DURATION OF VISUAL AFTERIMAGES by Richard E. Albert

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by

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ABSTRACT

M.A.

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The duration of the positive afterimage (PAI) of a short flash of light was measured under different conditions of dark-adaptation, stimulus intensity, and stimulus spectral composition. The number of positive phases was recorded. Longer durations and more phases of the PAI were recorded when the eye was most completely darkadapted, independent of spectral makeup of the stimulus. A red test stimulus produced fewer phases and shorter durations of the PAI, but the red stimulus was also the weakest stimulus in effective brightness. A second experiment tested for transfer in the PAI. Monocular testing produced a long PAI when the non-tested eye was exposed to light for 20 minutes before the test; the PAI was shorter if the non-tested eye was dark-adapted for the 20 minutes before the test.

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INTRODUCTION

The afterimage of a textured field illuminated by a short, brilliant flash of light consists of several distinct phases. As many as seven phases have been described, all of which fall into two categories: 1) the positive afterimage (PAI), in which the brightness relations are identical to the stimulating field, and 2) the negative afterimage, in which the original brightness relations are reversed. The positive phases are most easily identified, and they usually follow a set pattern. The initial flash is quickly followed by two positive phases which can be seen as separate only if the stimulus is moving. Then there is a noticeable dark interval, followed by a long positive phase, the Hess (3rd) positive phase (Brown, p. 480). For a stationary stimulus, the third positive phase is the second distinct phase that one sees.

Early researchers suspected that some form of interaction among retinal elements was responsible for the oscillatory nature of the afterimage, and their experiments were designed to isolate the effect of different retinal elements. McDougall (1904) studied the afterimage of a rotating bar of light in both red and white light. In white light, the afterimage consisted of a series of light and dark bands, followed by a dark space and then a grey band. The grey band disappeared in red light, while the light and dark bands remained. Since it was known that rods were not responsive to red light (McDougall, p. 95), McDougall considered the light and

dark bands to be "cone bands," and the grey band to be a "rod band." But because the "rod band" showed some colour under bright light, McDougall felt that it was really a combined rod-cone effect (McDougall, p. 97). Judd (1927), using a 14 msec stationary light source as a stimulus, studied the effect of different coloured filters on the second positive, or Purkinje, phase of the PAL. He found that shorter wavelengths were most successful in producing this phase; he could not obtain any Purkinje phase in red light (Judd, p. 527). Karwoski and Warrener (1942, p. 145) using a rotating stimulus similar to McDougall's did see a Purkinje phase with red light. Judd's results may have been due to the difficulty in separating the Purkinje phase from the first positive (Hering) phase with a stationary stimulus (Judd, p. 509). Feinbloom (Brown, p.488), measured the increase in duration of the afterimage sequence as a function of luminance and found that the rate of increase was slowest for red light.

With stimulation of long duration or very high intensity, red light does not have as much of an effect on the duration of the afterimage. Weve (1925), using 5-10 sec stimulation, found that <u>Ss</u> with normal colour vision did not report any difference in the length of the afterimage as a function of wavelength. One colour-blind <u>S</u> reported little or not afterimage with red stimulus light, but his other afterimages were as long as those of observers with normal colour vision. Brindley (1962) used 8 coloured stimuli ranging from deep red to deep blue and a 0.67 sec stimulus of 3×10^6 mL. The red

stimulus blurred faster than other coloured stimuli, but afterimages of red stimuli as long as 8 minutes were reported (Brindley, p. 170). Weve ignored oscillations of the afterimage, and Brindley did not report any; neither mentioned whether the afterimage was positive or negative.

The afterimage undergoes changes as the <u>S</u> dark adapts, and these changes may be evidence of neural interaction. Padgham used binocular matching to measure the brightness of the afterimage, "presumably the third positive phase," as a function of dark adaptation (DA) (Brown, p. 495). He found that brightness was not increased beyond five minutes DA, and concluded that this phase may depend on a cone process. Feinbloom (Brown, p. 487) found that the afterimage duration increased, at a decreasing rate, with increased DA.

The duration of the afterimage increases with an increase in the primary stimulus luminance (Brown, p. 493). Alpern and Barr (Brown, p. 488) investigated the relation between primary stimulus energy and duration of any detectible afterimage. They found that the afterimage duration increased with increased stimulus energy, and that the data fitted two lines, each related linearly to the logarithm of the stimulus energy. They attributed one segment to the rods and the other to the cones.

