

THE PHOTOPIGMENT BLEACHING HYPOTHESIS OF COMPLEMENTARY AFTER-IMAGES: A PSYCHOPHYSICAL TEST

JACK M. LOOMIS¹

Department of Psychology, University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

(Received 15 June 1971; in revised form 26 October 1971)

A WIDELY accepted explanation of complementary (negative)² after-images is based on the assumption that photopigment bleaching, in one way or another, alters the sensitivity of the mechanisms underlying color perception with the result that a white stimulus (under neutral adaptation) takes on a complementary hue. The purpose of the present study was to test this assumption by comparing the complementary after-images resulting from two different sequences of adapting stimulation, equated for bleaching effects but totally disparate in color appearance.

The conditions of the experiment are made possible by the existence of a temporally-induced color phenomenon, called here the Bidwell color after its discoverer (BIDWELL, 1897, 1901). Specifically, if a red (green, blue) flash is followed by a white flash, properly timed, only a blue-green (purple, orange) flash is perceived, the red (green, blue) being totally masked. Recycling the sequence of dark (D) phase, color (C) phase, white (W) phase several times per second results in sustained perception of a flickering color that is roughly complementary to the hue of the C phase alone or of the sequence D, W, C. This temporally induced color is quite stable and can be produced under a wide range of luminances and durations of the three phases (GOLDSTEIN and MASSA, 1963; KESTON, 1965; SPERLING, 1960; WHEELER and LAFORCE, 1967). Its origin is not well understood, but knowledge of its origin is unnecessary for the line of argument taken here.

Its application to the present experiment was as follows: subjects were exposed to C and W light in each of the two spatially distinct sequences of D, W, C, D, . . . producing a flickering C appearance and of D, C, W, D, . . . producing the flickering Bidwell \bar{C} (complement of C) appearance. Subjects then reported on the color of the negative after-images produced by these two adapting sequences, which were equivalent in their bleaching effects.

METHOD

The two opposite cycles of C and W phases were produced simultaneously by rotating a sectored disc (D) (Fig. 1a) just in front of a piece of translucent plexiglass (S) onto which light from a 500-W slide projector (P) was back-projected (Fig. 1c). The two color channels were defined by the outer and inner trans-

¹ Present address: Smith-Kettlewell Institute of Visual Sciences, 2232 Webster St., San Francisco, Calif. 94115.

² The term "negative after-image" is often reserved for after-images, the brightness relations of which are reversed with respect to the adapting color. A "complementary after-image" is one, the hue of which is roughly complementary (as defined by additive color mixture) to the adapting color. Because they are obtained under similar conditions, the two are generally given the same theoretical treatment, as will be done here.

mitting annuli on the disc which were covered with gelatin color filters (Red: Wratten 25A; Green: Wratten 58; Blue: Wratten 47). The white phase for both channels was determined by the sector of white paper one or two layers thick, depending on the luminance desired. Clockwise rotation of the disc produced the sequence D, W, C in the field defined by the outer annulus and D, C, W in the field defined by the inner annulus. A masking partition (M) limited the subject's field of view to a small part of the rotating disc (Fig. 1b). Subjects saw two flickering colored rectangles (with slightly curved sides as defined by the cut-out sectors) against a flickering white surround. With clockwise rotation, the right-hand rectangle (outer annulus) appeared C and the left-hand one (inner annulus) appeared \bar{C} . These colors were reversed by counter-clockwise rotation. Viewing was done binocularly with undilated natural pupils at a distance of 23 cm.

