

Gaze direction modulates visual aftereffects in depth and color

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Abstract

Prior physiological studies indicate that gaze direction modulates the gain of neural responses to visual stimuli. Here, we test gaze modulation in the perceptual domain using color and depth aftereffects. After confirming retinotopy of the effects, we employed a balanced alternating adaptation paradigm (adaptation alternates between opponent stimuli) to demonstrate that opposite color and depth aftereffects can co-develop at the same retinal location for different gaze directions. The results provide strong evidence for (a) gaze modulation of aftereffects, (b) generality of gaze modulation across two visual attributes, and (c) perceptual correlates of the modulation of neural activity by gaze direction.

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1. Introduction

Due to frequent spontaneous saccades, the retinal image undergoes repeated and continual relocation. The problem of spatial constancy—how we derive and maintain a highly stable visual world despite this highly dynamic visual stream—has long been one of the central concerns of vision science. As the position and orientation of the retina changes due to movements of the eye within its orbit, the head atop the shoulders, or the body with respect to its surroundings, the spatial mapping necessary to correctly and consistently interpret a visual scene is in constant flux. Information regarding the position of the eye must provide a context for the transformation of retinal coordinates into environmental locations.

Physiological evidence suggests that a critical basis for this computation may be provided by adjusting the gain of visual neurons in a gaze-dependent manner. It

has been shown with monkeys that presenting the same visual stimulus at the same retinal position can give rise to very different neuronal responses depending on an animal's gaze direction (Andersen & Mountcastle, 1983). A given neuron will still respond maximally when the stimulus is presented at its tuned retinal location, but the amplitude of activity at that location and presentations elsewhere in the visual field will systematically vary with gaze. These gaze-modulated receptive fields were first observed in parietal cortex (Andersen, Essick, & Siegel, 1985) and have been shown to be associated with performance on visually guided motor tasks (Andersen & Mountcastle, 1983). “Gain field” neurons, synthesized from these kinds of gaze-modulated receptive fields, could be the basis for a head-centered representation of visual space and may indeed be the neural substrate of such coordinate transformations (Pouget & Sejnowski, 1997; Zipser & Andersen, 1988). These findings have not been limited to visio-motor systems. Recent physiological studies have shown similar neural modulation in areas V1 (Trotter & Celebrini, 1999), V3 (Galletti & Battaglini, 1989) and MST (Shenoy, Bradley, & Andersen, 1999; Squatrito & Maioli, 1997).

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Are these types of gaze-modulated neural responses in perceptual areas reflective of perception, and if so are they psychophysically detectable? To explore this possibility, we utilize visual aftereffects, which have the benefit of being both generally retinotopic, and sensitive to spatial-visual context across gaze shifts. To put this another way, aftereffects are convenient for this study because they tend to be focused at a specific retinal location (the adapted location) and are also somewhat robust to eye movements.

For our studies we used a depth-ordering aftereffect (DOAE) and a color aftereffect (CAE). In the DOAE, adaptation to overlapping regions simultaneously presented at different disparity-cued depth planes causes a neutral test stimulus (both regions presented at equal depth) to appear opposite their adapted orientation. This is a variation of Blakemore and Julesz's original depth aftereffect (Blakemore & Julesz, 1971) in which adaptation to a depth plane nearer than fixation caused a neutral depth plane to appear farther away while adaptation to a depth plane beyond fixation caused a neutral plane to appear closer. Our preliminary observations suggested that our depth-ordering version of stimuli tended to yield clearer percepts, thus providing a more consistent aftereffect. The stimuli used for these experiments were overlapping horizontal and vertical

rectangles composed of random dots whose depths were defined by disparity without monocular cues (Fig. 1).

We also tested the color aftereffect (CAE), in which prolonged adaptation to a patch of one color causes a gray test stimulus to appear in the opponent color (adaptation to green produces a red aftereffect). It is known that the CAE is not subject to interocular transfer (Coltheart, 1973)—adaptation in one eye does not produce an aftereffect for a stimulus viewed only with the other. This suggests that the effect occurs somewhere prior to the integration of binocular information. The DOAE is based upon adaptation to depth planes defined by binocular disparity cues, necessitating information from both eyes. While both effects are likely to occur relatively early in the visual system (V1 or V2) the depth effect involves a greater degree of neural integration and probably occurs later.

Even before the physiological data suggested a mechanism for it, Mayhew reported a compelling example of a gaze-dependent motion aftereffect in humans (Mayhew, 1973). After alternate their gaze between a clockwise rotating disc on the left and a counterclockwise rotating disc on the right while maintaining a fixed head position, observers reported the direction of motion aftereffect (MAE) observed for a static disc presented in each gaze direction. Mayhew found that the direction