Barlow and Sparrock (1964) feel that the oscillatory nature of the afterimage is due to its stabilization on the retina. They compared the PAI to a stabilized image, found considerable similarity in the oscillatory character, and concluded that the PAI oscillations

were due to the mechanisms responsible for the stabilized image phenomena. As long as the visual pigment remained bleached, the receptors would continue to send a message up the visual system, and the continued input to the ganglion cells would cause inhibitory feedback to the receptor cells. Hence, the oscillation would not be due directly to rod-cone interaction, in their explanation. Earlier Granit had reached a similar conclusion, based on the neurophysiological work of Fröhlich and others. In Granit's scheme, stimulation of the receptors sets up a depolarizing generator potential in..the receptor, which is maintained during stimulation. The generator potential determines the rate of spike potential transmission. Thus any change in the spike rate would be due to some kind of negative feedback (Granit, p. 13).

There is some neurophysiological evidence of rod-cone interaction which might make oscillatory phenomena possible. Granit (1955) and Barlow (1957), using different techniques, measured Purkinje shifts in single retinal ganglion cells. The Purkinje shift is a change in spectral sensitivity, toward shorter wavelengths, which accompanies the change from bright light (cone vision) to dim light (rod vision). Their data indicate that both rods and cones are connected to a single ganglion cell. Polyak (Granit, p. 65) and Dowling and Boycott (1966, p. 106) have demonstrated such connections anatomically.

Ratliff (1965) has made a comprehensive study of the lateral interconnection present in the eye of <u>limulus</u>. This primitive eye consists of many identical receptors, each with one fiber leading to

a single nerve. Each receptor is laterally connected to its near neighbours, forming a primitive plexiform layer. Ratliff illuminated an area of the <u>limulus</u> eye and recorded the electrical activity of one receptor in the center of the illuminated field. The light intensity was then abruptly changed. After the initial burst of spikes, the firing level oscillated before reaching a new base level. Ratliff mathematically demonstrated how the oscillations could be explained by assuming that the connections between receptors are inhibitory in nature. The human retina is complicated by several different kinds of cells at each level, so an explanation of oscillation due to simple lateral inhibition of like receptors would not necessarily be valid in the human retina. However, the similarity between the subjective intensity levels of the oscillation of the PAI and the recorded electrical activity in the limulus eye is striking.

Alpern (1965) showed that like retinal elements interact with each other; that is, rods with rods, blue cones with blue cones, etc. He measured the threshold of a 5 msec test flash masked 50 msec later by a 5 msec after-flash. After-flashes of certain colours had virtually no effect on the threshold of certain cone mechanisms (e.g. a yellow after-flash with a blue test flash). He concluded that there is no rod-cone interaction in the after-flash effect. In a similar second experiment (Alpern and Rushton, 1965), he established the independence of each cone mechanism from one another in the after-flash effect. DeValois and Abramov (1966) suggested that these connections probably occur at the earliest level in the visual pathway, because of the

preponderance of connections between unlike receptors by the bipolar level. From their electron microscope work, Dowling and Boycott (1966, p. 105) feel that horizontal cells might mediate this afterflash effect. They suggest that each horizontal cell might connect specific retinal elements (e.g. one cell connecting blue cones only), although they do not have the direct evidence to support this claim.

In summary; there is anatomical, physiological, and behavioural evidence for interaction of visual elements at the retinal level. This interaction may be of lateral, centrifugal, or centripetal nature; some of it seems to be of the inhibitory type.

The present experiment was designed to study the effect of several stimuli on the PAI, particularly on the number of phases, in an attempt to obtain further data on the kind of interaction that occurs in the retina. Different methods of pre-test DA were used, to see if differences in adaptation would have any effect on the PAI. A second experiment, consisting of a simple transfer test, was run to see if there was any central influence in the oscillatory nature of the PAI.