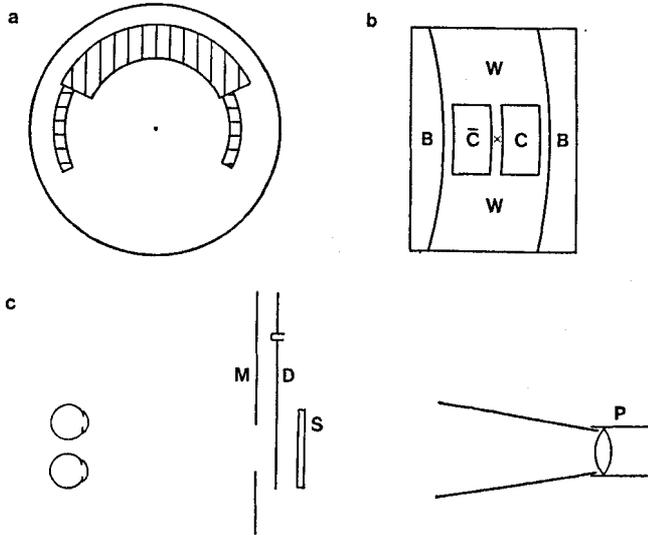


FIG. 1. (a) Black cardboard disc used to provide the stimulating sequence. (III) White translucent paper. (≡) Gelatin filter (red, Wratten 25A; green, Wratten 58; blue, Wratten 47). (b) Subject's field of view. (B) Black surround. (W) Flickering white surround. (C) Flickering rectangle of hue C (red, green, or blue). (\bar{C}) Flickering rectangle of hue \bar{C} (blue-green, purple, or orange). (c) Apparatus. (P) 500 W slide projector. (S) Plexiglass screen. (D) Disc. (M) Masking partition.

The disc was rotated at 362 rpm. The white phase (130°) lasted 83 msec, each C phase (50°) lasted 32 msec, and each dark phase (180°) lasted 115 msec. Each of the colored rectangles subtended approximately 3° horizontally \times 7° vertically; the W background subtended $8^\circ \times 16^\circ$. The luminances, as measured by MacBeth illuminometer, and retinal illuminances (calculated using tabled values of pupil size) of the different phases for each disc are given in Table 1; the nonzero value of the dark phase was produced by the ambient illumination of the black cardboard.

TABLE 1. MEASURES OF LUMINANCE (RETINAL ILLUMINANCE) FOR THE VARIOUS PHASES OF EACH DISC

	C Phase	W Phase	D Phase
Red (Wratten 25A) disc	122 ft-L (2180 td)	248 ft-L (4010 td)	0.4 ft-L (19 td)
Green (Wratten 58) disc	238 ft-L (3876 td)	72 ft-L (1388 td)	0.6 ft-L (28 td)
Blue (Wratten 47) disc	16 ft-L (393 td)	72 ft-L (1388 td)	0.6 ft-L (28 td)

As a control (which later proved unnecessary) for unwanted differences between the inner and outer sequences of the disc, half of the subjects (for each color C) were presented with clockwise rotation of the disc (C on the right; \bar{C} on the left); and half, counter-clockwise rotation (C-left; \bar{C} -right). They fixated binocularly on a small dot positioned between the two rectangles. They viewed the adapting stimulus configuration for 3 min (2 min for C = red), after which a swing shutter was dropped in front of the window. This also served as the postadapting field; it was light gray and under the fluorescent illumination had a luminance of 9 ft-L (250 td). Subjects were instructed beforehand to report any colored afterimage that appeared immediately after the shutter was dropped. They then alternately opened and closed their eyes (1 cycle every 4 sec) to enhance and prolong whatever after-image was present, being interrogated on its appearance every 15 sec during the 120 sec reporting interval. To avoid biasing their reports, the experimenter was careful not to suggest any specific possibilities for the appearance of the after-image. Subjects were instructed to avoid any eye movements while their eyes were open since eye movements tended to dissipate the after-image. Subjects reported where the different parts of the after-image were with respect to their fixation point.

A total of 70 subjects, primarily University of Michigan undergraduates both male and female, were paid for their participation in the experiment. Each subject served in only one condition (red, green, or blue disc). All had been screened for normal color vision (A O S Pseudoisochromatic plates under standard artificial daylight illumination), and none had any knowledge of the purpose of the experiment.

RESULTS

There are several adaptation theories, one of which is the bleaching hypothesis, that predict identical after-images to the two adapting sequences throughout the post-adapting interval. Not one of the 48 subjects who reported seeing an after-image confirmed this expectation.

