

Adapting to an aftereffect

Bhavin R. Sheth

Department of Electrical and Computer Engineering,
University of Houston, Houston, TX, USA, &
Center for NeuroEngineering and Cognitive Science,
University of Houston, Houston, TX, USA



Shinsuke Shimojo

Computation and Neural Systems/Division of Biology,
California Institute of Technology, Pasadena, CA, USA, &
JST.ERATO Shimojo Implicit Brain Function Project, Japan



We report a new type of orientation-contingent color aftereffect in which the color aftereffect is opposite to the classical McCollough effect, i.e., the perceived color of the aftereffect is the same as the inducer's color. Interleaved exposure to red, horizontal and achromatic (gray), horizontal gratings led to a long-lasting aftereffect in which achromatic horizontal gratings appeared reddish. The effect, termed the anti-McCollough effect, although weaker than the classical aftereffect, remained stable for a moderate duration of time (24 hours). Unlike the classical aftereffect, which is known to not transfer interocularly, the new after-aftereffect transferred 100%, suggesting that its locus in the brain was downstream of the classical effect. It is likely that neurons in a higher-order area adapted to the classical color aftereffect that was represented in a lower-order area, thus forming an aftereffect of an aftereffect, i.e., an after-aftereffect. Our finding has implications as to how neural activity in lower- and higher-level areas in the brain interacts to yield conscious visual experience.

Keywords: neural adaptation, visual hierarchy, consciousness, visual awareness, conditioning

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Introduction

Adaptation results from sustained exposure to a stimulus, thereby leading to an aftereffect. Sustained association of two independent sensory features leads to a negative aftereffect that is contingent upon the presented pair of features. For instance, a few minutes of inspection of a red, horizontal grating typically causes a post-inspection, achromatic, horizontal grating to appear greener than its orthogonal (vertical) achromatic counterpart—this aftereffect is widely known as the McCollough effect (McCollough, 1965; Stromeyer, 1969). Following induction, exposure to an achromatic grating of the same spatial composition (i.e., orientation, spatial frequency) as the adapter (inducer) causes a rapid washout or extinction of this effect (Skowbo, Gentry, Timney, & Morant, 1974), namely, the washout brings back the perception of an achromatic horizontal grating to veridical.

Rather than exposure to the extinction stimulus after the induction is complete, what if observers are periodically exposed to achromatic gratings during their induction to chromatic gratings itself? Error correction accounts of adaptation generally state that aftereffects are the brain's corrective response to recent perceptual contingency; in the case of the McCollough effect (Dodwell & Humphrey, 1990), they predict that because a specific color and a

specific orientation remain associated even in this new induction paradigm, the system still generates an error and a McCollough effect, perhaps weaker, will still result. On the other hand, associative sensory–sensory conditioning theories (Allan & Siegel, 1993; Murch, 1976) would base the kind and the magnitude of aftereffect on the precise values of the paired features in a classical conditioning type paradigm. They would predict that presentation of the extinction stimulus (the achromatic gratings in the present case) during the conditioning (or induction) will preclude any change from occurring in the system; therefore, there will not be any aftereffect following the adaptation. Of importance, neither of these theories predicts an aftereffect in the opposite direction from the classical McCollough effect.

Experiment 1: The anti-McCollough effect

We exposed observers to the extinction stimulus, namely, achromatic inducers, in alternation with the classical adapter, i.e., red, horizontal (or vertical) gratings, during the adaptation procedure, and observed the effect this manipulation had on the resulting aftereffect.

Methods

Participants

Six observers with normal or corrected-to-normal vision participated in the horizontal inducer experiment; all were naive to the purpose of the experiment. Three new observers (one author, remaining were naive) participated in the vertical inducer experiment.

Stimuli

All experiments were performed on a MAC G4 computer connected to a 21-in. LaCie monitor with a refresh rate of 75 Hz and a resolution of 1280 × 1024 pixels. Viewing distance was 57 cm, such that 34 pixels subtended 1 degree of visual angle. Observers sat comfortably in a chair in front of the screen in a dark room (<0.01 cd/m²) and were required to maintain gaze on the screen although not to any specific point on it. Software was scripted in MATLAB (Mathworks, Inc.) utilizing the psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Procedure

The experimental procedure consisted of three components in the following chronological order: a pre-induction test, induction, and a post-induction test 10–30 min following the end of induction; they are described below.

Induction

The stimulus during the induction phase of the horizontal inducer experiment consisted of the presentation of a horizontal grating, consisting of red (CIE coordinates, $x = 0.602$, $y = 0.344$) and black stripes (3.4 cycles/deg) alternating with an achromatic horizontal grating (gray and black stripes) of the same luminance (12.7 cd/ m²) every 10 s for a total adaptation duration of 20 min. On the vertical inducer experiment, red vertical gratings were alternated with achromatic vertical gratings, with stimulus and timing parameters the same as on the horizontal inducer experiment. The chromatic and achromatic patterns were on for the same amount of time.