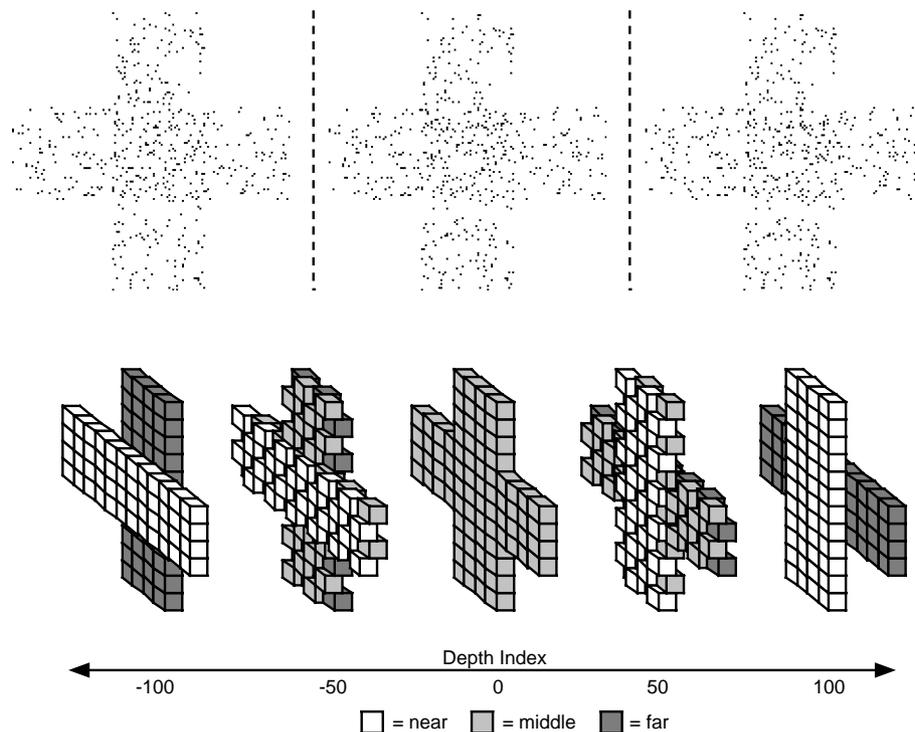


Fig. 1. Stimuli for the depth ordering aftereffect. (Top) Cover the image on the right and fuse the image on the left with image in the center. One of the bars should appear nearer than the other. Now cover the image on the left and fuse the image on the right with the image in the center. The bars should appear to have reversed their depth ordering. This is provided as a demonstration. For the actual experiments, images were presented in red-blue anaglyph. (Bottom) The depth index specifies what percentage of random dots specifies a particular depth orientation. A negative index corresponds to the vertical bar appearing farther, a positive index means the vertical bar is nearer.

of the aftereffect varied with gaze direction, each always opposite to that of its adapting stimulus. Two simultaneous, opposite aftereffects at the same retinal position could not be explained by a purely retinotopic mechanism and the physiology to suggest a mechanism for gaze integration was unknown at the time. A recent study, enlightened by physiological findings, has demonstrated gaze modulation of motion, tilt, size aftereffects, although the size of the modulation was modest (approximately 15%; Nishida, Motoyoshi, Andersen, & Shimojo, 2003). Unlike Mayhew's study, gaze-dependent opposite aftereffects were not demonstrated.

We revisit gaze alternation between opponent adapting stimuli as a means of examining the gaze modulation of aftereffects in depth and color. These effects likely occur in different neural pathways of visual processing (Livingstone & Hubel, 1984) and may reflect on the generality (or specificity) of gaze-modulation in visual processing. While Mayhew's original demonstration provided a compelling example of gaze modulation, the spatial extent and selectivity of the effect were never quantified. Here we reexamine and augment the original paradigm to measure the degree of modulation for each effect. After measuring the spatial tuning of these aftereffects, we conducted experiments in which observers adapted by repeatedly alternating fixation at fixed time intervals between a location in one direction (right), which contained an adaptation stimuli, and a location in the other (left), which contained only a fixation point. Observers were then asked to make a saccade to a neutral location (center) before shifting their gaze to a test pattern presented at one of the two adapted locations, or the neutral location. We found significant gaze-dependent modulation of both color and depth aftereffects.

In other experiments, observers regularly switched their gaze location between opponent stimuli at the two locations (red on the right and green on the left, or horizontal-in-front on the right and vertical-in-front on the left), alternately adapting to opposite stimuli at the same retinal location (in the fovea). Again, after being asked to saccade to a neutral central location, observers were presented with a test stimulus at one of the three locations (Fig. 2). We found evidence of gaze modulation of aftereffects, i.e. opposite directions of aftereffect in two gaze directions, in the case of both color and depth.

2. Experiments

Before directly examining the gaze-modulation of these aftereffects, we first sought to establish a means of measuring the size of each effect under fixed gaze. Methodology for probing of the two aftereffects is discussed in detail below.

2.1. Depth apparatus

All experiments were performed on Macintosh computers running MATLAB (MathWorks Inc., Natick, MA) and the Psychophysics Toolbox extensions (Brainard, 1997). Stimuli were displayed on an LCD screen (60 Hz refresh; 32.3 cm × 21.6 cm) at a viewing distance of 57 cm (1 cm on screen = 1° of visual angle). Observers wore red green stereo-glasses and room lights were turned off. The apparatus was the same in all depth experiments.