Experiment I

Experiment I tested the effects of various methods of dark adaptation (DA) on duration and phases of the positive afterimage (PAI) of a 1 msec flash of light. Three methods of DA were used: 1) 20 minutes in complete darkness (the "total dark" condition); 2) 20 minutes wearing red goggles (the "red" condition); and 3) 20 minutes wearing neutral density (ND) goggles, which transmitted approximately the same luminous intensity as did the red goggles (the "ND" condition). There were three different conditions for testing the FAI: 1) with the <u>S</u> wearing red goggles (the "red goggle" condition); 2) with the <u>S</u> wearing ND goggles (the "ND goggle" condition); and 3) with the <u>S</u> wearing no goggles (the "no goggle" condition). Each adaptation condition was paired with each test condition; thus each <u>S</u> was tested under 9 conditions. The test consisted of timing the duration of the PAI. The number of phases of the PAI was also recorded.

Apparatus

The stimulus was a black circle, 20.5 cm in diameter, on a featureless white background. Distance from <u>S</u> to stimulus was 90 ± 8 cm; the stimulus subtended 13° at the eye. A luminous dot was placed in the center of the stimulus, to simplify focusing in the dark and insure proper orientation of the S. Light was provided in 1 msec flashes by a Metz 502 Mechablitz photoflash unit, 166 ± 3 cm from the stimulus. The flash part of the unit consisted of a xenon-argon lamp, "daylight-

balanced," but really stronger in the lower (blue) part of the spectrum (Handbook of Chem. and Physics, pp. 2494-6, 2626-7). The flash was rated at 4000 effective candle-power-seconds. The unit was placed in a box to limit its illumination to the area around the stimulus (about $3\frac{1}{2}$ ' x 5'). With this setup, the effective luminance reaching the eye was about 10^{-2} mL. The <u>S</u> wore Cesco welder's goggles, model 557-W, with either Kodak Wratten no. 29 (red) or no. 96 (ND) filters as lenses. Times were recorded to the nearest .01 sec on a Standard electric timer.

Subjects

Subjects for experiment I were six female and four male college students, ranging in age from 18 to 27 years. Each <u>S</u>s vision was normal or corrected to normal.

Design

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A 3 x 3 factorial design (adapt x test) was used. A modified latin square method, as described by Winer (p. 517), determined the order of testing for 7 subjects. The remaining three <u>S</u>s followed randomly determined orders. In this way practice and other long-term effects were kept to a minimum.

Procedure

All <u>Ss</u> received preliminary training, consisting of a short period of DA followed by a few flashes of light. For the first few times, the <u>S</u> viewed the flash and described his afterimage. All <u>Ss</u> readily identified the positive phase (a black circle on a lighter background), as well as the negative phase (a lighter stimulus on a darker background). When the <u>S</u> could easily identify the positive phases, he was instructed to time them. Timing consisted of closing a switch when the <u>S</u> saw the PAI and opening it when the PAI was not present. When the <u>S</u> felt that he could time the positive phases accurately, the experiment started.

Each run proceeded as follows. A few minutes in normal room light was allowed before each DA began, providing a base line for adaptation. The <u>S</u> was dark-adapted for 20 minutes under one of the 3 DA conditions. After 20 minutes of DA, the <u>S</u> was seated in front of the stimulus. The light was turned out, and the <u>S</u> prepared for the test condition as quickly as possible. This usually consisted of changing goggles. The <u>S</u> was then instructed to look at the luminous dot in the center of the stimulus. This was impossible with the red filters; in this case he focused on the dot before putting on the goggles. The experimenter would ask the <u>S</u> if he had the switch in his hand. Upon hearing the affirmative, the <u>E</u> would say "ready," followed two seconds later by the flash. The <u>S</u> then timed the PAI. The delay between the end of the DA period and the test flash was held as short as possible, but it ran up to 45 seconds at times.

Results

Ss wearing red goggles during the test period reported fewer phases and shorter durations of the PAI than they did under the other test conditions (Tables I, II). Under the red goggle test condition, only two of 10 Ss reported seeing more than one phase, and in one case the S was not looking at the stimulus at the time of the flash. The no goggle test condition produced the greatest number of phases -- two or more distinct phases were reported 25 times in 30 trials (Table II). Two or more distinct positive phases were reported in 15 of 30 tests with the ND goggles. These figures were significantly different from one another (Friedman $X^2 = 16.7$, df = 2, p < .01). Each test condition was significantly different from each other condition at $p \leq .02$ by the Wilcoxin matched pairs test.