TABLE 2. NUMBER OF SUBJECTS REPORTING AFTER-IMAGES OF THE TWO ADAPTING RECTANGLES

	Both	A-I of C	A-I of \bar{C}	No A-I	Other
Red disc					
C = Red	11	5	5	4	3
\bar{C} = Blue-green					
Green disc					
C = Green	5	5	1	5	0
\bar{C} = Purple					
Blue Disc					
C = Blue	4	5	4	13	0
\bar{C} = Orange					

An equally important finding is that for many subjects, particularly in the red and green conditions, the rectangular after-image perceived was roughly complementary to the hue of the rectangle perceived during adaptation. Thus the subject who adapted to red:left, blue-green:right would see the after-images faint green:left, pink:right. Subjects who saw both after-images in their proper positions at some time in the post-adapting interval are listed under the Both column in Table 2. Some subjects saw an after-image of only one of the two sequences (D, C, W or D, W, C) and are listed under the columns A-I (after-image) of C or A-I of \bar{C} . A sizable number of subjects saw no after-image at all and 3 subjects (in the red condition) gave reports that are difficult to classify. All three observed blue-green on both the left and the right, seemingly in support of the bleaching hypothesis. However, none of them reported anything approaching two identical blue-green rectangles at all times of the reporting period. There were indications that these subjects, one of whom also reported a

red after-image, were permitting eye-movements and were reporting after-image position with respect to an external referent, rather than the fixation point.

It will be observed that reports of after-images were most frequent in the red disc condition. It is in this condition also that after-images were observed for the longest period. For most of those subjects who saw both after-images, it is interesting that the development and decay of the red and blue-green after-images followed different time courses. It was commonly reported that the blue-green appeared before the red and also faded more quickly. Few subjects observed an after-image immediately after the shutter was dropped. Many of the subjects reported seeing after-images (especially the red one produced by the Bidwell blue-green adapting color) after 90 sec; a few reported one or both after-images at the end of the 120 sec interval.

In both the green and blue disc conditions, after-images were less frequently observed and rarely perceived beyond the first 60 sec. As in the red condition, after-images generally were not seen until 10 sec or so after the shutter was dropped.

Although the after-images perceived were always roughly complementary to the hue of the adapting rectangle in both the red disc and green disc conditions, such was not the case for blue. In fact, the reason for including the blue disc in the experiment was that in preliminary work, the experimenter observed a red-orange after-image to the blue adapting rectangle (D, W, Blue sequence) and a light green after-image to the Bidwell yellow-orange rectangle (D, Blue, W sequence). The color names reported by the naive observers who saw an after-image of some sort in the blue disc condition are shown in Table 3. About two-thirds saw the more expected complementary after-images with the rest seeing colors more like those observed by the experimenter.

TABLE 3. REPORTED AFTER-IMAGES TO THE C (BLUE) and \bar{C} (ORANGE) ADAPTING RECTANGLES IN THE BLUE DISC CONDITION. SUBJECTS NOT LISTED REPORTED NO AFTER-IMAGES

Subject	C = Blue	\bar{C} = Orange
2	Orange	—
3	Pink	Green
5	Orange	Green
9	Purple-Pink	—
10	Orange	—
11	—	Blue-green
15	Orange	—
17	Pink	Blue
18	—	Blue-green
19	—	Blue
20	Red	—
21	—	Blue-green
24	Orange	Blue

Two further observations made by the experimenter are of some interest. The first is that the Bidwell color is not perceived when the C and W phases are presented in proper sequence to separate eyes, suggesting that it is a consequence of unilateral interactions. The second observation is that adaptation of one eye to the red disc configuration, for example, leads to after-images (pink and blue-green) for only that eye; in other words, adaptation does not transfer interocularly.

DISCUSSION

The essence of the bleaching hypothesis is that the bleach photoproducts in each of the three classes of cones codetermine the state of chromatic adaptation. Regardless of the precise mechanism by which the state of adaptation is controlled, it is clear that the states of adaptation corresponding to two stimulating sequences should be identical if the three-dimensional bleaching vectors (indicating the proportions of unbleached photopigment for each of the three cone types) are equivalent. Since the condition of bleaching equivalence is fulfilled here without the concomitant equivalence of after-images, the bleaching hypothesis may be rejected as inadequate. This does not mean that bleaching plays no role in determining the state of adaptation at these low bleaching levels (approximately 5 per cent), but merely that it is not the sole determinant. By necessity there is some other activity in the visual system, presumably neural, that is contributing to the determination of the adaptation state.

