no evidence that the aftereffects result from contrast adaptation. In a third experiment, we used S-cone isolating stimuli to discover whether there are S-cone dimming and brightening aftereffects. We found no aftereffects. However, in a fourth experiment we replicated Krauskopf and Zaidi’s (1986) finding that adaptation to S-cone sawtooth stimuli affects thresholds for increment and decrement detection. The mechanism underlying the dimming and brightening aftereffects thus seems to be independent of the mechanism underlying the concurrent polarity selective reductions in contrast sensitivity.

Introduction

The dimming and brightening aftereffects were discovered by Stuart Anstis in 1967. They are aftereffects that follow adaptation to a temporal luminance sawtooth (Figure 1). If the adapting sawtooth is one that brightens gradually and dims rapidly (Figure 1, right)—a “ramp-on” sawtooth—there is a dimming aftereffect. If the adapting sawtooth is one that dims gradually but brightens rapidly (Figure 1, left)—a “ramp-off” sawtooth—there is a brightening aftereffect. The aftereffect is dynamic, spatially localized, and relatively short-lived, lasting of the order of a few seconds. It is fairly robust to variations in adapting temporal frequency, occurring with roughly equal magnitude for adapting sawtooth waveforms between 0.5 and 4 Hz (Arnold & Anstis, 1993).

Anstis and colleagues have characterized the properties of the dimming and brightening aftereffects in some detail. They have found that:

1. The magnitude of the aftereffects decreases somewhat with retinal eccentricity, but is still clear up to at least 40° (Arnold & Anstis, 1993).
2. The aftereffects may be induced by sawtooth modulation in a surrounding region, and the induction has components of both simultaneous and successive contrast (Anstis, 1979).
3. The aftereffects are minimal either in a very small stimulus or in a ganzfeld stimulus (Anstis, 1967).
4. The aftereffects are still observable through a 2 mm artificial pupil, and are therefore not caused by a pupillary response (Anstis, 1967).
5. The dimming and brightening aftereffects can cause apparent motion in spatial luminance ramps (Anstis, 1967; Anstis & Reinhardt-Rutland, 1976).

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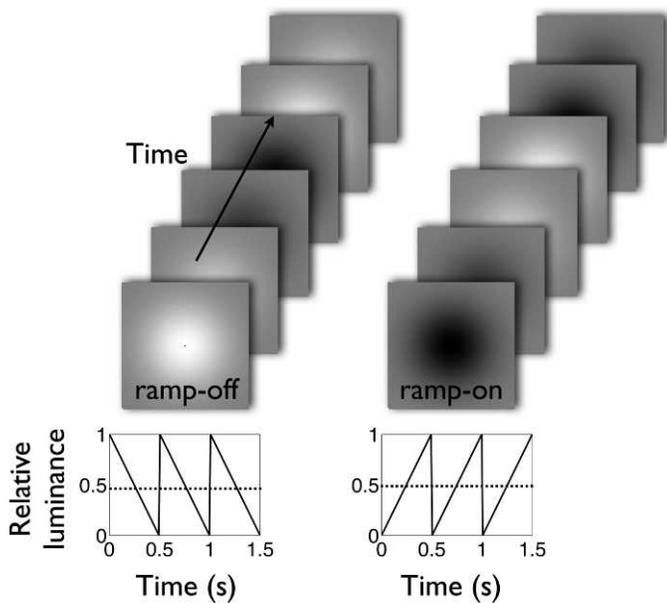


Figure 1. 2 Hz ramp-off and ramp-on sawtooth waveforms. A ramp-off sawtooth is represented on the left, as a waveform and as a series of snapshots along the waveform. A ramp-on sawtooth is represented on the right.

The locations within the visual system of the neural channels that give rise to the dimming and brightening aftereffects are unknown. However, there are several unusual properties of the aftereffects that narrow down the range of possibilities. The receptive fields of the neural mechanisms that underlie the aftereffects are very large. Anstis and Harris (1987) measured the receptive field size by using a checkerboard where alternate squares were modulated through opposite-polarity sawtooth waveforms. If, at a given eccentricity, the adapting squares of the checkerboard are smaller than the receptive field so that several opposite-polarity checks fell into the same receptive field, there should be no resultant aftereffect. Anstis and Harris measured the size of the receptive fields underlying the aftereffect at different retinal eccentricities by measuring the extent of the aftereffect into the periphery as the size of the squares of the adapting checkerboard was varied systematically. They found that the estimated diameter of the receptive fields (in minutes of arc) underlying the dimming and brightening aftereffects can be described by the following formula:

$$\begin{aligned} \text{Receptive field diameter} \\ = 13.62 \times \text{retinal eccentricity (degrees)} + 6.9 \end{aligned}$$

Anstis and Harris (1987) concluded that the diameter of the receptive fields is 20.9 times greater than the diameter of the cells underlying acuity (probably the midget cells), with 430 times their area.

Since the size of the receptive fields of the neural mechanism underlying the aftereffects is so large, a

plausible site for the neural mechanism's location is at high levels of the visual system where receptive fields are large—for example, area MT. However, this idea in a simple form is undermined by the fact that the dimming and brightening aftereffects show no interocular transfer (Anstis, 1967; Anstis & Harris, 1987). Cells in MT typically have balanced input from the two eyes and are only rarely monocularly driven (Maunsell & Van Essen, 1983). The two properties of the aftereffects—the large receptive-field sizes and the lack of interocular transfer—suggest an intriguing possibility for the neural mechanism involved: that it is low-level but has large receptive fields—perhaps a rare or currently undescribed class of retinal ganglion cells or early cortical cells. The aim of the present study was to measure more of the properties of the dimming and brightening aftereffects to further characterize the neural mechanism involved.