Times recorded by <u>S</u>s tested wearing red goggles were short under all adaptation conditions and were much shorter than the times recorded in the other two testing conditions (Table I). 23 of 30 trials were of less than two seconds duration, and the average time was about 1.5 sec. Times for the ND test condition averaged 4.1 sec., and <u>S</u>s recorded an average duration of 8.6 sec when no goggles were worn during the test. These time data were significantly different from one another (analysis of variance, test effect: F = 19.5, df = 2,18, p < .01).

Differences in adaptation also produced differences in the PAI. The PAI was longest under the total dark condition and shortest under the ND condition (Table I). Number of phases followed the same pattern, with the greatest number recorded under the total dark condition and the least in the ND condition (Table II). Both times and phases were significantly different from one another (times: analysis of variance, adapt effect: F = 16.9, df = 2,18, p < .01; phases: Friedman, $X^2 = 11$, df = 2, p < .01). The difference between times recorded under the ND adapt and the red adapt condition failed to reach significance (Scheffé test, F = 2.41, df = 1, 18, NS), but all other time differences between two adapt or two test conditions were significantly different from one another. All comparisons between different number of phases for specific adapt or test conditions were significant, by the Wilcoxin matched pairs test, at $p \leq .05$.

I was interested in the appearance of the third positive phase of the PAI as a function of the test light. For this purpose the phase data were re-analyzed in a modified form. With a stationary afterimage, it is difficult to separate the flash from the first two rapidly following phases (personal observations, Judd, p.509, Brown, p. 487). The third positive phase, which is separated from the first phases by a relatively long dark, or "negative", phase, is clearly observable, as are later phases. Hence the third positive phase is the second distinct phase. To emphasize the appearance of this phase in the data, a table in which all observations of 2 or more phases were listed as "2" was made (Table III), with a report of "2" interpreted as indicating the occurrence of the third positive phase. Whenever a <u>S</u> did not record any phases at the time of testing but later reported that he had seen a flash of noticeable length (about 1 sec), one phase was recorded in the data. This correction was carried over to Table II. Applying the Friedman test to the modified data showed that the test condition was highly significant ($X^2 = 17.2$, df = 2, p <.001) for the appearance of the third positive phase, while the adaptation was not important ($X^2 = 1.2$, df = 2, NS). The no goggles test condition produced the largest number of third positive phases, followed by the no goggles and the red goggles conditions in that order. All differences between test conditions were significant at p $\leq .05$ by the Wilcoxin test. Adaptation with ND lenses tended to produce fewer third positive phases than the other conditions (10 vs. 15 and 16), although the difference between the number of phases in the ND adaptation condition and the number of phases for any other adaptation condition was not significant by the Wilcoxin test (T>O, N = 6 for all comparisons).

Experiment II

Experiment II was designed to discover whether the influences on the PAI were of central, peripheral, or mixed origin. A simple test of transfer was used. Ss were monocularly tested for the PAI after 20 minutes of DA. Two conditions of DA were used: 1) The "adaptation" eye covered by an eye patch and the test eye covered by the no. 96 ND filter (the "dark" condition), 2) the test eye covered by the ND filter and the "adaptation" eye uncovered, but in the goggle frame (the "open" condition), Each S was given both conditions, and the same eye was tested in both conditions for each S. During the test flash, the "adaptation" eye was covered with an eye patch, and the test eye was uncovered. Choice of eye and order of conditions for each S was randomly determined. 10 male and 4 female Ss, 5 of whom had participated in Experiment I, were used for Experiment II. New Ss were trained as in Experiment I, and old Ss were given a few practice runs. With the exception of the monocular testing, the details of the testing condition of Experiment II were identical to those of Experiment I. The apparatus for Experiment II was the same as that used in Experiment I.

Results

<u>Ss</u> reported longer times and more phases of the PAI in the open than in the dark condition (Table IV). The average PAI duration in the open condition was significantly longer than the average duration in the dark condition (t = 3.19, df = 14, p < .01). Times for <u>Ss</u> who reported the same number of phases in both conditions also showed this trend (t = 2.26, df = 8, p < .10). The difference in duration did not seem to depend on whether the <u>S</u> reported the same or different number of phases of the PAI (t = .915, df = 13, NS).

