induced by DMBA (14) and enhances skin tumor formation induced by benzo(a) pyrene (15). Under other conditions, however, an increased susceptibility to chemical carcinogenesis related to impaired immune states has not been confirmed (16). Poly I  $\cdot$ poly C may be operating by counteracting the immunosuppressive effect of the carcinogen and may generally enhance the ability of the host to exclude antigenically different tumor cells. Poly I • poly C and other polynucleotides may be of use in enhancement of interferon production or immunological capability and may thereby represent a means of investigating the role of these processes in chemical carcinogenesis.

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## **Critical Flicker-Fusion of Solid** and Annular Stimuli

Abstract. Critical flicker-fusion thresholds were measured with both solid disks and annular stimuli. The former subtended 1, 4, and 8 degrees of visual angle, and the latter subtended 4 and 8 degrees. The illuminated region of the 4-degree annulus provided the same area of stimulation as that of the 1degree disk. The illuminated region of the 8-degree annulus provided the same area of stimulation as the 4-degree disk. Annular stimuli significantly reduced critical flicker-fusion thresholds relative to those obtained with disk stimuli of the same area. The effects are not explicable in terms of heterogeneous retinal sensitivity. Laws relating critical flicker-fusion to area seem to be valid only under the restricted condition of homogeneous stimulation.

Studies of the effects of various factors upon the critical flicker-fusion (CFF) threshold are among the most numerous in vision research (1). Thresholds are known to depend upon both the parameters of stimulation and certain characteristics of the organism, such as age, visual adaptation, and integrity of the visual pathways. Among the most reliable CFF relationships are those describing the effects of stimulus intensity, area, and position on the retina. The differential functioning of rods and cones is demonstrable through measurements of CFF thresholds over a range of luminances and positions from fovea to extreme retinal periphery (2, 3). There is also spatial integration in that CFF thresholds are systematically elevated by increases in stimulus area (4). Theoretical statements have been summarized (5).

This study was prompted by a paradox that prevails in studies of the effects of stimulus area upon CFF. Since, with one known exception (6), all such investigations have employed solid circular stimuli, distinctions between effects due to stimulus size and those due to the retinal locus of stimulation have not been clear. The CFF threshold increases as the size of the stimulus is increased, but it decreases as stimuli are positioned further toward the periphery. The former effect is usually attributed either to spatial-summation effects or to the increased probability of stimulating the most sensitive retinal elements (5). The reduction in CFF which attends the displacement of stimuli toward the periphery is generally

explained in terms of the reduced temporal resolving power of rods relative to that of cones (3).

In an attempt to distinguish between the effects of size and those of position, I employed both solid and annular stimuli. The diameters of the disk stimuli subtended 1, 4, and 8 degrees of visual angle while the outer diameters of the annuli subtended 4 and 8 degrees. The stimulating area of the 4-degree annular stimulus was the same as that of the 1-degree disk, and the stimulating area of the 8-degree annulus was the same as that of the 4-degree disk. Luminance was varied over 2.4 log units, the dimmest stimulus being a value that just allowed clear recognition of a constantly presented 1-degree disk after subjects had been adapted to darkness for 5 minutes. Annular stimuli were not visible at this intensity but were visible at a value 0.32 log higher. From the dimmest value (approximately 5 mlam), luminance was increased in log steps of 0.32, 1.0, 1.32, 1.64, and 2.08; that is, a range from 0 to 2.4 log units of intensity. To effect these increases, I used Wratten neutral-tint filters.

Stimuli were presented by a Scientific Prototype Three-Channel tachistoscope, modified to reduce the viewing distance to 14 inches (35 cm). Four subjects, restrained by a chin rest and a forehead support, viewed stimuli. Viewing was monocular and a dim red 0.5-degree patch was constantly present for foveal fixation. Stimuli were presented in 1-second bursts to further restrict fixation.