Pre- and post-induction tests

Pre- and post-induction tests were identical in all respects and utilized the method of constant stimuli. On each trial, one vertical and one horizontal grating (3.4 cycles/deg) appeared side by side, each randomly occupying either the left or the right half of the screen. The observer had to judge in a binary choice task which of the two gratings (left/right) was greener and respond accordingly by pressing one of two adjacent keys on a

computer keyboard. The keypress ended the trial. No feedback was provided.

The levels of red and green hues in the two gratings were independently varied from trial to trial, so that the hue of each grating varied from slightly green or greenish to slightly red or reddish across the trials, while maintaining the level of luminance. There were 5 hue levels (reddish → greenish) for each grating (2) and 30 trials for each condition, giving a total of 300 (= 5 × 2 × 30) trials each on the pre- and post-induction tests. Trials were presented in random order. For a given observer, hue levels were identical on the pre- and post-induction tests.

Analysis

The raw data obtained were averaged, fitted with a psychometric function and analyzed statistically for significance. Details are given below.

Psychometric functions

Responses were fitted with a psychometric curve,

$$F(x) = 0.5 + \frac{(a + bx)}{2\sqrt{1 + (a + bx)^2}}, \quad (1)$$

by minimizing the square error. Free parameters a and b were estimated by a least-squares criterion and the point of subjective equality (PSE) or threshold estimate was obtained as $(-a/b)$. Thus, each threshold estimate represented the physical hue at which the horizontal test grating was perceived to be of the same greenness as the vertical one.

Statistical analysis

Computer simulations using the bootstrap method to test the significance of the difference in the pre- and post-induction thresholds enumerated all possible pairs of psychometric functions from the pooled distribution and weighted them by their binomial probability. Each of the possible pairs of psychometric functions yielded a pair of threshold estimates. The difference in threshold between the two psychometric functions (PSE_{pre} 50–PSE_{post} 50) was compared with the distribution of the threshold differences between the pairs of psychometric functions generated using the bootstrapping method (Foster & Bischof, 1991). The upper and lower threshold-difference values of the distribution that would exclude the upper and lower 2.5% of the bootstrapped population, respectively, were taken as the confidence limits.

Results

Observers binocularly inspected a horizontal grating for 20 min while it alternated between chromatic (red and