10 of 15 <u>S</u>s reported seeing the third positive phase (second observable phase) in the open condition, while only 6 reported seeing it in the dark condition (this is not a significant difference by any appropriate test). Descriptions given by the <u>S</u>s agree with this trend; one <u>S</u> reported the second phase in the dark condition as "mushy" and the open second phase as "clear". (This <u>S</u> reported 2 phases in both cases). Another saw an "ill-defined" second phase in the open condition, and saw no such phase in the dark condition. Yet others reported both test conditions as identical.

Discussion

Experiment I

Experiment I was conducted in an attempt to obtain some information about the organization of the human retina by analyzing the oscillations of the PAI of a short flash of light. Three variables were used: brightness of the stimulus light, spectral character of the stimulus light, and condition of dark adaptation. This discussion will analyze the effect of these 3 variables on the PAI. The effect of some of the relevant details which were held constant throughout the experiment will also be discussed.

The red and ND goggles were equated for transmission of the luminous energy; both pass about 10% of the incident energy for the spectral makeup of the photoflash unit used. However, the effective brightness of the two lenses are far from equal, due to the difference in spectral character of the lenses. The ND lens passes light of all wavelengths in the visible spectrum about equally, while the red lens passes light above 600 Mp only. In the 600 mp plus range, both the rods and cones are much less sensitive to light (based on threshold data, Bartlett, p. 159) than they are over the entire spectrum as an average. Because of this difference in sensitivity, the red goggles serve to effectively eliminate the functioning of the rods, their purpose in the first place; but the differences in effective brightness must be considered in analyzing the data. For all adaptation conditions, the duration of the PAI was greatest when the <u>S</u> was tested wearing no goggles; the shortest durations were recorded under the red goggle test condition. The number of phases reported followed the same pattern. These results are correlated with the effective brightness of the stimulus light, regardless of spectral makeup. It is tempting to explain the disappearance of the third (and later) positive phases under the red test condition by assuming that the rods do not function in this condition. But because spectral energy of longer wavelengths is less effective on the retina than a total spectral distribution, one cannot rule out the possibility that the amount of spectral energy that produced later phases in the ND test condition was not strong enough, in the red test condition, to produce a later phase.

The confounding of effective brightness with spectral makeup can be used to explain the adaptation results as well. Longer durations and more phases were recorded when the <u>S</u> was totally dark-adapted than when he was partially dark-adapted; and adapting with the red goggles produced more phases and longer durations than adapting with the ND goggles. When the <u>S</u> adapts with red goggles, his rod photopigments are nearly 100% regenerated, while his cones remain in a state of partial DA. With ND goggles, both rods and cones remain partially light-adapted. So a given luminance in the test condition should be effectively brighter to the eye with the rods nearly 100% adapted; and PAI durations and number of phases followed this effective brightness prediction. The increase in duration of the PAI was much greater

than the increase in number of phases reported under the total DA condition. The longer duration seems to be due to the complete regeneration of the cones, which the partial DA conditions did not allow. The number of phases does not seem to have been as effectively changed by the total regeneration of the cones; there may be a relation between amount of photo-chemical regeneration in the rods and number of phases, but again the difference could be due to effective brightness.

The subjective appearance of the PAI during the oscillation was described as a disappearing and re-appearing circle or a circle with an edge which was alternately clear and fuzzy. Since the stimulus was dark (non-reflecting), and the surround was light (reflecting), the fovea was not stimulated. The disappearance of the circle may be interpreted to mean either fading of the stimulated surround, or stimulation of the unstimulated foveal region. In the second case, it is reasonable to suspect the occurrence of some sort of lateral connection, whether through the ganglion cells or at the receptor level, as responsible for the oscillation of the PAI. In the red test condition, and occasionally in the ND test condition, the absence of all later phases was reported as a decrease in brightness of the surround, rather than an increase in brightness of the central area. This difference between the oscillatory and non-oscillatory PAI is another reason to suspect that an insufficient illumination level played the dominant role in the absence of later phases of the PAI in the red test condition.

Experiment I seems to support a combination of nearly fully regenerated photopigments and lateral interaction as the necessary con-

ditions for an oscillatory afterimage of a short flash of light. Evidence of specific connections was not obtained. It is possible that both rods and cones needed to be stimulated to produce an oscillatory afterimage, but this proposition was not proved.