Krauskopf and Zaidi (1986) revealed a second effect of adaptation to sawtooth modulation. They found that adaptation to a luminance sawtooth caused polarity-selective reductions in contrast sensitivity. Following adaptation to a ramp-on sawtooth, there was a selective reduction in sensitivity to contrast increments. Following adaptation to a ramp-off sawtooth, there was a selective reduction in sensitivity to contrast decrements. It is not known whether the mechanism responsible for the dimming and brightening aftereffects is the same as that responsible for polarity-selective reductions in contrast sensitivity. But if adaptation to the same neural mechanisms were responsible for both effects, then we would expect that the dimming and brightening aftereffect would involve a progressive change in perceived contrast as well as a change in perceived luminance.

The aim of Experiments 1 and 2 was to determine whether the dimming and brightening aftereffects do result partly from the loss of contrast sensitivity that follows adaptation to temporal modulation of spatial contrast, or whether they are independent and purely aftereffects of luminance. The aim of Experiments 3 and 4 was to characterize the cone inputs to the mechanisms underlying the aftereffects, specifically to determine whether or not there is any S-cone input.

Experiment 1

In Experiment 1 we investigated whether the amplitude of the dimming and brightening aftereffects are independent of the polarity selective loss of contrast sensitivity found by Krauskopf and Zaidi (1986). Our method was analogous to that used in their study. We adapted subjects to both ramp-on and ramp-off sawtooth modulation, and then measured the magni-

tude of the aftereffects by measuring the amplitude of a nulling gradient required to perceptually null them on an incremental test field, a decremental test field, and a blank test field. If the aftereffects did depend on polarity-selective losses in contrast sensitivity, we would expect to see, for the size of the aftereffects, an interaction between the polarity of the adapting waveform and the polarity of the test field.

Methods

The stimuli used in Experiment 1 are represented in Figure 2. Subjects adapted to centrally presented Gaussian areas of sawtooth luminance modulation. The background luminance was 50.75 cd.m^{-2} , and the time-averaged luminance of the adapting sawtooth was the same as that of the background. The luminance of the adapting stimulus ranged from close to 0 to 101.5 cd.m^{-2} . The temporal frequency of the adapting waveform was 2 Hz. The *SD* of the Gaussian-adapting stimulus was 0.8° , and the image defining the background field was $41^\circ \times 31^\circ$.

In the condition where the test field was blank, the test field was uniform and of the same luminance as the background to the adapting stimulus. If the test field condition was incremental, a bright Gaussian test blob was presented with a peak luminance of 60.9 cd.m^{-2} against the 50.75 cd.m^{-2} surround. If the test field condition was decremental, a dark Gaussian test blob was presented with a minimum luminance of 40.6 cd.m^{-2} . The *SD* of the Gaussian test blob was the same as that of the adapting stimulus.

During the experiment the subject was instructed to fixate a centrally presented cross at all times. At the beginning of each block there was 2 min of adaptation to the adapting sawtooth. Following the initial period of adaptation, the first test stimulus was presented for 800 ms. The subject's task was to decide whether he saw a brightening or a dimming during the test interval, and to indicate his response with an appropriate button-press. Following the test interval, there was a 4 s period of top-up adaptation and then the next trial began. Test and adapting episodes were immediately consecutive, but the temporal phase of the adapting stimulus, and hence the instantaneous luminance at the end of each top-up period, was randomly assigned for each experimental block.

During the test interval, a physical luminance gradient was presented to null the dimming or brightening aftereffect. The nulling luminance gradient was temporally linear and had the same spatial Gaussian profile as the adapting stimulus. The nulling luminance gradient was applied to the test field in each condition. The incremental test field, for example, therefore either linearly increased its contrast (became a

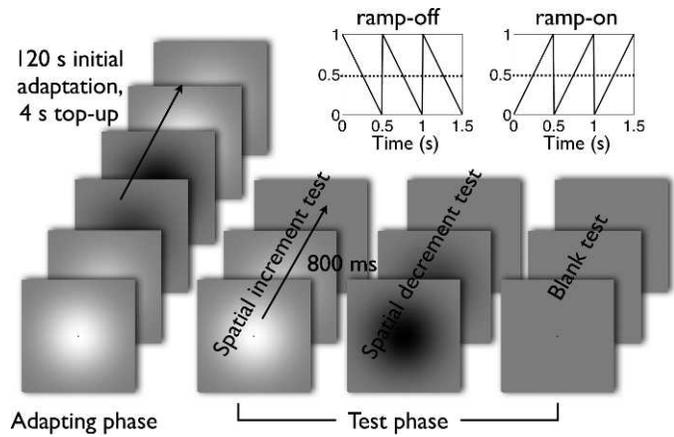


Figure 2. Stimulus and method for Experiment 1. There was an initial period of adaptation to sawtooth modulation (either a ramp-off sawtooth or a ramp-on sawtooth, depending on the block), followed by a test interval of 800 ms in which, depending on the condition, either an incremental test field, a decremental test field, or a blank test field was presented. On each trial the test field was initially at a fixed baseline luminance (an increment or decrement with the background of 10.15 cd.m^{-2} , or isoluminant with the background, depending on the condition), to which a nulling luminance gradient was then applied. The amplitude of the nulling gradient was adjusted via a staircase procedure until the subject was equally likely to report the progressive change of perceived brightness during the test interval as a brightening or as a dimming. When the participant applied a nulling gradient to the test blob therefore changed physically though the test interval. For an incremental test blob for example, the test blob would begin the test interval as a spatial increment of 10.15 cd.m^{-2} relative to the background. If the participant applied a brightening nulling gradient to null a dimming aftereffect on a particular test interval, the test blob would then increase linearly in luminance through the rest of the test interval, reaching a maximum at the end of the test interval that depended on the amplitude of the nulling gradient applied. The nulling gradient is represented in the figure as a loss of contrast of the test blobs, but this is just one of the possible physical scenarios caused by the nulling gradient.