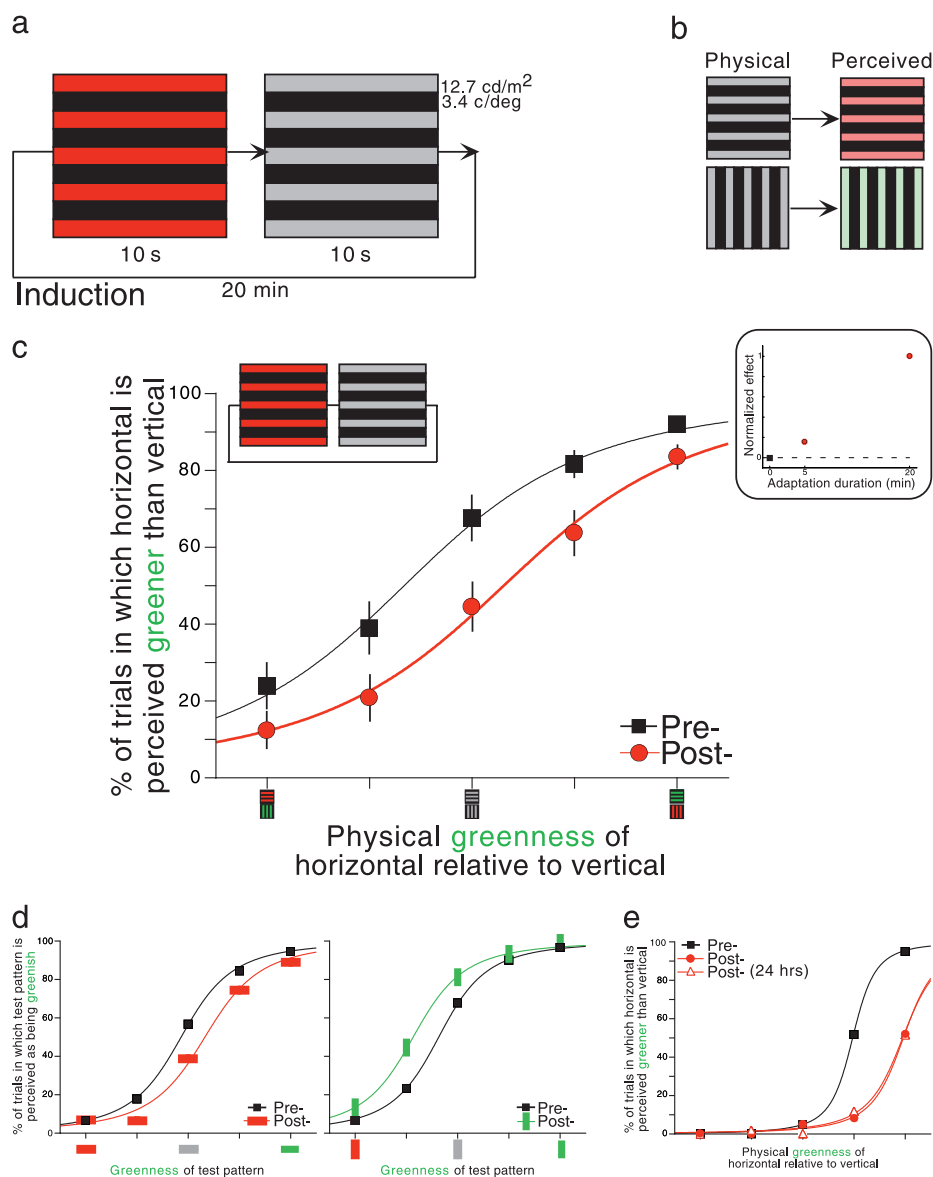


Figure 1. The anti-McCollough effect. (a) The sequence of induction stimuli is shown. A red and black horizontal grating and an equiluminant achromatic horizontal grating were alternated every 10 s for a total of 20 min (60 alternations total). (b) Observers' typical percept following the induction is sketched here: Achromatic horizontal stripes appear reddish, achromatic vertical stripes appear greenish in comparison. (c) Group ($n = 6$) pre- and post-induction responses and fitted psychometric functions on the dual grating test (see text). Increasing values along the abscissa represent increase in the amount of green in the horizontal stripes or a decrease in the amount of green in the vertical stripes, by 0.14 cd/m^2 increments. Each data point is the mean of 360 trials. After induction on the sequence in panel a, horizontal stripes appeared redder than vertical stripes of identical chromaticity or CIE value (red circles). Probit analysis and computer simulations using the bootstrap method (Foster & Bischof, 1991) confirmed the difference between the pre-induction and post-induction pooled group data was significant ($p < 0.02$). Inset shows the strength of the effect as a function of induction period duration (0, 5, and 20 min) (d) Group ($n = 3$, 180 trials total/data point) pre- and post-induction responses and fitted psychometric functions on single orientation tests. On a given trial of the test, a single oriented (horizontal/vertical) grating of varying hue was presented, and the observer judged in a binary choice task if the grating appeared reddish or greenish. The tests used the method of constant stimuli. Following induction, achromatic horizontal stripes appeared redder and achromatic vertical stripes greener than before induction. (e) The effect was long-lasting and stable. The post-induction data and psychometric function fit for a naive observer immediately (10 min; filled red circles) and 24 hours (open red triangles) after induction were almost identical.

black) and achromatic (black and white, or BW) states every 10 s (Figure 1a). We measured the impact of this sustained induction on perception (see Methods). Contrary to the theories mentioned above (Allan & Siegel, 1993; Dodwell & Humphrey, 1990; Murch, 1976), the induced horizontal orientation appeared significantly less green (thus interpreted as more red) in comparison with its non-induced, orthogonal (vertical) counterpart ($p < 0.02$; for details of statistical procedure, see Statistical analysis section; Foster and Bischof, 1991; Figures 1b and 1c) for each of the six observers. The effect barely diminished 24 hours after induction (Figure 1e). Tests using single gratings showed that the change in percept illustrated in Figure 1c resulted from a change in the perceived color of the induced as well as the non-induced (orthogonal) orientations in the test. The horizontal grating appeared redder and the vertical grating appeared greener after induction than before (Figure 1d). We term the resulting aftereffect the *anti-McCollough* effect, as it is in the direction opposite the McCollough effect. In essence, the anti-McCollough effect that resulted from adaptation to a red and achromatic horizontal grating sequence simulated a regular McCollough effect that results from adaptation to a red vertical grating.

The results of an analogous experiment using vertical inducers ($n = 3$) in place of horizontal were similar. There was a significant ($p < 0.05$) anti-McCollough effect (i.e., induced vertical appeared less green than non-induced horizontal).

Discussion

Interleaving achromatic and chromatic oriented inducers gave rise to an aftereffect that was opposite to that observed earlier with chromatic inducers alone. In order to inquire about the mechanism underlying this new effect, we first examined what factors in the inducer stimulus sequence were critical to obtain the aftereffect in the opposite direction. The key difference between the classical induction sequence and ours is the presence of the achromatic inducer. Therefore, one would posit that the achromatic inducer is important to the anti-McCollough effect. We verified this postulate in Experiment 2.

