Rod-Cone Interaction in Human Scotopic Vision

Abstract. *Thresholds of a test flash were measured at various time intervals from onset of a conditioning flash under parafoveal scotopic conditions; rods or cones were selectively stimulated by utilizing either 420- or 680-nanometer light. Rod-cone interaction was indicated because conditioning flash presentation increased test threshold above control level for heterochromatic as well as for homochromatic stimulus pairs. The time course of these t..reshold changes indicates that the rod system has a longer latency than the cone system.*

Several lines of research have dealt with the possibility of rod-cone interaction in the visual system of the primate. Anatomical evidence suggests several pathways that could permit an interaction between rod and cone signals within the retina (*1*); electrophysiological evidence obtained from the monkey has indeed demonstrated such an interaction at the ganglion cell level (*2*).

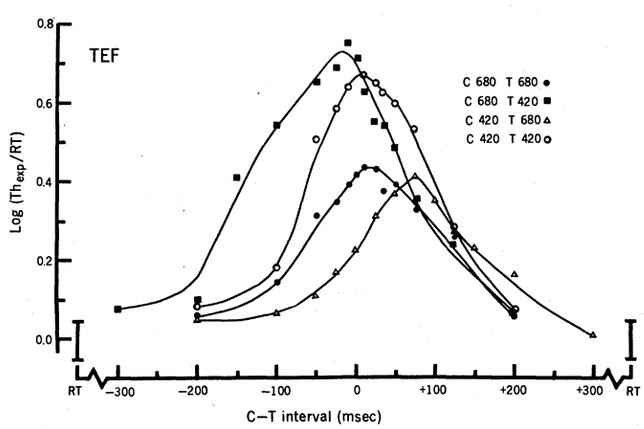
Human psychophysical investigations, however, have yielded conflicting results. In some studies, the apparent color (*3*) of a photopic stimulus changes when a scotopic stimulus is spatially superimposed upon it. In other studies in which either apparent brightness or threshold techniques were used, the results were equivocal (*4*), or they suggested rod-cone *independence* (*5, 6*). In our study, the threshold of a test flash of light was measured at various intervals with respect to the onset of a conditioning flash (*7*); each light flash selectively stimulated either rods or cones because of its wavelength. Regardless of the type of receptor stimulated by either flash, conditioning presentation increased test threshold above control level, thus indicating rod-cone interaction.

By means of a four-channel Maxwellian view optical system (*8*), the two flashes were presented concentrically at 7° in the temporal field of the right eye against a continuously exposed scotopic (4.6 log troland white light) background. The wavelength of the 1°40′-circular, 25-msec conditioning flash was fixed at either 420 or 680 nm by means of an interference filter (Baird-Atomic) with a half bandwidth of 7 to 10 nm. Conditioning flashes were presented at an intensity of 1.0 log units above their threshold value, levels at which the 420-nm stimulus was judged to affect just rods and the 680-nm stimulus to affect primarily cones (*9*). The test flash was a 55′-diameter circular target of 10 msec in duration whose wavelength was fixed at either 420 or 680 nm in order to stimulate, respectively, just rods or cones (*9*).

Our data were collected over approximately 30 experimental sessions, in any of which only one wavelength conditioning, and one wavelength test flash were employed. The observer first adapted to the dark for 25 minutes, and subsequently adapted to the continuously exposed background for 1 minute. According to a predetermined randomization schedule, the conditioning and test flashes were then presented together at a given delay interval, once every 4 seconds (*10*). By pressing a double-throw lever that would either increase or decrease test flash intensity by 0.01 log units, the observer would adjust the flash to a threshold value (for comparison purposes, the observer could "blank out" either test or conditioning flash at will). The experimenter then changed the interval between flashes, and this procedure was repeated. After every second pairing of the two flashes, threshold for the test flash alone was determined as a control, the RT or "resting threshold" condition.

Figures 1 and 2 summarize all the data for observers TEF and MDS, respectively. Test flash threshold is plotted as a function of temporal displacement between flashes (a zero interval indicates simultaneous onset of the two flashes) with both test and conditioning flash wavelength as parameters. For all situations, test flash threshold is expressed as a log ratio of the RT control condition. The RT (indicated with a 95 percent confidence interval) would be the expected threshold level for the test flash if the conditioning flash produced no effect.