brighter increment), or linearly decreased its contrast (became a dimmer increment) through the test interval, depending on whether the subject applied a brightening nulling gradient or a dimming nulling gradient, respectively. Physically, the test blob on each presentation underwent either a progressive increase or a progressive decrease in luminance and in contrast. Subjectively, however, once the subject had found an appropriate null for the dimming or brightening aftereffect, the test blob appeared to have steady luminance, appearing as either a steady increment, a steady decrement, or a steady blank field, depending on the condition.

The amplitude of the nulling gradient was adjusted after each trial according to the subject's response. If the subject reported that he saw a brightening, the amplitude of the nulling gradient was altered in the dimming direction, and vice-versa if he reported a brightening. Two interleaved ZEST (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994) staircases controlled the amplitude of the nulling gradient, and the staircase to be used was randomly selected on each trial. A block terminated after 60 trials.

In one session there were six blocks, each lasting approximately 8 min. There were three conditions (incremental test fields, decremental test fields, and blank test fields), and opposite-polarity-adapting sawtooth waveforms were tested in separate blocks. Between each block there was a 2-min resting period to allow adaptation to wear off. The subject completed two sessions separated by at least 2 days. Results are based on the average of the two sessions.

The experiment was conducted using a VSG2/4 graphics card (Cambridge Research Systems, Rochester, UK), controlled using Matlab (The Mathworks, Inc., Natick, MA). Stimuli were presented on a GDM 2000TC CRT monitor (Sony, Tokyo, Japan). The gamma functions of the monitor were linearized using a UDT photometer (United Detector Technology, Hawthorne, CA), and the linearization was checked using a Spectrascan PR650 spectroradiometer (Photo Research, Inc., Chatsworth, CA).

Four subjects took part in the experiment. One subject was an author (JB), and three subjects were naive to the purposes of the experiment. Two subjects were male and two were female, and their ages ranged between 21 and 34. All subjects had normal color vision (assessed by the Ishihara Plates) and had normal or corrected-to-normal visual acuity.

Results

Results are shown in Figure 3. The size of the aftereffect in each condition is quantified as the average of the amplitude of the brightening luminance change (at the center of the test blob) that nulled the dimming aftereffect, and the amplitude of the dimming luminance change that nulled the brightening aftereffect, each of these changes being expressed as a percentage of the background luminance. An ANOVA revealed a significant main effect of adapting sawtooth polarity ($p = 6.5 \times 10^{-15}$), meaning that we have measured significant dimming and brightening aftereffects. The effect size is about 50%. However, there was no significant effect of test-field polarity ($p = 0.20$), and no significant interaction between the polarity of the adapting sawtooth and the polarity of the test field ($p = 0.5$). For adapting waveforms of each polarity, the sizes

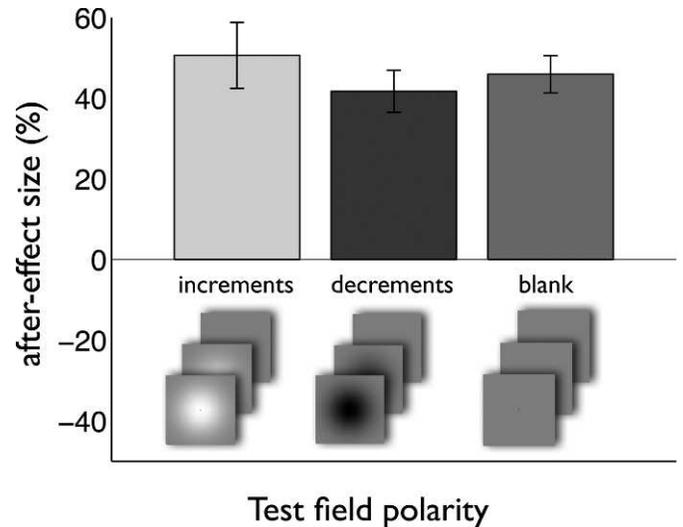


Figure 3. Results of Experiment 1. The size of the aftereffects are indicated by the bars. The error bars subtend twice the *SE* of the mean for the four subjects. The three bars correspond to the three test field conditions: initially bright, or incremental, test fields (left); initially dim, or decremental, test fields (center); and initially blank test fields (right). There are significant aftereffects for all conditions, but there is no significant effect of test field.

of the aftereffects on the blank test field, the incremental test field, and the decremental test field were not significantly different. Our results do not provide any support for the hypothesis that the dimming and brightening aftereffects result from the same polarity-selective changes in contrast sensitivity that Krauskopf and Zaidi (1986) observed for detection of increments and decrements.