Experiment 2: The role of chromatic and achromatic inducers

In a series of related experiments, we investigated the importance of the oriented achromatic inducer to the generation of the anti-McCollough effect.

Methods

Participants

All observers had normal or corrected to normal vision.
 Experiment 2a—Three observers participated.
 Experiment 2b—Five observers participated.
 Experiment 2c—Seven observers participated.
 Experiment 2d—Five observers participated.

Stimuli and procedure

Induction (20-min duration; 10-s alternation) differed from that of Experiment 1 as follows.

Experiment 2a

The alternating inducers were red and gray homogeneous full-field, unoriented stimuli. Pre- and post-induction tests utilized the method of constant stimuli. On a given test trial, a single, homogenous, full-field stimulus of mildly saturated (greenish/reddish) hue was displayed. In a binary choice task, the observer had to judge if the stimulus appeared greenish or reddish and respond accordingly.

Experiment 2b

The alternating inducers were a saturated red homogeneous full-field stimulus and an achromatic (BW) horizontal grating. Stimuli and procedure on the pre- and post-induction tests were identical to those in Experiment 1.

Experiment 2c

The alternating inducers were a saturated red and black horizontal grating and a gray homogeneous full-field stimulus. Stimuli and procedure on the pre- and post-induction tests were identical to those in Experiment 1.

Experiment 2d

The alternating inducers were highly saturated and desaturated red horizontal gratings. Stimuli and procedure on the pre- and post-induction tests were identical to those in Experiment 1.

Analysis

Analysis was the same as in Experiment 1.

Results

On a 20-min-long induction sequence consisting of alternating chromatic (red) and achromatic (BW), homogeneous full-field, unoriented inducers (Experiment 2a), there was no color afterimage observed on a post-induction test 10 min later (Figure 2a; $p > 0.8$). These findings replicate earlier studies (Day & Webster, 1989).

Induction on the same homogeneous full-field, red inducer as in Experiment 2a and an achromatic (BW)