2.2. General notes on depth stimuli

The adaptation stimuli consisted of 840 random dots arranged in two $5.0^\circ \times 1.67^\circ$ overlapping bars (one horizontal, one vertical; see the top of Fig. 1 for an example). Each dot was displayed in both red and blue, and the horizontal disparity between each dot's red and blue components was adjusted to convey depth. All dots appeared at one of three depths corresponding to horizontal crossed disparities of 6.6, 10.0, and 13.2 arcmin (far, middle, and near). For the adaptation stimuli the two bars were presented at different depth planes (100% of dots composing the horizontal bar appearing near, 100% of dots composing the vertical bar appearing far, and vice versa). Throughout the experiment, observers fixated a 0.29° circle presented at the far depth plane (6.6 arcmin red-blue horizontal disparity) which was always visible through the adaptation stimuli.

To quantify this effect, we defined a "depth index" for the test stimuli corresponding to the percentage of dots in the stimulus that are not at the middle (10.0 arcmin) disparity. Positive depth index is assigned to stimuli in which the vertical bar appears nearer than the horizontal bar, negative depth index is assigned to those in which the horizontal bar appears nearer than the vertical bar. For example, a stimulus with a depth index of +60 would have 60% of the dots that compose its vertical bar at the near-depth disparity (the other 40% at the middle-depth disparity) and 60% of the dots that compose its horizontal bar at the far-depth disparity (the other 40% at the middle disparity). Conversely, a stimulus with a depth index of -60 would have 60% of the dots that compose its vertical bar at the far-depth disparity, 60% of the dots that compose its horizontal bar at the near-depth disparity, and the other 40% of both bars at the middle disparity. The vertical-near/horizontal-far adaptation stimulus has a depth index of +100 (100% of the vertical-bar-dots near, 100% of the horizontal-bar-dots far) and the horizontal-near/vertical-far adaptation stimulus has a depth index of -100 (100% of the vertical-bar-dots far, 100% of the horizontal-bar-dots near). For a perfectly neutral test stimulus, 100% of the dots representing both the vertical and horizontal bars were presented at the middle disparity. This stimulus receives a depth index of zero (Fig. 1).

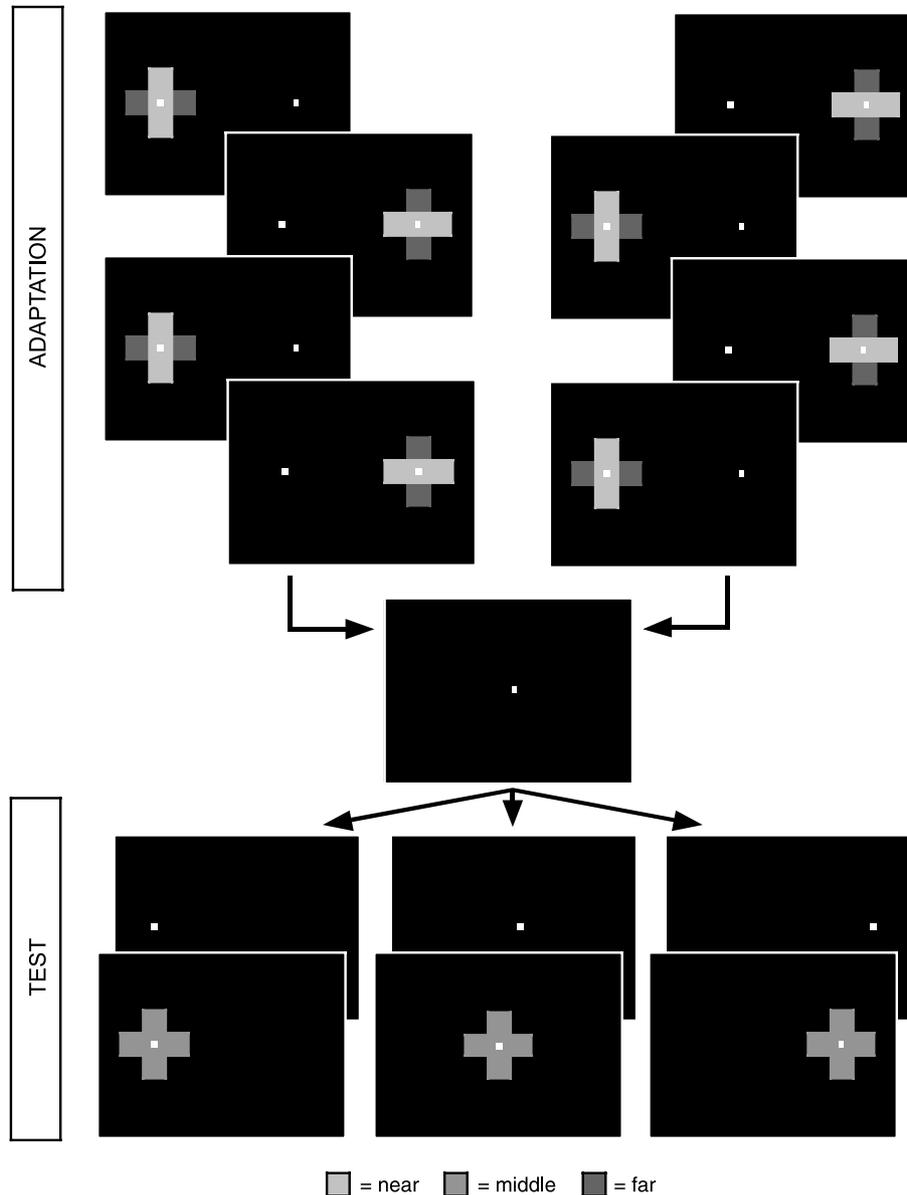


Fig. 2. The experimental paradigm. The stimulus begins on either the right or the left. The subject alternates gaze location, following the stimulus throughout adaptation. Before testing, observers saccade to a neutral location at the center, and are then tested at one of three locations.