When the stimuli are paired homochromatically, threshold begins to rise when test precedes the conditioning flash by 100 msec, reaches a maximum at approximately the +10-msec interval, and then returns to the control value. With 420 nm (rod) test flashes, significantly greater threshold elevations above RT are found than with 680-nm (cone) test flashes. Of greatest interest are the results obtained with heterochromatic stimulation. With the 680-nm test flash and a 420-nm conditioning



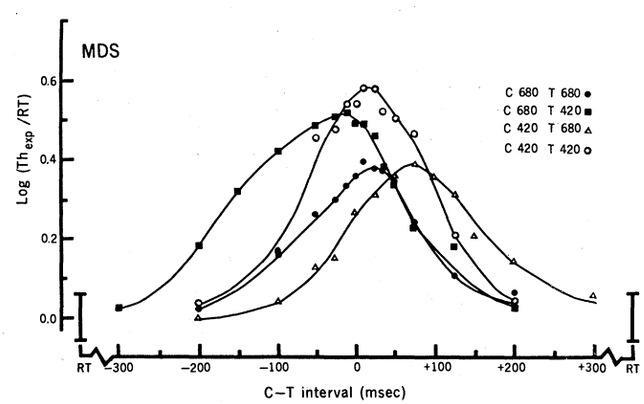


Fig. 1 (left). Test flash threshold (TH) as a function of conditioning-test flash (C-T) interval for observer TEF. Threshold is expressed on ordinate as a log ratio of the RT (resting threshold, test flash alone) condition. The vertical bars indicate 95 percent confidence intervals for RT. The four different curves represent different stimulus wavelength combinations as indicated. Fig. 2 (right). Test flash threshold as a function of conditioning-test flash interval for observer MDS. See legend of Fig. 1.

flash, a function similar to the homochromatic cone function is obtained, except that it shifts to the right, peaking at a much longer time interval. With the 420-nm test flash and a 680-nm conditioning flash, the function shifts to the left of the homochromatic "rod" function, peaking at negative time intervals. In summary then, any of the four wavelength combinations result in significant deviations from the RT condition. To the extent that 420-nm stimuli indeed affect rods and 680-nm stimuli affect cones, the data thus suggest rod-cone interaction.

We might attempt to account for the data in terms of rod-cone independence by assuming that all flashes stimulate both classes of receptors, but that the 680-nm stimuli have a stronger effect upon cones, the 420-nm stimuli upon rods. It would be expected, accordingly, that homochromatic conditions would result in the greatest similarity between receptor populations stimulated by test and conditioning flash and thus would result in the greatest threshold changes. The data are not consonant with such an argument because the primary effect of conditioning wavelength is on the time course and not the magnitude of threshold change (*11*). In consideration of physiological evidence indicating that the rod system has a longer latency than the cone system (*2*), this time shift suggests rod-cone *interaction,* not independence. Let us assume in the present situation that for a fixed wavelength test flash, an interaction between test and conditioning flashes occurs with a definite time course. It would be expected that a cone conditioning flash would produce its effect earlier in time than a rod conditioning flash because of the shorter latency of the cone system. The data in Figs. 1 and 2 are very much in agreement with this conclusion, as are the electrophysiological data obtained at the ganglion cell level (*2*). Whether this interaction between rod and cone stimuli occurs just at the ganglion cell level or at multiple sites within the primate visual system, however, can only be determined by further electrophysiological investigation.

THOMAS E. FRUMKES
MARIAN D. SEKULER
EUGENE H. REISS
Department of Psychology, Queens College of the City University of New York, Flushing 11367