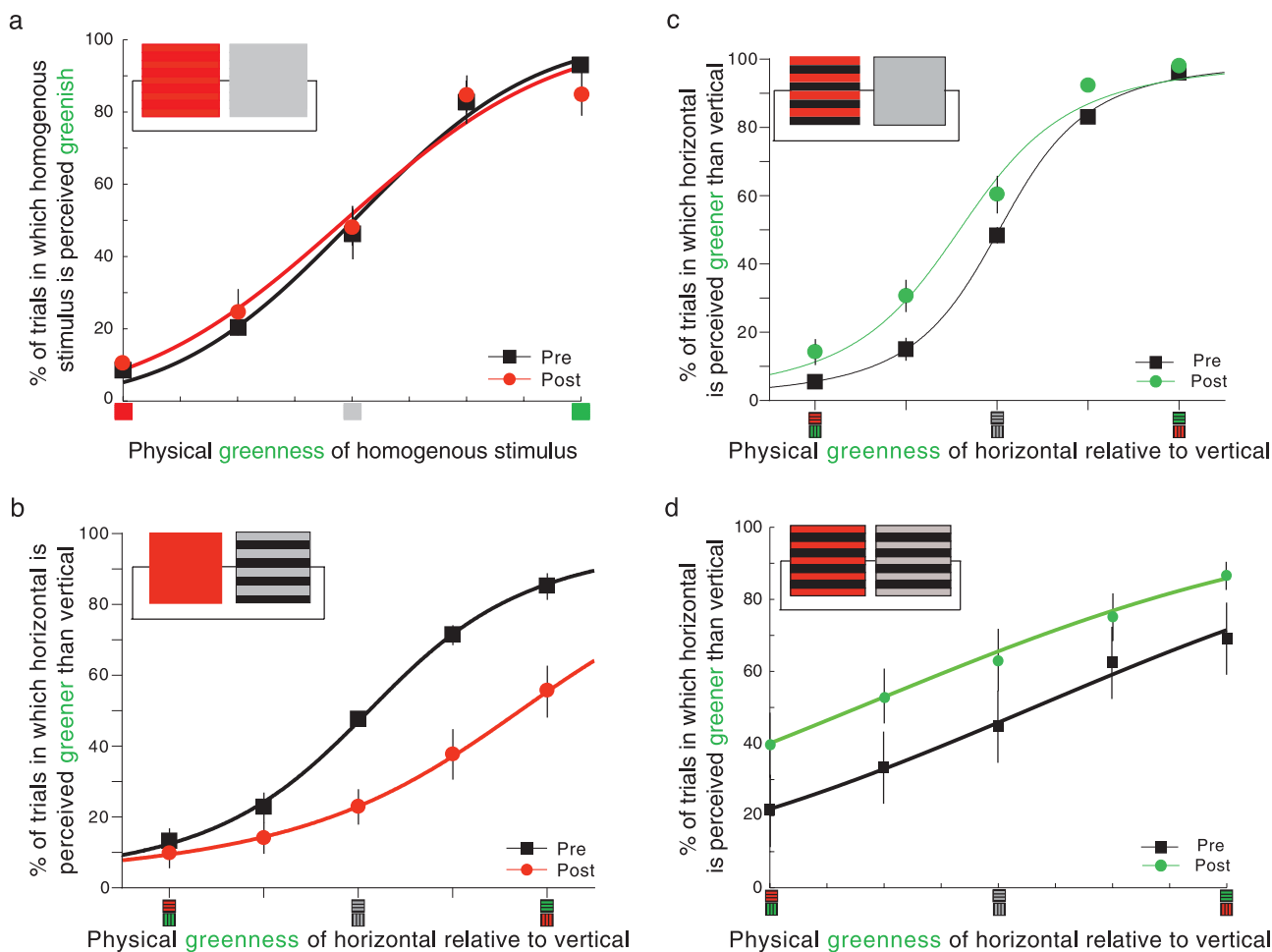


Figure 2. The critical role of the achromatic inducer in the anti-McCollough effect. (a) Induction on alternating homogeneous full-field red and gray stimuli (10 s each; 20 min total) did not yield a significant aftereffect ($p > 0.8$), as illustrated by the closeness of the psychometric function fits of post-induction (red) and pre-induction (black) sets of data. (b) Induction on a homogeneous full-field, red stimulus interleaved with an achromatic horizontal grating (10 s each; 20 min total) yielded an anti-McCollough effect as illustrated by the rightward shift ($p < 0.01$) of the post-induction (red) group ($n = 5$) data with respect to the pre-induction (black) data. (c) Induction on a sequence of a red grating interleaved with a homogeneous full-field, achromatic stimulus (10 s each; 20 min total) yielded a classical negative McCollough effect as illustrated by the leftward shift ($p = 0.08$) of the post-induction (green) group ($n = 7$) data with respect to the pre-induction (black) data. (d) Induction on alternating saturated and desaturated red gratings yielded a classical negative McCollough effect as illustrated by the leftward shift ($p < 0.05$) of the post-induction (green) group ($n = 5$) data relative to pre-induction (black).

horizontal grating (Experiment 2b) yielded a robust anti-McCollough effect (Figure 2b; $p < 0.01$). This suggests that an achromatic grating is sufficient to generate the anti-McCollough effect.

Experiment 2c provides further evidence of the unique importance of the achromatic inducer and its orientation. Switching the oriented/unoriented nature of the two inducers influenced the perceived color of the aftereffect: an induction sequence consisting of an oriented chromatic grating interleaved with a homogeneous full-field achromatic inducer yielded a classical McCollough effect ($p = 0.08$; Figure 2c). This result suggests that an achromatic grating inducer is necessary to obtain the anti-McCollough effect.

Experiment 2d shows that the lack of chromaticity of the achromatic inducer is critical to the perception of aftereffect color. Induction on a saturated red, horizontal

grating alternated with a desaturated red grating in place of an achromatic one eliminated the anti-McCollough effect and replaced it with a classical aftereffect (Figure 2d; $p < 0.05$). The presence of the desaturated red inducer naturally weakened its greenish appearance, supporting the proposal that a consistent, clear green afterimage during induction is critical to the anti-McCollough effect.

Combined, the data from Experiments 2a–2d argue that an oriented, achromatic inducer controls the perceived aftereffect color.

Discussion

Long-term neuronal fatigue (Harris, 1980; McCollough, 1965) can explain negative aftereffects in general, whereas

theories of error correction (Dodwell & Humphrey, 1990) and theories of conditioning (Allan & Siegel, 1993; Murch, 1976) can explain contingent negative aftereffects (Favreau, Emerson, & Corballis, 1972; Lovegrove & Over, 1972; Lovegrove, Over, & Broerse, 1972; McCollough, 1965). To our knowledge, these theories are unable to account for the anti-McCollough effect.

In order to account for it, one would have to start from the following two observations. First, the achromatic inducer is critical (Figure 2). Second, as expected, a negative afterimage is formed during the induction process—the achromatic inducer is perceived to be of complementary color to the chromatic inducer. A proposal that we would like to raise is that this color afterimage, which appears to accumulate and to enhance during the course of the induction, induces an aftereffect complementary to it (Day & Webster, 1989; Murch & Hirsch, 1972). Within this framework, the putative “after-aftereffect” generated is the anti-McCollough effect. Our proposal, while plausible, raises a question: How does an after-aftereffect induced by a presumably weak afterimage come to perceptually dominate a (negative) aftereffect induced by a stronger, highly saturated chromatic stimulus?