2.3. Color apparatus

All experiments were performed on Macintosh computers running MATLAB (MathWorks Inc., Natick, MA) and the Psychophysics Toolbox extensions (Brainard, 1997). Stimuli were displayed on a CRT Monitor (LaCie electron21, 60 Hz refresh; screen dimensions: 38.4 cm \times 29.0 cm) at a viewing distance of 55 cm. The apparatus was the same in all color experiments.

2.4. General notes on color stimuli

The adaptation stimuli consisted of $3.47^\circ \times 3.47^\circ$ squares of red (RGB(255,0,0), CIE xyY(0.6357,0.3411, 11.19)) and blue-green (RGB(0,255,255), CIE

xyY(0.2145,0.3015,37.20)). To avoid issues with edge overlap, test stimuli consisted of smaller $2.08^\circ \times 2.08^\circ$ color squares. Throughout the experiment, observers fixated a $0.28^\circ \times 0.28^\circ$ square of white.

To quantify this effect along a single dimension, we constructed a “color index” for the values used in the test stimuli. The palette of test colors was chosen along the RGB interpolation of the red and blue-green adaptation stimuli. All colors used as test stimuli were then measured by X-Rite Color Monitor Optimizer, plotted in xy-space of the CIE xyY color system, and fitted with a linear regression. Each test color was then orthogonally projected onto the regression line and assigned a color index corresponding to its distance from the scale’s origin, which was set at the orthogonal projection point of

monitor white (RGB(255,255,255)). Positive color indexes signified redder values and negative indexes signified more blue-green values. The red adaptation stimulus corresponded to a color index of +0.3366 while the blue-green adaptation stimulus corresponded to a color index of -0.0805.

2.5. Analysis

All experiments used the interleaved fixed-step-size staircase method. Eye movements were not monitored. Observers responded after each trial by pressing one of two adjacent keys. Each key specified a fixed judgment (horizontal/vertical near or red/blue-green) and the stimulus was then adjusted accordingly to achieve cancellation of the effect in subsequent trials. For each experimental condition observers ran two staircases, one beginning at each adaptation stimulus. Staircases terminated after observers had reversed their responses five times. The point of subjective equality for each condition was determined by the average of six points (the last three reversal points from each staircase). PSEs were compared using two-tailed, non-paired *t* tests. A typical experiment lasted between 15 and 20 min. Reaction times were not measured.

3. Experiment 1

Our first task was to quantify the effects and to demonstrate their spatial tuning on the retina without a gaze-shift. Observers maintained central fixation throughout the experiment as they were presented with an adaptation stimulus in the fovea and test patterns at five retinal locations.

3.1. Participants

Two authors and five naive observers with normal or corrected to normal vision were used in all experiments.

3.2. Depth stimuli

Observers began each experimental session by adapting to the vertical-in-front stimulus at the center of the screen for 20 s. At the beginning of each trial, that stimuli would re-appear for 3 s, then disappear and 0.5 s later, a test stimuli would appear at one of five locations (8.4° left, 4.2° left, 0°, 4.2° right, 8.4° right). The test stimuli would be visible on the screen for 0.7 s.

3.3. Depth task

Observers were asked to judge, in a 2 AFC task, whether the horizontal bar of the test stimulus appeared in-front of or behind the vertical bar. They were

instructed to hold their gaze on the central fixation circle throughout the experiment.

3.4. Depth results

All observers exhibited strong retinal tuning for the depth ordering aftereffect, with tightly peaked tuning curves centered at the fovea (Fig. 3, top). As a rough probe for gaze-modulation, in another experiment we had observers adapt to a stimulus in the fovea, and then saccade to a new location before presentation of the test pattern in one of five locations around the new fixation point. This showed strong retinal tuning as well, and the size of the measured effect at the fovea after refixation was diminished (Fig. 3, top, gray line).

3.5. Color stimuli

Observers began each experimental session by adapting to the red stimulus at the center of the screen for a prolonged 20 s. At the beginning of each trial, that stimuli would re-appear for 5 s, then disappear and 0.5 s later, a test stimuli would appear at one of five locations (6.9° left, 3.5° left, 0°, 3.5° right, 6.9° right). The test stimuli would be visible on the screen for 0.7 s.

3.6. Color task

Observers were asked to judge, in a 2 AFC task, whether the test stimulus appeared reddish or blue-greenish. They were instructed to hold their gaze on the central fixation square throughout the experiment.

3.7. Color results

All observers exhibited strong retinal tuning for the color aftereffect, with tightly peaked tuning curves centered at the fovea (Fig. 3, bottom).

4. Experiment 2

To quantify gaze modulation of the DOAE, observers alternated gaze direction during adaptation between a single stimulus (horizontal field-in-front) at one position (right) and a fixation point at the other (left). The strength of the aftereffect (vertical field-in-front) was then tested at the two familiar locations and a neutral location (center).