A similar but not so rigorously maintained argument can be made against the hypothesis that the vector representing the time-averaged activities of the three receptors determines the state of adaptation. Under the assumptions that each cone response is a function only of its quantum-catch rate and that time-averaging of the cone response (by the mechanism which determines the adaptation state) is done over an interval of at least 230 msec (the duration of 1 cycle), one predicts after-image equivalence for the two adapting sequences. Since equivalence is not obtained, this hypothesis is rejected provided that the two assumptions are valid. The averaging assumption is supported by the observation that chromatic adaptation proceeds very slowly; no perceptible after-image is obtained with adapting intervals of less than 30 sec. The assumption about the cone response has no direct support but it is difficult to imagine how failure of the assumption would favour one sequence over the other so as to produce mutually complementary after-images

The finding that the after-images to the two complementary adapting rectangles are themselves mutually complementary is suggestive of the kind of theory required for negative after-images. Tentatively it seems that adapting sequences that appear different have different adaptive effects. Moreover, in the red and green disc conditions, a flickering Bidwell color has the same qualitative adapting effect as does flickering light of that hue. That the after-image is complementary to the adapting color for these conditions is reminiscent of opponent-process theories of color coding, such as that of HURVICH and JAMESON (1957; JAMESON and HURVICH, 1956), where activity in one process increases the relative sensitivity of the opposing process.

An adequate account of these data must also explain several qualitative facts that distinguish the after-images observed in this study from those observed following steady low-intensity adaptation. The first concerns the temporal course of after-image development and decay, particularly in the red disc condition. Not only was there some lag before the after-images appeared but the two adjacent after-images often followed different time courses. The second fact is that several subjects reported red and green after-images in the blue disc condition, rather than the anticipated yellow and blue.

Despite the evidence here against bleaching and receptor adaptation, there is other evidence that, at least under some conditions, one or both do underlie after-images. CRAIK (1940) demonstrated that both positive and negative after-images were observed following adaptation to a 60 W bulb in spite of the fact that the eye was pressure-blinded during the 2-min adapting period. Craik concluded that this was proof of a photochemical basis of negative after-images but BROWN and MURAKAMI (1968) have shown that both the horizontal

cells and receptors survive pressure-clamping of the retina thus making peripheral neural adaptation a possibility.

Less equivocal evidence for bleaching was adduced by BRINDLEY (1959). He found that for an interval of up to 2 sec, two light flashes equated for total energy (8×10^4 cd sec/m²) but with the energy distributed differently over the interval, gave rise to after-images (positive and negative) that were indistinguishable after the first 15 sec of the post-adapting period. This was true even though the two adapting stimuli had very dissimilar appearances.

In attempting to reconcile these findings with the present ones, it is assumed that both bleaching and neural adaptation underlie complementary after-images and that various experimental conditions favor one or the other form of adaptation.

The experiment by Craik is qualitatively different from Brindley's and the present one in that most of the cone photopigments must have been bleached away. In this case it is reasonable that bleaching was responsible for the after-images. Of more interest to those in color vision is the question of what kind of chromatic adaptation is involved over the normal range of retinal illumination (10–10,000 td) where bleaching is rather small. Although the bleaching level in the present experiment assuming the steady state equations are valid (RUSHTON and HENRY, 1968) is as high as 15 per cent in the red-disc condition (8 per cent green; 3 per cent blue), the differential bleaching of one pigment by the chromatic flash is at most 5 per cent in the green disc condition (3 per cent red; 3 per cent blue). From the results obtained, it is clear that neural adaptation predominates over bleaching under these conditions. It is possible, however, that the different time courses for the two adjacent after-images reflect second-order bleaching adaptation.

Brindley obtained his results on the reciprocity of time and intensity with a stimulus energy of 8×10^4 cd sec/m² but because of insufficient information (size of the source image in the pupil plane) the retinal illuminance and bleaching values are not available. Even a uniformly illuminated pupil of 2 mm would give a 6 per cent bleach so it is likely that bleaching was appreciable. However, the critical difference between that experiment and the present one is the duration of the adapting period. If one makes the reasonable assumption that at high intensities (over 10^5 td) neural adaptation is slow in comparison to bleaching, one can understand how the differential neural activity in a 2-sec adapting period may not be sufficient to produce any appreciable difference in neural adaptation; for adapting periods longer than 2 sec, the now appreciable difference in neural adaptation is enough to cause a nonequivalence of the after-images, of which the major source of adaptation is bleaching. This suggestion has some merit, for it explains why Brindley's critical duration estimate of 2 sec is far short of 10 sec, a period for which Rushton (RUSHTON, 1958; RUSHTON and HENRY, 1968) has found through densitometry that time-intensity reciprocity obtains for bleaching.