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Experiment II

Experiment II was designed to learn whether there was any central component in the oscillatory afterimage phenomenon. As the eye which was tested underwent identical DA for each test, and as the eye which was dark adapted under varying conditions was never tested, the consistent differences which appeared between the two conditions indicated that some aspect of the visual system central to the retina has an effect on the appearance of the afterimage. Day (1958) has argued against transfer measures as measures of central aspects of visual after-effects, but his argument is based mainly on the type of experiment where one eye is being stimulated, and the second eye is experiencing the phenomenon simulatneously. He argues that "leakage" through the optic tract from one hemi-retina to the other should not be considered a "central" phenomenon, although even this leakage is evidence of interaction more central than that of the retina. In Experiment II, however, there is no optic nerve feedback due to simultaneous light stimulation of the non-tested eye; any change in sensitivity of the tested eye due to the non-tested eye must have occurred during the adaptation period.

The visual system received much more light during the open adaptation condition than during the dark condition. In the dark condition, one eye was receiving 10% of its normal input, and the other eye was receiving 0% of its. The average input, relative to normal, was 5%. In the open condition, the eye wearing the ND goggles was again receiving 10% of its normal input, while the other eye was

receiving 100% input. The average input in this case was 55% of normal. Yet the open condition produced longer PAIs. This result makes more sense if one looks at the DA level of the tested eye relative to the average level of adaptation of the visual system. In the dark case, the ND eye was receiving more than the average input during the adaptation period (it was dark adapted less than the average level); in the open case, the ND eye was receiving less than the average input (dark adapted more than the average level). Since the open condition continually produced longer afterimages, one might hypothesize that the state of DA in the CNS is related to the average of the photochemical levels of adaptation of the two eyes, and that the afterimage of one eye expresses the relation of the state of DA of the individual eye to the average DA level. Thus, in the dark condition, the ND eye is less adapted than the average; and it would produce a short afterimage. In the open case, the ND eye is adapted much more than the average level; and its resulting afterimage would be longer than that of the ND eye in the dark condition. This view strongly suggests a central aspect to DA, and Granit (1955) took a similar stand and gave some neurophysiological evidence for his position (p. 145).

The basic oscillatory nature of the PAI did not seem to be changed by this central effect, as both one and two phase reports were recorded in both conditions. The central influence on the PAI seems to be in setting the base level from which the extent of the effect of a given flash of light is to be measured.

In conclusion, the oscillatory nature of the PAI of a short flash of light seems to be effected by the intensity and spectral character of the stimulus and the level of dark adaptation of both eyes. A red stimulus light reduces both duration and number of phases of the PAI, but it was not determined whether the absence of all later phases of the PAI was due to the elimination of the rod response at long (red) wavelengths or to the low level of activity of the cones at long wavelengths. If the <u>S</u> is tested monocularly and if each eye is at a different level of DA, the duration and number of phases depend on the average level of DA of the two eyes, and the relation of the DA level of the tested eye to this average level.

