suggested that the antigonadotrophic effect of the pineal gland was due to an increased synthesis and release of melatonin by the gland (*1*). Whereas this may be true for some species, it does not seem to be true for the hamster, where melatonin treatment had the same effect as pinealectomy. There are several possible explanations for the results. Possibly melatonin inhibited the synthesis or the release, or both, of the true pineal antigonadotrophic factor. Other substances, especially polypeptides, are considered by many workers to be the pineal factors which account for the antigonadotrophic activity of the gland (*10*). Furthermore, several workers have suggested that the indoleamines (including melatonin) within the pineal may be concerned with the release of other substances by the gland (*11*). A second explanation for the present results is that melatonin may have rendered the hypothalamo-pituitary axis resistant to inhibition by the pineal antigonadotrophic factor. Finally, melatonin may be directly stimulatory to the gonads in the hamster. Regardless of the mechanisms involved, the results of this study suggest that melatonin is not the pineal antigonadotrophic factor in the golden hamster.

R. J. REITER, M. K. VAUGHAN
D. E. BLASK, L. Y. JOHNSON
Department of Anatomy, University of Texas Health Science Center at San Antonio, San Antonio 78284

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Rod Origin of Prolonged Afterimages

Abstract. *Afterimages fade against any unchanging background but generally reappear if the background changes suddenly. Under some conditions, however, a change of background color fails to revive a faded afterimage. This happens only if the interchanged backgrounds equally stimulate the rod receptors. It follows that afterimages seen under these conditions are generated by rods.*

After exposure to an intense light, strong enough to bleach most of the visual pigment, an afterimage may be seen for half an hour or more. The appearance of the afterimage depends on the brightness and color of the background against which it is observed. In the dark, or when the eyes are closed, it glows dimly against the dark surround (the positive afterimage); against a uniform bright background it appears dark (the negative afterimage). But an afterimage does not long remain visible against any steady background. Instead, an initially crisp image fades progressively, and totally disappears within a few seconds. After it has faded, any sudden change in background intensity will revive it: dimming the background discloses a positive afterimage; making it brighter creates a negative afterimage (*1*). These afterimages are not generated in the brain but originate within the eye itself. If only one eye is bleached, it is the intensity of the background seen by that eye which determines the appearance of the resulting afterimage, so that once the afterimage has faded, changes of background intensity that are seen only by the unbleached eye are powerless to revive it (*2*). If an eye is bleached while temporarily blinded by pressure on the eyeball, the brain can contain no record of the bleaching exposure, yet an afterimage may appear when the pressure is released (*3*). This afterimage must be generated within the eye.

The normal eye contains two classes of receptor that might generate an afterimage: the cones, which are the receptors of daylight and color vision, and the rods, which permit vision in dim light. After exposure to an intense bleaching light, cones recover their sensitivity in about 5 minutes, rods much more slowly. Rods allow no color discrimination and are relatively insensitive to long-wave light, so that for rods, a dim blue and a bright red may be indistinguishable. We show that after bleaching, once the cones have had time to recover their sensitivity, differently colored backgrounds which are indistinguishable by rods but very different for cones may be interchanged without reviving the afterimage. This afterimage must therefore be generated by rods alone (*4*).

With a 30 second exposure to a white light of 2.2 million trolands we bleached nearly all the visual pigment in a circular region of retina subtending 10° and centered 10° above the line of sight. The observer then directed his gaze at a small red spot near the bottom of a large (21°) red (620 nm) circular field, the "conditioning" background (*5*). The afterimage of the bleaching light appeared as a dark disk in the center of the field, but if fixation was maintained for a few seconds it gradually faded. After it had faded the observer depressed a lever which abruptly replaced the red conditioning background with light of a different wavelength; this substitution usually revived the afterimage. After viewing the afterimage against the substituted background for about half a second, he restored the red conditioning background and allowed the afterimage to fade once again. He then adjusted the intensity of the substituted background light, by means of a graded neutral filter, and again depressed the lever to observe the afterimage against the substituted background at its new intensity. The observer's task was to

find an intensity of the substituted background such that no afterimage at all was visible at the changeover.

During the first few minutes after the bleaching exposure, while cones as well as rods were still insensitive, any change of background color exposed the afterimage, whatever the intensity of the substituted background. But after the lapse of 7 to 8 minutes, when the cones had completely recovered their sensitivity, it became possible to locate a narrow range of intensities which failed to expose the afterimage. Above this range of "interchangeable" background intensities the observer saw a negative afterimage; below it, a positive. The observer made repeated determinations of the range of interchangeable backgrounds, until the afterimage faded irretrievably about 20 minutes after the bleaching exposure. In Fig. 1 the arrowheads show, for each wavelength of the substituted background, the limiting radiances that were interchangeable with the red conditioning background (*6*). Each pair of limits is the average of settings made by a practised observer during recovery from a single bleaching exposure.