4.1. Depth stimuli

Observers began each experimental session with an adaptive period of gaze alternations between the horizontal-in-front stimulus (with fixation circle) 9.7° to the right of center, and the fixation circle alone 9.7° to

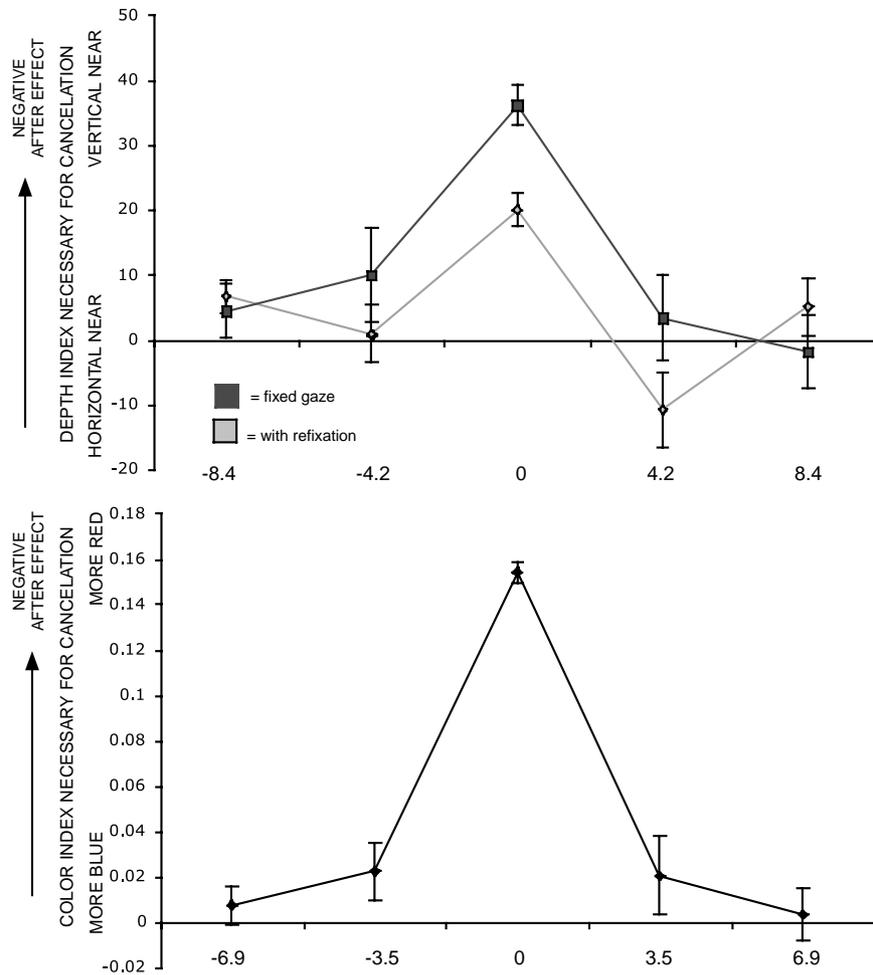


Fig. 3. Retinal tuning of the color and depth ordering aftereffects. (Top) Observers adapted to a horizontal-in-front stimulus in the fovea after which they maintained fixation (black) or shifted to a new fixation point 12.6° to the right or left (gray), and a test stimulus was presented at one of five retinal locations. (Bottom) Observers adapted to a red stimulus in the fovea after which a test stimulus was presented at one of five retinal locations. For both effects, the magnitude was greatest at the adapted retinal location and dropped off quickly to the left and right. Error bars represent standard error of the mean for the six reversal points used in determining the point of subjective equality.

the left of center (3 s right, 3 s left, 10 alternations). Only one stimulus (horizontal-in-front with fixation circle, or fixation circle alone) was visible at a time. At the beginning of each trial, observers underwent a shorter period of gaze alternating adaptation (1.5 s right, 1.5 s left, 6 alternations), after which the fixation circle appeared at the center of the screen for 0.5 s (prompting a saccade). The fixation circle then moved to one of three locations (9.7° right, 0° , 9.7° left) for 0.5 s before the test stimulus appeared at that location. The test stimulus was visible on the screen for 1 s.

4.2. Depth task

Observers were asked to judge, in a 2 AFC task, whether the horizontal bar of the test stimulus appeared in-front of or behind the vertical bar. They were instructed to follow the fixation circle and keep it fixated throughout the experiment.

4.3. Depth results

All observers showed significant attenuation of the effect at the non-adapted location (on the left; the average effect at this location was only 45% as large as in the adapted gaze direction; $p < 0.05$). The attenuation of the effect at the neutral location (in the center; nearer to the adapted location) was less than in the non-adapted direction, but still significant relative to the effect at the adapted location (the average effect at this location was 53% as large as in the adapted direction; $p < 0.001$), and not significantly different from the aftereffect at the non-adapted gaze location (Fig. 4, top).