Experiment 2

Results of Experiment 1 indicate that the dimming and brightening aftereffects are independent of the polarity-selective changes in contrast sensitivity found by Krauskopf and Zaidi (1986), but might there still be a component of the aftereffects that results from adaptation to modulations in spatial contrast? In Experiment 2 we consider the possibility that the dimming and brightening aftereffects have a contrast component in which progressive changes in contrast generate, as an aftereffect, the impression of an opposite change in perceived contrast. In Experiment 1, each ramp-on adapting sawtooth introduced first an abrupt reduction, and subsequently (after an instant when the field was physically uniform), a progressive increase in spatial contrast, whereas the ramp-off adapting sawtooth presented the same frames in opposite temporal succession. In Experiment 2 we

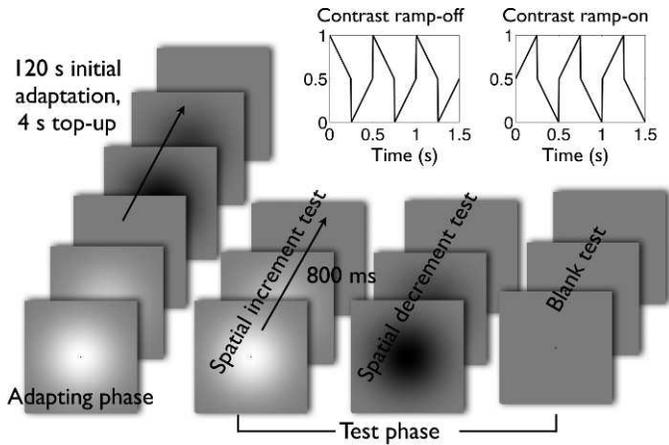


Figure 4. Method for Experiment 2. The procedure and method of measurement was similar to that for Experiment 1 (see Figure 2 legend). The adapting waveform in Experiment 2 was a sawtooth of contrast, rather than of luminance, as in Experiment 1. The adapting waveforms represented in the top center and right of the figure show the moment-by-moment luminance of the adapting stimulus, as a fraction of the maximum luminance ($101.5 \text{ cd}\cdot\text{m}^{-2}$).

investigate whether adaptation to repeated cycles of always declining spatial contrast would produce, as an aftereffect, the impression of a progressive increase in perceived contrast.

We avoided confounding contrast change with luminance change by flipping the spatial contrast of the adapting stimulus halfway through each sawtooth cycle.

Thus for adaptation to progressively increasing contrast, we progressively increase the luminance of a spatially incremental Gaussian blob during the first half of each cycle, and then progressively decrease the luminance of a spatially decremental Gaussian blob during the second half of each cycle. This is the “contrast ramp-on” case shown in Figure 4. For adaptation to progressively decreasing contrast, the succession of contrasts was reversed, yielding the “contrast ramp-off” case shown in Figure 4. If there is a contrast component to the dimming and brightening aftereffects, any effect of contrast adaptation should be revealed as an aftereffect in a direction that depends on the contrast polarity of the test field. For instance, a contrast opponent aftereffect following adaptation to increasing contrast would give rise to perceptual dimming in a test field of incremental spatial contrast, but to perceptual brightening in a test field of decremental spatial contrast, and would have little or no aftereffect for the blank test field.

Methods

The adapting stimulus is represented in Figure 4. For the contrast ramp-on sawtooth (top, right), spatial

contrast increases gradually in both directions from zero and then is reset to zero rapidly, with spatially incremental and spatially decremental contrasts appearing in alternate half-cycles. For the contrast ramp-off sawtooth (top, center), the time course is reversed: The contrast decreases gradually from maximum and is then rapidly reset to maximum. Weber contrast ($\Delta I/I$) was symmetrical about zero, and varied between 0 and +1 for incremental contrast and between 0 and –1 for decremental contrast. The waveforms shown in Figure 4 indicate the moment-by-moment luminance of the stimulus, as a fraction of the maximum $101.5 \text{ cd}\cdot\text{m}^{-2}$; zero contrast is shown as a test intensity of 0.5, which is the background intensity on the normalized scale.

In other respects the method was the same as for Experiment 1. There were 2 min of initial adaptation, and the test interval and interval for top-up adaptation was the same as for Experiment 1. As in Experiment 1, the aftereffect was measured by a nulling gradient where the amplitude of the nulling gradient was controlled by interleaved ZEST staircases, adjusted according to the subject’s responses.

As in Experiment 1 there were six blocks. We tested incremental, decremental, and blank test fields, and contrast ramp-on and contrast ramp-off adapting waveforms were tested in separate blocks. The subjects were the same as for Experiment 1, and again, they completed two sessions separated by at least 2 days.

Results

Results are shown in Figure 5. We have not measured any significant aftereffects in this experiment. An ANOVA showed no significant effect of the polarity of the adapting sawtooth ($p = 0.19$). There was no significant interaction between the contrast polarity of the adapting sawtooth and the polarity of the test field ($p = 0.97$). Compared to the aftereffect size of about 50% seen in Experiment 1 (Figure 3), any possible aftereffect resulting from the adapting waveform used in Experiment 2 must be very small indeed (Figure 5).

Taken together, the results of Experiments 1 and 2 show that the dimming and brightening aftereffects do not result from adapted changes in sensitivity to contrast. Instead, they seem to be entirely aftereffects of luminance.

Experiment 3

One way of narrowing down the range of possibilities for the neural mechanism that underlies the dimming and brightening aftereffects is to investigate

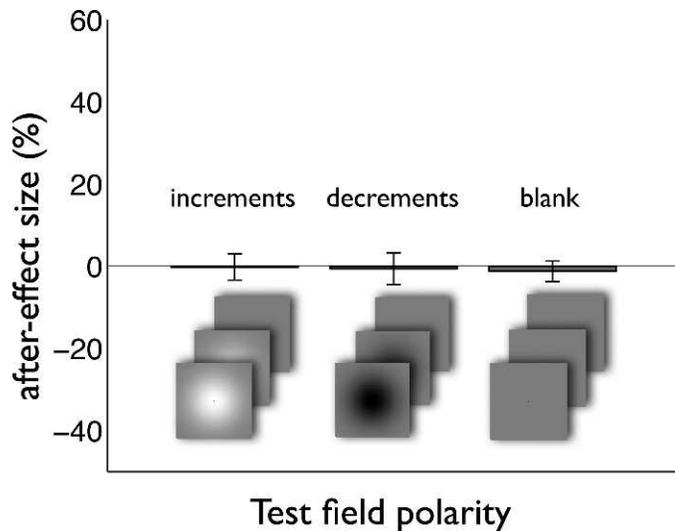


Figure 5. Results of Experiment 2. As in Figure 3, bars show results for initially bright test fields, initially dim test fields, and initially blank test fields. There are no significant aftereffects of increasing or decreasing contrast, no effect of test field polarity, and no significant interaction between the polarity of the adapting sawtooth and the test field polarity.