The conclusion that over the range of low to moderate adapting intensities the process of chromatic adaptation is a neural one makes intelligible the invariance of metameric matches over the same range (BRINDLEY, 1970). If metamerism is determined at the level of photopigment absorption, but the process underlying the change in color appearance of a test stimulus following adaptation is strictly neural, then color matches cannot be upset. The breakdown of metameric matches following high-intensity adaptation (BRINDLEY, 1970) is another matter; the adaptation process involved clearly operates at a level at least as distal as photopigment absorption of light quanta.

The unequivocal demonstration of a neural basis for the complementary after-images observed here is not too surprising in light of a number of recent studies showing that

complementary colored after-effects to stationary and moving patterned arrays clearly depend upon some form of neural adaptation, possibly cortical (MCCOLLOUGH, 1965; HEPLER, 1968; STROMEYER, 1969; STROMEYER and MANSFIELD, 1970). Although these after-effects differ in several ways (saturation, persistence, and, in some cases, interocular transfer) from the complementary after-images observed here and in typical steady adaptation, it is interesting that after-effects to blue and yellow-orange adapting patterns tend to be red and green, rather than the expected orange and blue (STROMEYER, 1969).

SUMMARY

Previously, it was known that brief-duration lights, which bleach appreciable photopigment, produce after-images that depend only on the bleaching and not on the visual appearance of the lights. This study demonstrates that under opposite conditions—long-duration light stimulation with little bleaching—after-images are correlated with visual appearance and are quite independent of bleaching. Such after-images, which exhibit no interocular transfer, must be produced by a process of slow neural adaptation that is controlled chiefly by a correlate of color appearance.

Acknowledgements—The author gratefully acknowledges the advice of Dr. DAVID H. KRANTZ during the preparation of this paper. The experiment was conducted while the author held a United States Public Health Service Traineeship and a National Science Foundation Predoctoral Fellowship. Research was supported by NSF Research Grant GB 4947.

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Abstract—Normal observers color-adapted simultaneously to two spatially distinct sequences of light stimulation, equivalent in their bleaching effects but complementary to one another in hue. Following the adapting period, observers reported on the color appearance of the two adjacent after-images seen against a neutral background. The nonequivalence of the two after-images argues against the explanation of complementary after-images based on photopigment bleaching; in addition, the fact that the two after-images are mutually complementary further restricts the class of (neural) adaptation hypotheses.

Résumé—On adapte à la couleur des observateurs normaux simultanément avec deux séquences distinctes spatialement de stimulations lumineuses, équivalentes dans leurs effets décolorants mais complémentaires en tonalité. Après la période d'adaptation, les sujets décrivent l'apparence colorée des deux images consécutives adjacentes vues sur fond neutre. La non équivalence des deux images consécutives contredit l'explication des images complémentaires fondée sur la décoloration du pigment; en outre le fait que les deux images consécutives sont mutuellement complémentaires restreint la classe des hypothèses d'adaptation nerveuse.

Zusammenfassung—Farbnormal-sichtige Testpersonen wurden simultan auf zwei räumlich getrennte Sequenzen von Lichtreizen farbadaptiert, die in ihrem Bleicheffekt äquivalent aber komplementär in ihren Farbton sind. Nach der Adaptation berichtete die Testpersonen über den Farbeindruck der zwei aneinandergrenzenden Nachbilder, die gegen einen neutralen Hintergrund gesehen wurden. Die Nichtübereinstimmung der beiden Nachbilder ist ein Argument gegen die Erklärung der komplementären Nachbilder aufgrund der Ausbleichung der Photopigmente. Außerdem beschränkt die Tatsache, daß zwei Nachbilder zueinander komplementär sind, die möglichen Adaptationshypothesen.

Резюме — Нормальные наблюдатели одновременно адаптировались к двум пространственно раздельным световым стимулам, эквивалентным по их обесцвечивающему эффекту, но дополнительным друг к другу по цветовому тону. После адаптационного периода наблюдатели сообщали о том как выглядели цвета двух находящихся рядом последовательных образов, видимых на нейтральном фоне. Неодинаковость двух последовательных образов говорит против объяснения характера комплементарных послеобразов, основывающегося на обесцвечивании фотопигментов; в дополнение к этому, тот факт, что два последовательных образа взаимно дополнительные, далее ограничивает гипотезы адаптации (нейральной).