To address this issue, one may consider three different accounts. The first is intra-cortical connectivity confined within a visual area; the second account is based on hierarchical interactions across different areas; the third account is based on the fact that lower stimulus intensities decay slower, which in our experimental context means that the weakly saturated greenish aftereffect persists for a longer duration in the brain’s visual system than the colored inducer. The second and third accounts are not mutually exclusive, as we will discuss later. First, we will contrast the first two accounts.

Within the first framework (intra-cortical connectivity), cells preferentially tuned to red, horizontal stimuli and cells tuned to green, horizontal stimuli mutually inhibit one another via intra-cortical connections. It is more likely that the activity of the orientation-selective cells tuned to the saturated color of the external stimulus (colored grating) is greater than that of the orientation-selective cells tuned to the weakly saturated afterimage. This makes it less likely for cells tuned to the color of the afterimage to exert greater inhibition than cells activated by the stimulus, making it hard for this account to explain our psychophysical finding.

The second framework for interpreting the data is based on a hierarchical model of perception. To probe distinctive features of different levels in the visual hierarchy and interactions among them, the classical psychophysical paradigm of interocular transfer provides powerful clues. Visual effects that do not transfer interocularly typically have a lower neural substrate in the visual pathway in comparison with effects that do, and the classical McCollough effect is known to not transfer interocularly (Coltheart, 1973); further, effects that transfer interocularly

are likely to have a cortical substrate. We tested the degree of eye specificity of the anti-McCollough effect in the next experiment.

Experiment 3: Interocular transfer

We examined the extent to which the anti-McCollough effect induced on a single eye transferred to the non-induced eye and contrasted the magnitude of interocular transfer for the anti-McCollough and classical McCollough aftereffects.

Methods

Participants

Four observers with normal or corrected to normal vision participated in the monocular anti-McCollough induction, three in the monocular McCollough induction.

Stimuli

Stimuli were the same as in Experiment 1.

Procedure

The experimental procedure was nearly identical to that in Experiment 1 with the following three important exceptions.

Viewing was monocular at the time of induction. A commercially available eyepatch (Bernell Corp.) was placed over one of the eyes, depriving it of visual stimulation during the 20-min-long induction period. Second, pre- and post-induction tests were run separately for each eye. Thus, each observer ran two pre- and two post-induction tests. Finally, the duty cycle was modified. Instead of the 10- to 10-s alternating red and achromatic sequence as in Experiment 1, we used the following induction sequences: (1) McCollough sequence—red horizontal inducer: 18 s, achromatic horizontal inducer: 2 s, alternated for 20 min total, and (2) anti-McCollough sequence—red horizontal inducer: 2 s, achromatic horizontal inducer: 18 s, also alternated for 20 min total. Earlier experiments with binocular induction revealed that induction on the McCollough and anti-McCollough sequences typically led to McCollough and anti-McCollough aftereffects respectively (unpublished). All other variables were unchanged from Experiment 1.

Results

Induction on the McCollough sequence (18 s red, 2 s achromatic) typically though not always (see Discussion below) yielded a strong classical aftereffect (Figure 3a,