what cone types contribute to them. Input from the S-cones is segregated into different neural channels from the channels that underlie achromatic acuity and L-M cone chromatic opponency (Dacey, 2004). In Experiment 3 we investigated whether S-cones input to the channels underlying the dimming and brightening aftereffects by attempting to measure aftereffects from adaptation to S-cone isolating stimuli.

Methods

Our methods for Experiment 3 were analogous to those for Experiment 1, with the difference that all the stimuli used were S-cone isolating rather than achromatic. Though we call the aftereffects for S-cones “dimming” and “brightening,” perceptually they are expected to be revealed as changes in color. The “brightening” aftereffect would be a progressive color change from yellow-green to violet (along the vertical axis of the MacLeod-Boynton [1979] chromaticity diagram), and the “dimming” aftereffect would be a color shift in the opposite direction. We have kept the terms “dimming” and “brightening” for clear analogy with Experiments 1 and 2. The terms are more appropriate when considering S-cones in isolation, since they correspond to equivalent changes in S-cone intensity.

A representation of the stimuli used in Experiment 3 is shown in Figure 6. The chromaticity of the background and the time-averaged chromaticity of the adapting stimulus was metameric with equal-energy

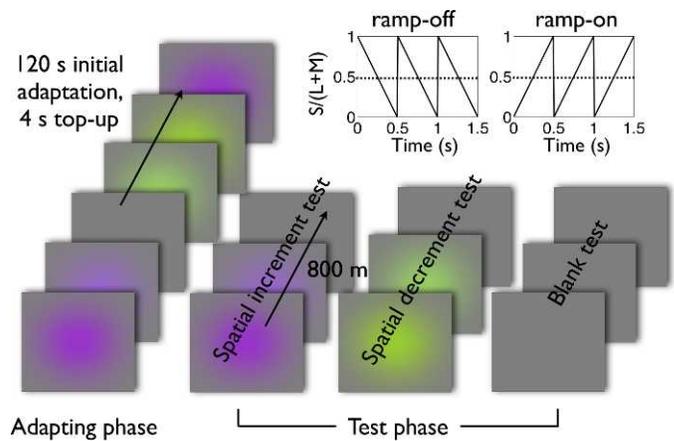


Figure 6. Stimulus and procedure for Experiment 3. The method was equivalent to that of Experiment 1 (see Figure 2), except the stimuli were S-cone isolating. The adapting waveforms shown in the upper center and upper right indicate the moment-by-moment $S/(L + M)$ value as a proportion of the total excursion.

white (MacLeod-Boynton [1979] chromaticity coordinates $S/(L + M) = 0.01606$, $L/(L + M) = 0.6654$). The chromaticity of the adapting sawtooth ranged from $S/(L + M) = 0.00236$ to $S/(L + M) = 0.02976$. In S-cone Weber contrasts, the range was $+0.85$ to -0.85 . All our stimuli were isoluminant for the standard observer, with a luminance of $27 \text{ cd}\cdot\text{m}^{-2}$. In separate blocks, S-cone incremental test fields, S-cone decremental test fields, and blank test fields were used. The incremental and decremental test fields had maximum S-cone Weber contrasts of 0.19.

Similarly to Experiments 1 and 2 there were 2 min of initial adaptation, 4 s of top-up adaptation on each trial, and the test interval was 800 ms. On each trial, the subject’s task was to decide whether he saw a chromatic equivalent of dimming or a chromatic equivalent of brightening with time. This was described to the subject as the test field changing either along a color gradient in the violet direction, or along a color gradient in the yellow direction. A chromatic nulling gradient was used to quantify the aftereffect, and as in Experiments 1 and 2, two interleaved ZEST staircases converged on the subject’s nulling amplitude in each block.

As in Experiments 1 and 2 there were six blocks. S-cone incremental, S-cone decremental, and blank test fields were tested, and the effect of adaptation to opposite-polarity S-cone sawtooth waveforms was measured in separate blocks. The same subjects took part in Experiment 3 as took part in Experiments 1 and 2. All subjects completed two sessions separated by at least 2 days.

The color calibration that allowed us to convert from MacLeod-Boynton (1979) chromaticity space to coordinates in the RGB space of the CRT monitor was

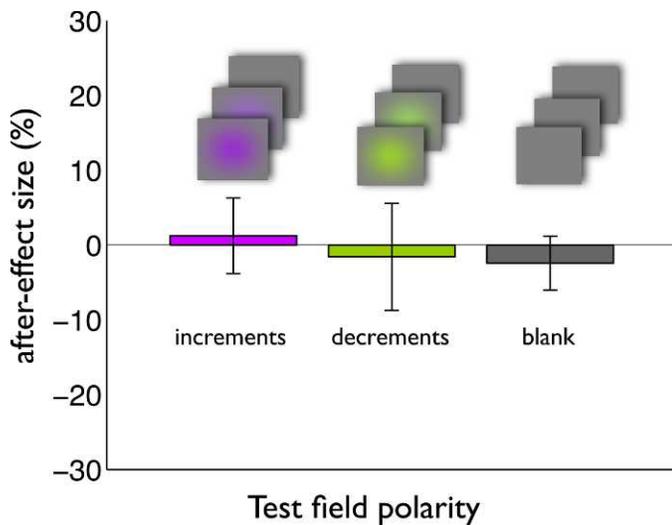


Figure 7. Results of Experiment 3. There is no significant effect of adapting sawtooth polarity; there are no significant dimming or brightening aftereffects for S-cone isolating stimuli.

achieved by measuring the spectra of the three guns using a Spectrascan PR650 spectroradiometer.