4.4. Color stimuli

Observers began each experimental session with an adaptive period of gaze alternations between the red stimulus (with fixation square) 13.8° to the right of center, and

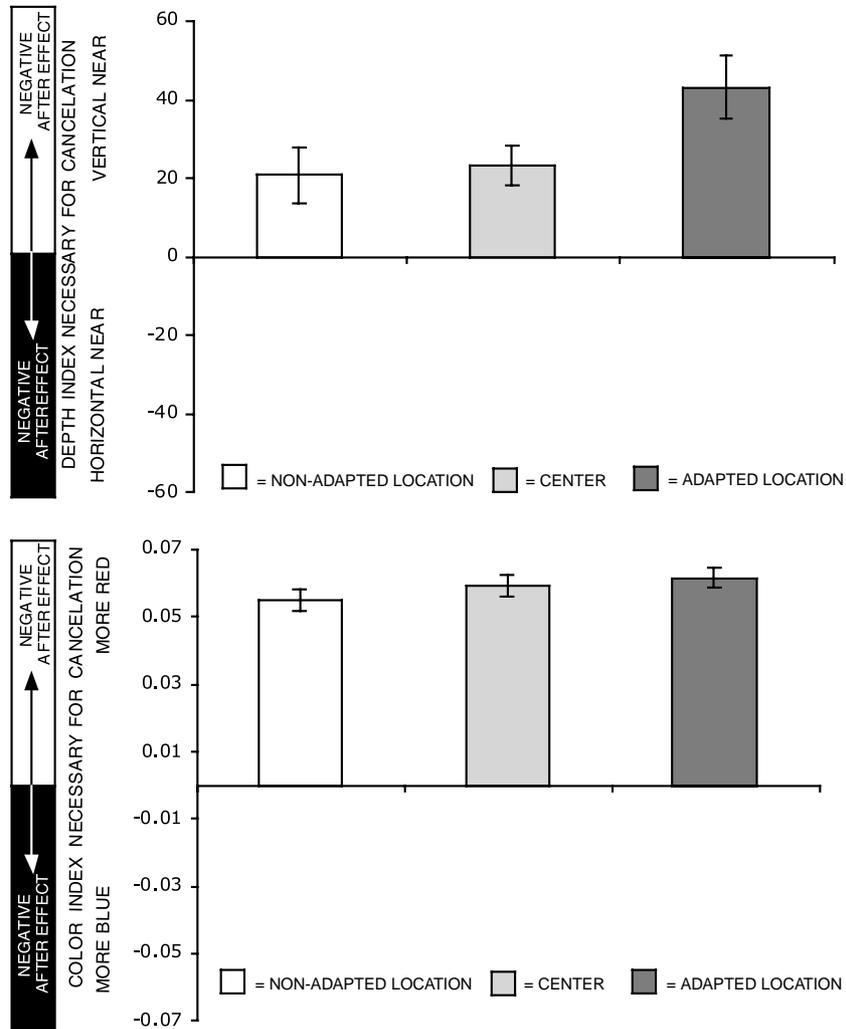


Fig. 4. Gaze modulation of aftereffects. (Top) Observers adapted to a vertical-in-front stimulus in the fovea on the right side of the screen. (Bottom) Observers adapted to a red adaptation stimulus in the fovea on the right side of the screen. In both experiments, after shifting gaze to the center of the screen, and then to one of three testing locations (left, right, center) observers were presented with a test stimulus. With both effects, observers showed the strongest aftereffect at the adapted gaze location and diminished effects at other gaze-locations. Error bars represent standard error of the mean for the six reversal points used in determining the point of subjective equality.

the fixation square alone 13.8° to the left of center (4 s right, 4 s left, 15 alternations). Only one stimulus (red adaptation stimulus with fixation square, or fixation square alone) was visible at a time. At the beginning of each trial, observers underwent a shorter period of gaze alternations (2 s right, 2 s left, 5 alternations), after which the fixation square appeared at the center of the screen for 0.5 s (prompting a saccade). The fixation square then moved to one of three locations (13.8° right, 0° , 13.8° left) for 0.5 s before the test stimulus appeared at that location. The test stimulus was visible on the screen for 1 s.

4.5. Color task

Observers were asked to judge, in a 2 AFC task, whether the test stimulus appeared reddish or blue-greenish. They were instructed to follow the fixation circle and keep it fixated throughout the experiment.

4.6. Color results

As with the DOAE, observers showed a significant, but in this case much smaller, degree of attenuation of the effect at the non-adapted location (on the left; average effect was 90% as large as in the adapted gaze direction; $p < 0.05$). This degree of gaze modulation is not unlike that observed for other simple visual aftereffects previously (Nishida et al., 2003). The neutral location showed less attenuation, and the measured effect there was not significantly different from either adapted location (Fig. 4, bottom).

5. Experiment 3

Is gaze modulation strong enough to induce opposite aftereffects in different gaze directions? A positive result

would be the strongest conceivable evidence for gaze-dependent modulation. In our third experiment, observers alternated gaze between two locations with opponent adapting stimuli (horizontal field-in-front on the right, vertical field-in-front on the left) before responding to a test stimulus at one of three locations (left, right or center).

5.1. Depth stimuli

Stimuli were the same as in Experiment 2, except that during the adaptive periods of gaze alternation, the vertical-in-front stimulus (with fixation circle) appeared on the left instead of the fixation circle alone. Thus observers alternated their gaze between the horizontal-in-front stimulus (with fixation circle) 9.7° to the right of center, and the vertical-in-front stimulus (with fixation circle) 9.7° to the left of center (3 s left, 3 s right, 10 alterna-

tions). At the beginning of each trial, observers underwent a shorter period of gaze alternations as in Experiment 2 (shown schematically in Fig. 2).