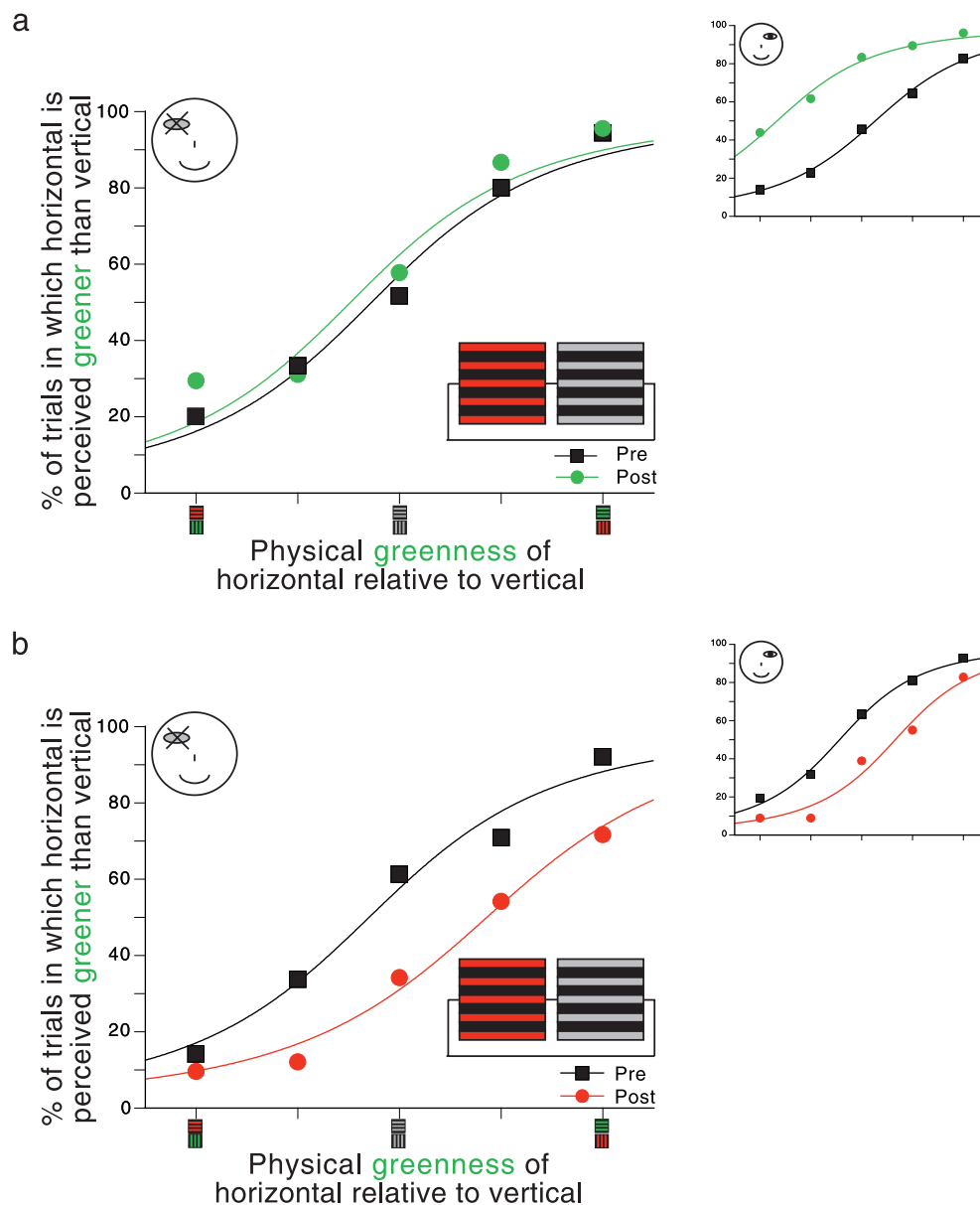


Figure 3. Interocular transfer of the anti-McCollough effect but not the McCollough effect. (a) Following monocular induction (18 s red, 2 s achromatic, 20 min total), there was a robust post-induction McCollough effect in the induced eye (inset) but no transfer to the non-induced eye ($n = 3$, 180 trials total/data point, $p > 0.2$). (b) Following monocular induction (2 s red, 18 s achromatic, 20 min total), there was a robust post-induction anti-McCollough effect in the induced eye (inset), which transferred unimpeded to the non-induced eye ($n = 4$; 240 trials total/data point, $p < 0.05$).

inset). However, there was negligible transfer to the non-induced eye ($p = 0.5$; Figure 3a), as expected from past studies (Coltheart, 1973). Of importance was the fact that the McCollough effect did not transfer interocularly *with our set of stimulus parameters*.

Induction on the anti-McCollough sequence (2 s red, 18 s achromatic) on the other hand typically, though not always, yielded a robust anti-McCollough aftereffect (Figure 3b, inset). In sharp contrast to the monocular specificity of the McCollough effect that we and others before us have observed, the anti-McCollough effect obtained on the induced eye did transfer (the magnitude

of the effect in the non-induced eye was larger numerically) to the non-induced eye ($p < 0.01$; Figure 3b) (Mikaelian, 1975).

Discussion

Although the McCollough effect does not transfer interocularly, which we confirmed with our parameters (Figure 3a), the anti-McCollough effect did; the anti-McCollough effect magnitude in the non-induced eye was larger than that in the induced eye (Figure 3b). Thus, the

findings of the interocular transfer experiment lend support to the proposal that the anti-McCollough effect has a higher level of representation in the brain hierarchy than the classical McCollough effect.

Stretching the exposure time of one of the inducers over the other had impact on the perceived color of the effect. Associating the color red and the horizontal orientation for 90% of the 20-min-long induction period caused post-induction achromatic horizontal stripes to appear greenish. In the same vein, if post-induction achromatic, horizontally oriented stripes appear reddish, it would argue for an induction sequence dominated by an association between the color green and the horizontal orientation. How could this occur with an induction sequence consisting of achromatic and red horizontal inducers displayed for 90% and 10% of the total induction period, respectively? We argue the following. The red inducer generated a strong greenish afterimage of the alternating achromatic inducer. The prolonged association between the perceived green and the horizontal orientation, rather than between the perceived (and physical) red and horizontal, resulted in an aftereffect in which the post-induction horizontal bars were perceived as reddish. That is to say, the greenish percept of the physically achromatic inducer is what triggered the anti-McCollough aftereffect.