Results

Results for Experiment 3 are shown in Figure 7. An ANOVA revealed no significant effect of adapting sawtooth polarity ($p = 0.73$). There was no significant interaction between the polarity of the adapting sawtooth and the polarity of the test stimulus ($p = 0.84$). There are no significant S-cone brightening or dimming aftereffects.

If there were significant dimming and brightening aftereffects we would expect the aftereffect sizes shown in Figure 7 to be positive, as in Figure 3 for the achromatic dimming and brightening aftereffects. The aftereffects for S-cone isolating stimuli are not significantly different from zero, and are not in a consistent direction. There does not seem to be a measurable S-cone input to the channels underlying the dimming and brightening aftereffects.

Experiment 4

The lack of the chromatic equivalent of dimming and brightening aftereffects for S-cone isolating stimuli found in Experiment 3 was curious, because the polarity-selective reduction in sensitivity to increments and decrements (Krauskopf & Zaidi, 1986) also applies to S-cone isolating stimuli (Krauskopf, Williams, & Heeley, 1982; Krauskopf & Zaidi, 1986). The results of Experiment 1 implied that the dimming and brighten-

ing aftereffects are independent of polarity-selective reductions in contrast sensitivity, but since both effects follow adaptation to the same stimulus, it is important to know whether they operate by entirely different mechanisms or share part of the same neural substrate. It is plausible, for example, that dimming and brightening aftereffects concurrently present in the detection interval of Krauskopf and Zaidi's (1986) experiment might cause the polarity-selective changes in ability to detect increments and decrements that they observed. If increment or decrement detection relies on perceived spatial contrast, the presence of a dimming aftereffect while detecting spatial increments might raise thresholds for increments by adding cancelling (dimming) decrements to the test locations. But if dimming or brightening aftereffects are absent for S-cone isolating stimuli (Experiment 3) that still exhibit the polarity selective changes in ability to detect increments and decrements, this implies that the two effects have a different origin. We therefore thought it important to replicate Krauskopf and Zaidi's findings in our subjects.

Methods

The stimuli used for Experiment 4 were similar to those used for Experiments 1, 2, and 3, except this time four parafoveal locations were adapted. There were four Gaussian sawtooth-modulated adapting blobs, distributed around a central fixation cross at an eccentricity of 5.3° . The SD of the Gaussians was 0.8° .

Following 2 min of initial adaptation, a Gaussian test blob was presented at one of the four adapted locations. The test stimulus replaced the adapting one at a phase of the adapting sawtooth that was randomized across blocks. The subject's task was to indicate the location of the test blob on each trial by an appropriate button-press. The duration of the test blob was 750 ms, and following the test presentation there were 4 s of top-up adaptation. For each block, two interleaved ZEST staircases converged on the subject's detection threshold; the staircases were terminated after 70 trials.

There were two versions of Experiment 4. One presented achromatic stimuli that modulated in luminance, and the other presented equivalent stimuli that isolated the S-cones. A representation of the luminance stimuli is shown in Figure 8. Other than the chromatic properties of the stimulus, the method for the S-cone isolating stimuli was the same as that for the luminance stimuli. The two versions of Experiment 4 were conducted in separate sessions, in a random order. Within each session there were four blocks. Thresholds for both incremental and decremental test fields were tested in separate blocks, as were both polarities of

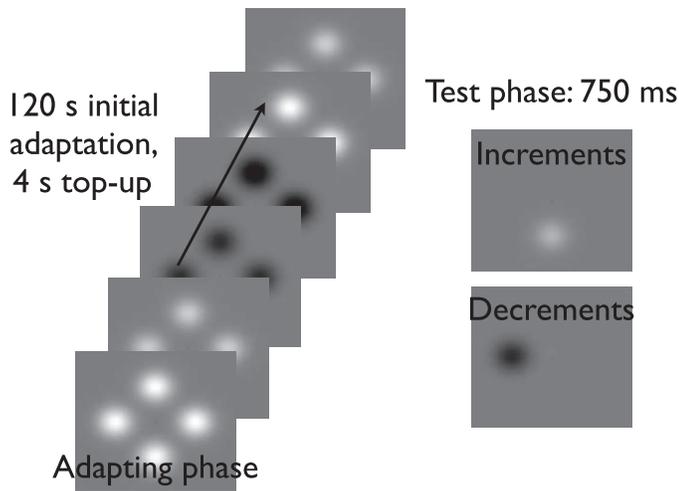


Figure 8. Stimulus and method for Experiment 4. The subject adapted to four Gaussian areas of the adapting sawtooth waveform. Test probes could be either incremental or decremental, depending on the block. In Experiment 4, both luminance stimuli (as shown here) and S-cone isolating stimuli were used.

adapting sawtooth waveforms. Each version (luminance or S-cone isolating) of the experiment was run twice, making a total of four sessions per subject. Each data point for a given subject was therefore based on the mean of four staircases across two sessions.