References

- Alpern, M. "Rod-cone independence in the after-flash effect," J. Physiol., <u>176</u>, 1965, 462-472.
- Alpern, M. and Rushton, W.A.H., "The specificity of the cone interaction in the after-flash effect," J. Physiol., 176, 1965, 473-482.
- Barlow, H.B., Fitzhugh, R, and Kuffler, S.W., "Dark adaptation, aboslute threshold, and Purkinje shift in single units of the cat's retina," J. Physiol., 137, 1957, 327-337.
- Barlow, H.B., and Sparrock, J.M.B., "The role of afterimages in dark adaptation," Science, 144, 1964, 1309-1314.
- Bartlett, N.R. "Thresholds as dependent on some energy relations and characteristics of the subject," in Graham, ed., <u>Vision and Visual</u> Perception, New York, Wiley and Sons, 1965, 154-184.
- Brindley, G.S. "2 new properties of foveal afterimages and a photochemical hypothesis to explain them," <u>J. Physiol.</u>, <u>164</u>, 1962, 168-179.
- Brown, J.L. "Afterimages," in Graham, ed., Vision and Visual Perception, New York, Wiley and Sons, 1965, 479-503.
- Day, R.H. "On interocular transfer and the central origin of visual aftereffects," Amer. J. Psychol., 71, 1958, 784-790.
- DeValois, R.L. and Abramov, I. "Color Vision", <u>Annual Review of Psycho-</u> logy, 17, 1966, 337-362.
- Dowling, J.E., and Boycott, B.B. "Organization of the primate retina: electron microscopy," Proc. Royal Soc. B, 166, 1966, 80-111.
- Granit, R. <u>Receptors and Sensory Perception</u>, New Haven, Yale University Press, 1955.
- Judd, D.B. "A quantative investigation of the Puckinje afterimage," Amer. J. Psychol., <u>38</u>, 1927, 507-533.
- Karwoski, T. and Warrener, H. "Studies in the peripheral retina: II. The Purkinje afterimage on the near foveal area of the retina," J. Gen. Psychol., 26, 1942, 129-151
- McDougall, W., "The sensations excited by a single momentary stimulation of the eye," Brit. J. Psychol., 1, 1904, 78-113.
- Ratliff, F., <u>Mach Bands</u>: <u>quantitative studies on neural networks in the</u> retina. San Francisco, Holden, 1965.

- Weve, H. "The colors of afterimages following strong light stimuli," <u>Brit. J. Ophthal.</u>, 9, 1925, 627-638.
- Winer, B.J. <u>Statistical Principles in Experimental Design</u>, New York, McGraw-Hill, 1962.



adaptation condition

FIGURE 1: Duration of the PAI as a function of the adaptation condition

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FIGURE II: Duration of the PAI as a function of the test condition



FIGURE III: Average number of positive phases reported as a function of adaptation condition





TABLE I

	ADAP	Mean for		
Test condition	red goggles	total darkness	ND goggles	test condition
red goggles	1.62	1.67	1.07	1.45
no goggles	5.08	17.15	3.71	8.65
ND goggles	2.93	8.35	1.12	4.13
Mean for Adaptation Condition	3.21	9.06	1.97	4.74

Duration of PAI(seconds) as a function of test and adaptation condition. Each entry is the average for 10 <u>S</u>s in Experiment I

TABLE II

Number of positive phases of the afterimage as a function of test and adaptation conditions. Each entry is the average for 10 Ss in Experiment I.

	, ADAI	Mean for		
Test	red	total	ND	Test
Condition	gogg1es	darkness	goggles	Condition
red goggles	1.0	1.0	1.1	1,03
no goggles	2.3	2.9	1.8	2.33
ND goggles	1.7	2.5	1.2	1.80
Mean for Adaptation Condition	1.67	2.13	1.37	

TABLE III

	ADAF	Mean for		
Test Condition	red	total darkness	ND	Test Condition
red goggles	1.0	1.0	1.1	1.03
no goggles	1.9	1.9	1.7	1.83
ND goggles	1.6	1.7	1.2	1.50
Mean for Adaptation Condition	1.50	1.53	1.33	

Average Number of positive phases of the afterimage as a function of test and adaptation conditions, Experiment I. Each entry is the "modified" average for 10 Ss.

TABLE IV

a) average duration in seconds of the PAI as a function of the adaptation condition in Experiment II. Durations are tabled for all <u>Ss</u>, for those <u>Ss</u> who reported the same number of positive phases in both adaptation conditions, and for <u>Ss</u> who reported a different number of phases in each adaptation condition.

	anadorandoranjananana Mora fa Unitada da Karada	AVERAGE All <u>S</u> s	E DURATION (S Same (9 <u>S</u> s)	SEC) different (<u>65</u> s)
Adaptation Condition	dark	1.46	1.45	1.48
	open	3.40	3.00	4.20

TABLE V

Analysis of variance of the durations of the PAI, Experiment I. Effects of adaptation and test conditions on duration of PAI.

Source of variance	MS	df	<u>s²</u>	F
adaptation (A)	912	2	456	16.9 *
test (T)	878	2	439	19.5 *
subjects (S)	366	9	40.7	
(S ж А)	486	18	27	
(S x T)	401	18	22.2	
(A x T)	370	۷ŀ	92.5	
(ЅхАхТ)	2670	36	74.2	

* p < .001