These interchangeable backgrounds were in general strikingly different from one another both in color and in brightness. To rods, however, they were indistinguishable. This is established by the correspondence of the interchangeable background radiances with the curve in Fig. 1, which represents lights of equal brightness for rod vision, as defined by the C.I.E. (Commission Internationale de l'Eclairage) scotopic luminosity function. Further evidence that interchangeable backgrounds are equal for rods was obtained by experiments with rare individuals known as rod monochromats (*7*), who are totally color-blind. To a rod monochromat, lights of different wavelength that stimulate the rods equally appear identical. We asked three rod monochromats to make each of the variously colored substituted background lights indistinguishable from the red by suitably adjusting their intensities (*8*). The average radiances chosen by the three rod monochromats at each wavelength (circles in Fig. 1) are close to those chosen by the normal observer as interchangeable with the red standard. Clearly, backgrounds are interchangeable if they are equal for rods.

In the normal eye this conclusion is

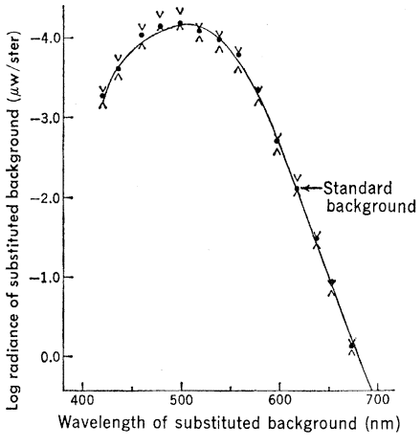

Fig. 1. Radiances of backgrounds interchangeable with a fixed red (620 nm, 7.83×10^{-3} μw/ster or 2.1 trolands). Tips of arrowheads indicate limiting radiances between which no afterimage is exposed (observer M.M.H.). Filled circles show radiances of lights which rod monochromats judged indistinguishable (average of three young observers). The curve represents lights of equal scotopic luminance (C.I.E. V_λ' function).

reinforced by determinations of interchangeable backgrounds at a range of conditioning background intensities (*9*). From the lowest visible radiances, where rods dominate vision, up to about 40 trolands, where cones predominate, the interchangeable radiances vary in proportion to the conditioning radiances, keeping equal to them for rods. Still higher radiances introduce complexities discussed elsewhere (*9*).

Once the cones have fully recovered their sensitivity, then, revival of the afterimage requires a signal from the rods: lights that are equal for the rods but different for the cones may be interchanged without exposing the afterimage. The behavior of the afterimage in these demonstrations may be understood by considering it as a consequence of (i) the reduced sensitivity of the bleached region and (ii) the fading process which allows the bleached region to take on the same appearance as the surrounding unbleached region in the presence of any steady background. After fading, any sudden change of illumination reveals the afterimage because the change is faithfully recorded by the sensitive unbleached retina, and not by the insensitive bleached receptors. The negative afterimage appears when the bleached region fails to record an increase in illumination; the positive afterimage is similarly generated by a decrease in illumination. During the first phase of recovery, both rods and cones are locally insensitive and can generate afterimages. After 7 minutes, the cones have recovered to the same fully dark-adapted sensitivity in the bleached area as in the rest of the retina. Being uniformly sensitive and uniformly stimulated, the cones cannot now create an afterimage, for they cannot signal a distinction between the bleached and unbleached areas (*10*). Only the rods can now revive the afterimage, and they cannot revive it unless they detect the change of background.

DONALD I. A. MACLEOD*
MARY HAYHOE*
Institute of Molecular Biophysics, Florida State University, Tallahassee

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5. It is important to prevent variations in pupil size from affecting the intensity of the retinal stimulus. Our light beams were focused to form images measuring less than 1 mm across at the center of the pupil. Results were unaffected when the pupil was dilated with Mydriacyl.
6. We measured the radiances by using a silicon photodiode (Tektronix J6502) that had been calibrated against a thermopile. Substituted backgrounds of different wavelength were selected by means of spectrophotometrically calibrated interference filters with half-height bandwidths less than 12 nm; the nominal wavelength for each filter is the wavelength whose scotopic luminosity is the same as the integrated scotopic luminosity of the light transmitted by the filter. Although the results of only one normal observer are shown in Fig. 1, we have checked our conclusions by testing three other normal observers at selected wavelengths.
7. Rod monochromats may possess some cones [H. Larsen, *Klin. Monatsbl. Augenheilkd.* **67**, 301 (1921)], but their cones are filled with rod pigment [M. Alpern, H. F. Falls, G. B. Lee, *Am. J. Ophthalmol.* **50**, 996 (1960)].
8. The rod monochromats equated the various lights by interchanging them in the same manner as the normal observer. When the lights were equal for rods, the rod monochromats could not detect the substitution.
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* Present address: Department of Psychology, University of California at San Diego, La Jolla 92037.

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