Results

The results of Experiment 4 are shown in Figure 9. The figure shows the mean thresholds across four subjects. For both achromatic stimuli and for S-cone isolating stimuli, there is a significant interaction between adapting sawtooth polarity and test probe polarity ($p = 1.12 \times 10^{-9}$ for achromatic stimuli; $p = 3.3 \times 10^{-5}$ for S-cone isolating stimuli). If the adapting sawtooth waveform is a ramp-on one, thresholds for an incremental step—the onset of a bright blob—are increased more than for a decremental step. If the adapting sawtooth waveform is a ramp-off one, the opposite happens.

We have thus replicated Krauskopf and Zaidi's (1986) finding that sawtooth adaptation has a sawtooth-polarity specific effect on increment and decrement detection, both for achromatic stimuli and for S-cone isolating stimuli.

Discussion

The results of Experiment 1 show that the magnitude of the dimming and brightening aftereffects does not

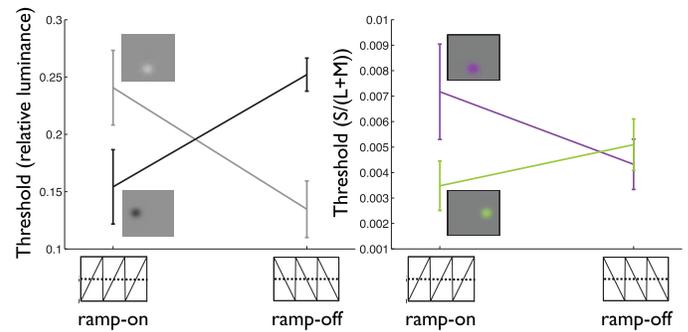


Figure 9. Results of Experiment 4. The x-axis indicates the polarity of the adapting sawtooth. The y-axis indicates test blob detection threshold, as a percentage of maximum luminance for the achromatic stimuli (left), and in MacLeod-Boynton $S/(L+M)$ units for the S-cone isolating stimuli (right). There is a significant interaction between adapting sawtooth polarity and test probe polarity, both for luminance stimuli and for S-cone isolating stimuli. Following adaptation to a ramp-on sawtooth, thresholds for increments are raised more than for decrements. Following adaptation to a ramp-off sawtooth, thresholds for decrements are raised more than for increments.

depend on test field polarity, or on the presence of a test field. The aftereffects are as large for incremental and decremental test fields as they are for blank test fields. These results are against the idea that the aftereffects result from loss of contrast sensitivity during adaptation, which gives rise to the polarity-selective threshold elevations found by Krauskopf and Zaidi (1986).

The results of Experiment 2 show that there are no aftereffects following adaptation to a sawtooth modulation of contrast. There are no “contrast increasing” or “contrast decreasing” aftereffects, i.e., contrast aftereffects analogous to the dimming and brightening aftereffects.

The results of Experiments 1 and 2, taken together, show a lack of involvement of contrast adaptation in the dimming and brightening aftereffects. They seem to be entirely aftereffects of luminance. This is surprising, because most visual neurons in the optic nerve and thereafter encode contrast rather than luminance (e.g., Troy & Enroth-Cugell, 1993).

The results of Experiment 3 show that there are no equivalent brightening or dimming aftereffects for S-cone isolating stimuli. However, in Experiment 4 we found, in agreement with Krauskopf and Zaidi (1986), that following sawtooth adaptation, there are polarity-selective reductions in sensitivity to increments and decrements, both for achromatic stimuli and for S-cone-isolating stimuli. The fact that the sawtooth-polarity selective effect occurs for S-cone-isolating stimuli, in the absence of dimming or brightening aftereffects for S-cone-isolating stimuli shows that these two effects of adaptation to sawtooth modulation have their origin in two different neural mechanisms.

Given the very large receptive fields of the neural mechanism underlying the dimming and brightening aftereffects, and given that they are aftereffects of luminance rather than of contrast, what are the candidate neural mechanisms? The large receptive field size would favor cell populations at high levels of visual processing. However, the lack of interocular transfer of the aftereffects favors monocular cells, and it is unclear how far through visual processing cells receiving purely monocular input persist.

Other possible candidates would be currently undiscovered cell populations in the retina, the LGN, or the monocular layers of the primary visual cortex that have very large receptive fields. Given the large variety of ganglion cells that are now known to exist (Dacey, 2004), we would expect that there are also minority populations of cortical cells with a corresponding variety of properties, yet to be discovered.

One possible candidate, which has already been discovered in the retina, is the melanopsin-containing ganglion cell. Of all the known types of retinal ganglion cell, the melanopsin-containing ganglion cell has the largest receptive field (Dacey, 2004). They are intrinsically light sensitive and have a peak sensitivity in the region of 482 nm (Dacey et al., 2005). However, they also receive a chromatically tuned input from the cones. They receive an S-cone off input and on inputs from the L- and M-cones. This being the case, if the melanopsin-containing ganglion cells are involved in the dimming and brightening aftereffects, we would expect aftereffects for S-cone-isolating stimuli. Our results for Experiment 3 show that there are no dimming or brightening aftereffects for S-cone isolating stimuli, and therefore no measurable S-cone input to the mechanism underlying the dimming and brightening aftereffects. This seems to rule out the melanopsin-containing ganglion cells as candidates for the neural mechanism underlying the dimming and brightening aftereffects.