Our arguments on the influence of temporal parameters on the sign of effect need to be tempered by, among other things, the tightness of the relationship between the two variables. One of the three observers whom we ran on the 18- to 2-s McCollough induction sequence (Methods) showed a strong anti-McCollough effect. Similarly, one of the four observers, who had shown a clear anti-McCollough aftereffect on the main 10 s-10 s induction sequence earlier, showed a strong McCollough effect on the 2- to 18-s anti-McCollough induction sequence. It bears mention that in both anomalous cases, the interocular transfer was consistent with perceived aftereffect color. Thus, although the sign of the effect typically had a lawful relationship (5/7 observers) with specific values of the temporal parameters of the induction sequence, the relationship between stimulus parameters such as timing and sign of effect is in need of further exploration.

General discussion

We report a novel aftereffect in which the aftereffect is of the same hue as the adapter. Exposure to colored gratings has long been known to lead to a long-lasting aftereffect that exhibits the complementary hue to the adapting color (McCollough, 1965); when interleaved with equal duration of exposure to achromatic gratings, we report an aftereffect that exhibited the same hue as the adapter (Figure 1). The aftereffect, termed the anti-McCollough effect, although weaker than the normal

aftereffect, remained stable for a moderate time duration (Figure 1). Further experiments showed that the achromatic inducer, its orientation, and hue all were crucial to perceived aftereffect color (Figure 2). In contrast to the normal aftereffect that does not transfer interocularly (Coltheart, 1973; Grossberg, Hwang, & Mingolla, 2002), the anti-McCollough effect transferred completely to the non-induced eye (Figure 3).

The so-called anomalous aftereffect, like the anti-McCollough effect, has the same hue as the inducing stimulus (MacKay & MacKay, 1973). In that study, one eye was adapted to an achromatic grating and the other eye to a homogenous colored field. The color-adapted eye exhibited the classical negative aftereffect, whereas the achromatically adapted eye exhibited an aftereffect that was of the same hue as the adapter. The experimental conditions and outcome in the current study were radically different from the earlier study. In the current study, both eyes saw identical adapters, achromatic and chromatic grating inducers were presented for an equal amount of time and in the end, the normal aftereffect lost out and only a non-classical aftereffect (anti-McCollough) was seen. Thus, the anti-McCollough effect cannot be entirely explained by mechanisms proposed to explain the anomalous aftereffect.

On the basis of Experiment 3, it is reasonable to believe that the classical negative aftereffect is represented in a low-level monocular visual brain area (e.g., layer 4 of area V1) (Day & Webster, 1989) and that the desaturated green percept of the achromatic horizontal grating presented in our induction paradigm induces an after-aftereffect, which is represented in a higher-level area (e.g., superficial layers of V1, or V2). Top-down feedback connections having a strong inhibitory influence might prevent the aftereffect represented in lower-level cells from reaching perceptual threshold. Regardless of relative aftereffect strength, if perceptual awareness is hierarchical (Hochstein & Ahissar, 2002), the after-aftereffect in the higher area will perceptually supersede the aftereffect represented in the lower area.

Alternatively, according to the third account, the greenish afterimage, having a low value of color saturation, might decay slower than the saturated colored stimulus. There are several plausible reasons for this. One, there is a reciprocal relationship of visual persistence with stimulus intensity (Di Lollo, 1984); although visual persistence is of the order of hundreds of milliseconds, it may be enough to cause the afterimage to outlive the stimulus in the visual pathway and induce the anti-McCollough effect-in experiments, we found that increasing the rate of alternation (1 s each) did not diminish the aftereffect. Alternatively, there might be a difference in the time constants of adaptation and de-adaptation at different levels of the visual pathway. Either way, the reddish aftereffect, i.e., the anti-McCollough effect, formed from adaptation to the greenish afterimage can outlive the classical aftereffect in the visual pathway.

Signal-strength-based theories of perceptual awareness postulate that the stronger and more reliable the activity of neurons in a brain area (e.g., firing rates, degree of interneuronal synchronization, or the relative power in a particular frequency band) in comparison with that in other competing brain areas, the more likely it is that perception will reflect the signal conveyed by their activity. In contrast, a second class of theories of perceptual awareness (Crick & Koch, 1995, 2003), which originate partly from the established tenet of a functional hierarchy in the brain, posits that a signal in a lower-order area is superseded in perception by signal in an area downstream of it. This is not surprising if the levels of activity in the two areas are comparable. The anti-McCollough effect goes beyond this idea by suggesting that the higher-order area supersedes even when its activity level is relatively weaker.

In conclusion, we report a new counter-intuitive effect—the anti-McCollough effect—that could be a promising means to examine hierarchical versus signal strength-based theories of perception. Moreover, this new after-aftereffect appears suited to shed new light on the classical issue of whether or not a percept, and not merely external stimuli, can affect yet another percept.

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Corresponding author: Bhavin R. Sheth.

Email: brsheth@uh.edu.

Address: Department of Electrical and Computer Engineering, University of Houston, Houston, TX 77204-4005, USA.

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