Thresholds were determined in ascending and descending series of measurements. In the former case, flicker rates were low enough to allow the flicker to be detected easily. Rates were increased from this value by a slow, continuous, and equal reduction in the duration of both the light and the dark components of the light-dark cycle. The light-dark ratio (LDR) on all trials was 1.0. A reverse procedure was employed in descending threshold determinations, beginning with repetition rates well above the fusion threshold and gradually reducing these rates until "flicker" was just detectable. For any given value of luminance and area of stimulus, the threshold was taken as the arithmetic average of two or three ascending and two or three descending threshold measurements. Whether two or three measurements were taken depended upon the variability of judgments to that point. From the beginning to the end of each 1-hour session, luminance was



Fig. 1. Relation between critical flicker-fusion thresholds (CFF) and log intensity. Curves are based upon thresholds averaged across four subjects. The left and right sets of curves are for disk and annular stimuli, respectively. The 4-degree and 8-degree annular stimuli (B) illuminated retinal areas equal to those illuminated by the 1-degree and 4-degree disks (A).

varied from the lowest to the highest value. Stimulus area and stimulus type (disk or annulus) were assigned unsystematically.

Since the functional equivalence of the results is invariant across subjects, Fig. 1 is based upon averaged data from the group. For any condition or subject, no standard deviation exceeded 2 flashes per second, and most were below 1.5 flashes per second. As has been observed, a reliable relation was obtained between CFF and log intensity and, for disk stimuli, between CFF and stimulus area. Increases in luminance or disk area lead to systematic elevations in the fusion point. However, annular stimuli give rise to significant reduction in the fusion threshold relative to results with disks. An annulus subtending an 8-degree perimeter on the retina results in CFF thresholds which are indistinguishable from those obtained with a 1-degree disk, although the area stimulated by the former is many times greater. Equivalent increases in total area produce significantly greater differences in the annular CFF thresholds than in the disk CFF thresholds. Moreover, the curves describing annular effects suggest that increases in luminance beyond the highest employed in this study will not produce commensurate increases in CFF thresholds. In other words, high-frequency attenuation appears to be greater in response to annular than to homogeneous intermittent stimulation.

Roehrig used annular stimuli of 6.9. 17.4, 33.3 and 49.6 degrees (6). He was concerned with the amount of a large area that was effective in determining the relation of CFF to area. Because of the very large stimuli employed in his study, the data warranted his conclusion that vast portions of area do not participate in the determination of the CFF threshold. My study suggests, however, that over a smaller range of areas, marked alternations in CFF will occur in response to relatively small changes in annular size.

Two different, although not necessarily incompatible, explanations have been traditionally offered to account for relations between CFF and area. One of them (7) assumes that the visual (retinal) mechanisms effect a kind of areal integration by which flicker rates exceeding the temporal resolving power of a small population of units can be accommodated by a larger number working in concert. The second explanation avers that the CFF threshold is set by the sensitivity of the most sensitive units stimulated. Thus, on a statistical basis, larger stimuli would be expected to contain a higher likelihood of activating more sensitive elements (8). Neither of these explanations is sufficient to embrace my findings. The first would predict that two stimuli of the same area and falling in approximately the same retinal region would yield approximately the same CFF thresholds. Yet, all stimuli were presented within a region not exceeding 4 degrees from the fovea and, within such a perimeter, CFF thresholds will not vary by more than 5 or 6 flashes per second (9). Despite this, differences between disk and annular CFF thresholds, with stimuli of identical area, were substantially greater than would be predicted. Analogously, since regional fluctuations in sensitivity could not produce differences as great as those obtained, the second traditional explanation is also insufficient. Thus, in light of the present findings, it may be that area and locus, of themselves, are artifactual sources of variation in CFF, or at least artifactual sources of substantial variation. Rather, those transretinal inhibitory influences, elucidated in Limulus (10) and operative in human vision (11) may be operative in the present instance as well. Effects such as those obtained could be produced by the spread of inhibition from a central retinal "OFF" region to peripheral loci of activation. In this respect, my findings may be treated as analogous to phenomena like Mach bands and metacontrast whereby the lateral spread of activity leads to inhibition or enhancement of activity in proximate regions.

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