Sensitivity changes after sawtooth adaptation

Although we found no reason to invoke changes in contrast sensitivity as a basis for the dimming aftereffect, in Experiment 4 adaptation to temporal sawtooth waveforms did cause polarity-specific elevations in threshold for detection of sustained spatial increments and decrements. Moreover, the direction of this effect is somewhat unexpected. Our results, much like those of Krauskopf and Zaidi (1986), show that pre-exposure to an adapting blob of progressively increasing luminance, punctuated by abrupt resets, selectively reduces sensitivity to spatial increments (sustained bright test blobs)—perhaps through a downward regulation in the sensitivity what might be loosely termed ON-channels—while pre-exposure to

progressively decreasing luminance selectively reduces sensitivity to spatial decrements (dim test blobs). But what signal is being used for detection of the sustained test blobs? Detection may be subserved by sustained signals responsive to the spatial increment or decrement defining the test blob, or it may rely on the temporal transient at the onset of the test blob. Thirdly, detection may result from temporal transients associated with small eye movements during the test blob exposure, or may require a combination of these with a sustained signal for spatial contrast.

How plausible are each of these alternatives in the light of our results? Sustained signals in response to spatial increments and decrements do exist in the retina (e.g., Awatramani & Slaughter, 2000; Cleland, Dubin, & Levick, 1971; Cleland, Levick, & Sanderson, 1973; Marocco, 1972; Roska & Werblin, 2001; Troy & Enroth-Cugell, 1993). However, the responsible cells may lack the contrast gain control that would allow them to be effectively adapted by the temporal sawtooth, whereas the large parasol or “magno” ganglion cells of the primate retina are highly responsive to temporal transients of appropriate polarity and do possess a contrast gain control (Benardete, Kaplan, & Knight, 1992).

If we were to suppose that the test blob is detected by magno cells responding to its onset transient, such a gain control is a candidate mechanism for the threshold changes of Krauskopf and Zaidi (1986) and of our Experiment 4 (see Kremers, Lee, Pokorný, & Smith, 1993 for ganglion cell responses to sawtooth modulation). But three considerations make such an account implausible. First, in our experiment, the test blob immediately replaced the adapting blob. Thus there was no temporal transient generated solely by the introduction of the test blob alone. The change in local luminance when the adapting blob was replaced by the test blob would be relatively large and not strongly dependent on test blob contrast. The procedure of Krauskopf et al. (1982) differed slightly from ours: Their test target was introduced after a delay (see their figure 1), thereby reducing or eliminating this masking of the onset transient. But the similarity of our results and theirs makes it plausible that onset transients were not critical for detection in either experiment. Second, in order to explain the results of Experiment 4 on the basis that onset temporal transient signals from magno cells are critical for detection, we must suppose that it is the slow ramp phase of the adapting stimulus cycle, and not the abrupt opposite temporal transient during adaptation, that selectively reduces the sensitivity of ON-magno or OFF-magno cells to the abrupt test stimulus onset. Third, the threshold change occurs not only with achromatic stimuli but also with S-cone stimuli, even though according to the best evidence, S-cone stimuli fail to excite the parasol or magno

ganglion cells that have the temporal modulation gain control (Sun, Smithson, Zaidi, & Lee, 2006). In any case, whether or not a contrast gain control in magno cells is a candidate mechanism for the threshold changes of our Experiment 4, it cannot provide a basis for the dimming aftereffect, as our earlier experiments have shown.

If we provisionally discount the role of the onset transient, it remains possible that detection relies on temporal transients associated with small eye movements, and that the selective threshold changes have their origin in those signals. Although subjects were instructed to maintain steady fixation on a centrally presented fixation cross, there would have been small eye movements which might have elicited temporal transients large enough to allow detection. However, our stimuli were large Gaussian blobs, presented in peripheral vision at an eccentricity of 5.3°. They differed from the stimuli of Krauskopf and Zaidi (1986) who used peripheral discs. The sharp edge in their stimuli means that eye-movement-induced temporal transients would have been stronger in their experiment than in ours. Yet the results of the two investigations are similar. A second difficulty with the idea that temporal transients from eye movements underlie detection is that the temporal transients associated with eye movements are both ON- and OFF-transients. If the stimulus is an increment, there is an ON-temporal transient where the increment moves on to an area of retina, and an OFF-temporal transient where the increment moves off a particular area of the retina. Adaptation to sawtooth modulation would reduce the size of the ON- or the OFF-transients, depending on the polarity of the adapting sawtooth, but the other would remain unadapted. However, are these opposite-polarity temporal transients of equal magnitude? There has been relatively little work on the relationship between ON- and OFF-channels and increment and decrement detection, but one intriguing study by Schiller, Sandell, & Maunsell, (1986) shows that increment detection in free viewing relies almost completely on ON-sensitive cells. They selectively blocked the ON-pathway in rhesus monkeys by applying the glutamate analogue 2-amino-4-phosphonobutyrate (APB). Following blocking, the ability of the monkeys to make correct saccades to peripherally presented incremental discs was severely impaired, even though the stimulus remained available long after its onset. Their ability to make saccades to decremental discs was unaffected. In light of this result, it is possible that the ON- and OFF-temporal transients elicited as a bright field moves over the retina are not equal in magnitude, but the ON-transient is stronger. It may be that OFF-cells do not readily signal a return to background from an increment, because they are outside of their optimal operating range. Since incre-

ments may be signaled primarily by ON-temporal transients from eye movements, a ramp-on adapting sawtooth that reduces the effective amplitude of ON-transients might selectively reduce the detectability of spatial increments. A ramp-off adapting sawtooth would reduce the effective amplitude of OFF-transients caused by eye movements, reducing the detectability of decrements.

Whatever the merits of these speculative explanations for the sensitivity changes following sawtooth adaptation, our experiments provide no support for any account of the dimming aftereffect based on those changes. The dimming and brightening aftereffects remain fundamentally mysterious.

Keywords: dimming aftereffect, brightening aftereffect, adaptation, contrast, S-cones

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