5.2. Depth task

As before, observers were asked to judge, in a 2 AFC task, whether the horizontal bar of the test stimulus appeared in-front of or behind the vertical bar. They were instructed to follow the fixation circle and keep it fixated throughout the experiment.

5.3. Depth results

On average, observers showed opposite and significantly different DOAE at the two adapted locations (+22.7 ± 8.8% (V-in-front) on the right vs. -22.3 ± 9.22% (H-in-front) on the left; $p < 0.001$; Fig. 5, top).

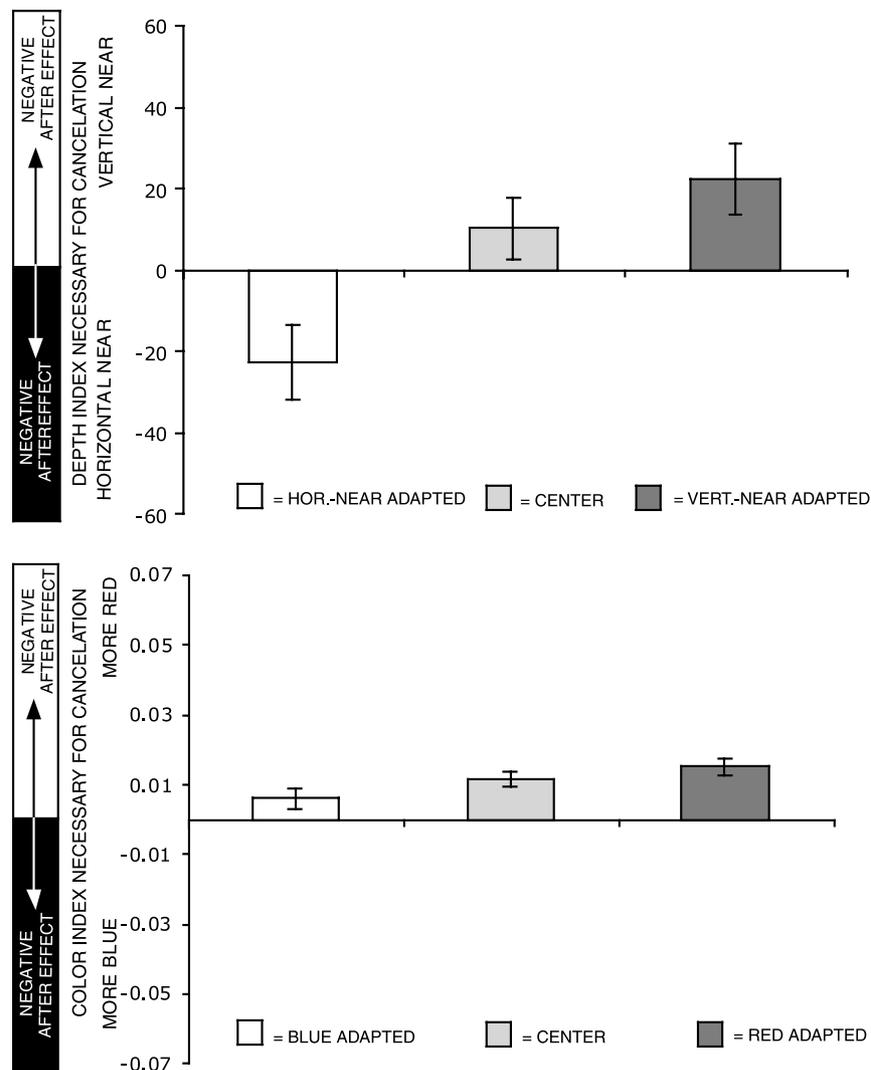


Fig. 5. Gaze dependent aftereffects. (Top) Observers alternated adaptation between a vertical-in-front stimulus on the right and a horizontal-in-front stimulus on the left. (Bottom) Observers alternated adaptation between a red stimulus on the right and a blue stimulus on the left. In both experiments, subsequent to adaptation, gaze was shifted to the center of the screen and then to one of three testing locations (left, right, center) and a test stimulus appeared. Error bars represent standard error of the mean for the six reversal points used in determining the point of subjective equality.

Thus adaptation to opponent stimuli at the same retinal position but in different gaze directions produced simultaneous, opposing aftereffects in the same retinal location.

5.4. Color stimuli

Stimuli were the same as in Experiment 2, except that during the adaptive periods of gaze alternation, the blue-green adaptation stimulus (with fixation square) appeared on the left instead of the fixation square alone. Thus observers alternated their gaze between the red stimulus (with fixation square) 13.8° to the right of center, and the blue-green stimulus (with fixation square) 13.8° to the left of center (4 s left, 4 s right, 15 alternations). At the beginning of each trial, observers underwent a shorter period of gaze alternations as in Experiment 2.

5.5. Color task

As before, observers were asked to judge, in a 2 AFC task, whether the test stimulus appeared reddish or blue-greenish. They were instructed to follow the fixation circle and keep it fixated throughout the experiment.