References and Notes

1. S. L. Polyak, *The Retina* (Univ. of Chicago Press, Chicago, 19[illegible] J. E. Dowling and B. B. Boycott, *Proc. Roy. Soc. London, Ser. B* **166**, 80 (1966).
2. P. Gouras and K. Link, *J. Physiol.* **184**, 499 (1966).
3. E. N. Willmer, *ibid.* **111**, 17 (1949); J. J. McCann and J. L. Benton, *J. Opt. Soc. Amer.* **59**, 103 (1969).
4. M. Ikeda and M. Urakubo, *ibid.*, p. 217.
5. M. Alpern, *J. Physiol.* **176**, 462 (1965).
6. G. Westheimer, *ibid.* **206**, 109 (1970).
7. A technique first used to study light adaptation B. H. Crawford, *Proc. Roy. Soc. London, Ser. B* **134**, 283 (1947).
8. T. E. Frumkes and J. F. Sturr, *J. Opt. Soc. Amer.* **58**, 1657 (1968).
9. With 420-nm stimuli, all flashes appeared colorless, were within the rod limb of a long-term dark-adaptation curve, and had much higher thresholds in the foveal than at 7°. With 680-nm stimuli, all flashes appeared red, no rod function was evident with long-term dark adaptation, and the flashes had appreciably lower thresholds in the fovea than at 7°. Increment threshold functions obtained according to the method of W. S. Stiles [*Doc. Ophthalmol.* **3**, 138 (1949)] indicated that within 1 log unit of threshold, 420- and 680-nm stimuli were affecting different receptor populations. With similar adaptation conditions and parafoveal stimulation, Westheimer (*6*) has noted a Stiles-Crawford effect with long wavelength but not with short wavelength stimuli.
10. No measurable long-term light adaptation was produced by conditioning flash stimulation with this recyling rate.
11. We might similarly attempt to account for our data in terms of an interaction between blue cones and red cones. Under situations where rod functioning does not exist (foveal photopic stimulation), an interaction between blue and red monochromatic stimuli has been demonstrated by W. R. Bush [*J. Opt. Soc. Amer.* **45**, 1047 (1955)] and E. J. Rinalducci [*ibid.* **57**, 1270 (1967)]. However, temporal displacements of the sort observed in Figs. 1 and 2 were not observed by these investigators.
12. Supported in part by NIH grant EY00575-07 awarded to W. S. Battersby, by NIH grant 805-FR-07064-05 awarded to Queens College, and by faculty research award 1368 from the City University of New York, and NIH training grant MH-10395.

16 July 1971; revised 22 October 1971

Twins: Early Mental Development

Abstract. *Mental development was appraised periodically for infant twins, and the twins displayed high within-pair concordance for level of mental development during the first and second years. Twins were also concordant for the spurts and lags in development in this period (monozygotic twins more so than dizygotic). From these results it was inferred that infant mental development was primarily determined by the twins' genetic blueprint and that, except in unusual cases, other factors served mainly a supportive function.*

For several years the Louisville Twin Study has recruited newborn twins for participation in a longitudinal study of growth and development. The twins are seen at 3, 6, 9, 12, 18, and 24 months of age, and at each age they are tested with the research version of the Bayley scales of mental and motor development. This report gives the results for the mental scale for 261 pairs of twins (*1*).

Infant mental development is a matter of particular interest in its own right. Infant test scores are essentially unrelated to adult intelligence except in cases of marked retardation, and in fact the correlations are relatively low between tests given at 6-month intervals during early childhood (*2*).

The interpretation of these results is that the functions measured during infancy undergo rapid changes as new capabilities emerge and become fully developed. But the rate of gain is not uniform for all children, and consequently for any particular infant there may be significant changes in relative maturity from one age to the next.

At this point, the test data for twins take on added significance. If the emergence of mental functions depends upon genetically determined growth processes, then the level of mental development attained at each age should be comparable for twins. Further, if these processes alternate between phases of accelerated growth and of drift, then the rate of gain between ages for both twins should be subject to the same spurts and lags. Finally, if gene segregation is a significant factor, then the exact duplication of genotypes for identical twins should make them more concordant than fraternal twins.

The Bayley scale was administered within 1 week of the twins' birthday for ages 3, 6, 9, and 12 months, and within 2 weeks for ages 18 and 24 months. The total sample included 225 white same-sex pairs and 36 white opposite-sex pairs. The number of valid tests actually obtained at each age was affected by missed visits due to illness, occasional substitution of other tests, and so forth, so the sample size is reported separately for each analysis. The mean scores and standard deviations for twins are given in Table 1, along with the comparable singleton means at each age as reported by Bayley (*3*).