5.6. Color results

After alternating adaptation between opponent color stimuli, observers showed considerably less overall color adaptation (0.011 vs. 0.058) with greater gaze-specific effects (average difference between the magnitude of effect at the two locations: 0.0093 vs. 0.0068) than in the single stimulus case as predicted. Observers again showed significantly different effects at the two adapted locations ($p < 0.0001$), though physically opposite aftereffects were not observed (Fig. 5, bottom). This may be due to net color adaptation in the fovea. If the level of gaze-modulation for CAE is only moderate (as observed in Experiment 2), a mismatch in the subjective intensity of the red vs. blue green adaptation stimuli may have resulted in the stronger red adaptation on the right overwhelming the blue-green adaptation on the left, and producing net red adaptation in both locations. Nonetheless, the relative aftereffects at the three measured locations clearly demonstrate gaze-modulation.

6. Discussion

Gaze alternation between opponent adaptation stimuli marks a significant departure from traditional aftereffect experimental paradigms, and may provide decisive evidence for gaze-modulation as well as a more sensitive measure of spatial tuning. By adapting the same retinotopic location alternately to opposite stimuli, strictly retinotopic adaptation should average out, leaving pri-

marily adaptation to effects that exist in non-retinal coordinate systems (such as head-centered or environmental systems). While it is impossible to insure that the competition between opposite stimuli indeed results in complete cancellation, at the simplest levels of visual processing the net adaptation should be very small, and even with net retinal adaptation, observing simultaneous opposite aftereffects would be impossible without gaze-modulation. Rather than measuring the combination of retinotopic and gaze-dependent adaptation under conditions of varied gaze, this paradigm seeks to measure the gaze-dependent component directly.

In all of these experiments, the strength of the aftereffect was measured to be greatest at the adapted gaze location and diminished at other gaze locations. In the single sided alternation paradigm, it is unlikely that retinal mismatch of adaptation and test stimuli induced by gaze shift could have accounted for any of the modulation observed, since all trials involved multiple saccades prior to testing and should have been equally susceptible to mismatch effects. By alternating gaze directions (but only one stimulus) throughout adaptation, observers in our experiments adapted to both gaze locations prior to each test. Since stimuli were always presented at the same retinal location, it would be difficult to attribute these findings to anything other than gaze modulation. It seems likely that humans share the gaze modulation observed in V1, V4, and MST of monkeys, and that perception reflects this neural modulation.

In the past, aftereffects have been shown to be contingent on a variety of visual attributes—orientation contingent on color (McCullough, 1965), motion on color (Favreau, Emerson, & Corballis, 1972), motion on depth (Nawrot & Blake, 1989), depth on motion (Anstis & Harris, 1974; Regan & Beverley, 1972). All of this suggests that the presence of these aftereffects depends on more than simply the retinal location of visual stimuli and exists within some more complicated framework. While we can postulate on how the contingent relationships between various features tie into issues of feature binding, gaze-dependence serves a more obvious purpose. It may provide a critical basis for the transformation from retinal to body-centered, and eventually environment, coordinates.

Physiological studies have demonstrated the existence of visually responsive neurons that adjust their gain in a gaze-dependent manner. Neurons of this type could provide a mechanism for the gaze modulation of visual aftereffects. Consider a population of color-tuned neurons (some responding to red, some responding to green) with receptive fields centered in the fovea and gain fields (the locations at which the gain of its tuning curve is the greatest) centered at the left adaptation location. The balance of output from this population of cells will represent color balance on the red-green axis. A red adapting stimulus presented at the left location will

cause a large increase in firing of red-tuned cells, whereas a green stimuli presented at the right adaptation location will evoke only a small increase in firing rate in the green-tuned cells (lower gain). The red-tuned cells will adapt-out their responses to a greater degree than the green tuned cells and, after adaptation, a neutral stimuli (equal parts red and green) presented at the left adaptation location will evoke a lesser response from the adapted red cells than the less adapted green cells. The neutral stimulus will appear green. Conversely, a similar population of cells with their gain fields centered at the right adaptation location, presented with the same adaptation stimuli (red-left, green-right), will represent a neutral stimulus on the right as being more red.

If we presume that perception is indeed reflective of underlying neural modulation such as that found in physiological studies, what does this imply about gaze modulation and possibly coordinate representation in the visual system? As mentioned above, the CAE is not subject to interocular transfer, localizing it very early in the visual pathways. It seems likely that the CAE is due to a reduction in the response of color selective neurons of V1 (or earlier) following adaptation. The results of these experiments would then suggest that very early on there occurs some integration of gaze information which modulates, albeit modestly, the response properties of color selective neurons. This is in line with recent findings of modest gaze modulation ($\approx 15\%$) of a variety of aftereffect (motion, tilt, size) that also likely occur as early as V1 or V2 (Nishida et al., 2003).

The depth ordering aftereffect probably involves a higher degree of visual processing, but could also occur as early as V1. In physiological studies in monkeys, stereoptic, depth-tuned neurons were found in V1, V2, V3, MT and MST (Poggio, 1994). The much greater degree of gaze-dependent modulation seen here with depth is not entirely surprising considering the degree of correlation and integration of position information at higher cortical levels that is involved in stereopsis.

The evidence here indicated that gaze direction modulates perception of aftereffects in both color and depth. These effects likely occur early in human visual processing and may be the perceptual correlates of the modulation of neuronal response in human visual cortex.

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