is more dependent on temperature than the nighttime respiration of the balanced microecosystem. Since daytime respiration is not measurable, its similarity or dissimilarity to nighttime respiration can only be assumed. If one assumes that daytime respiration, unlike nighttime respiration, increases with increase in temperature, then the drop in net photosynthesis at high temperature may be explained as reflecting an increase in daytime respiration. However, if daytime respiration is assumed to be independent of temperature, then the decrease in net photosynthesis at high temperature must be ascribed to some inhibitory effect of high temperature. In any event, the effect is not great, and photosynthesis certainly is not stimulated by increase in temperature. A similar temperature relationship was found by Golueke (*5*) in the net photosynthesis of a planktonic community consisting of *Chlorella, Scenedesmus,* and bacteria.

The results of the present work suggest that the more a system approaches the integration of a balanced ecosystem, the less its respiration is affected by temperature. Such a hypothesis could be readily explained by postulating that within a highly integrated community, where the physiological and geochemical cycles have evolved an almost complete interdependence, the multiplicity of metabolic pathways assures the cyclic flow of energy and material regardless of the temporary closing of one or several pathways by temperature extremes. In a single organism, or in a group of organisms which are less well adapted to each other and to their environment, the fewer pathways may be more easily affected by temperature (*6*).

ROBERT J. BEYERS
Institute of Marine Science,
University of Texas, Port Aransas

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6. This paper is based in part on a dissertation, "The metabolism of twelve aquatic laboratory microecosystems" submitted to the faculty of the University of Texas in partial fulfillment of the requirements for the Ph.D. degree (H. T. Odum, supervising professor). I thank H. T. Odum and A. Phelps for their invaluable assistance. These studies were aided by the National Science Foundation through grants NSF G 3978 and G 13160. I also held an NSF predoctoral fellowship during the period of this investigation.

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Persistent Fear Responses in Rhesus Monkeys to the Optical Stimulus of "Looming"

Abstract. The approach of an object corresponds with a spatiotemporal optical stimulus consisting of a symmetrical expansion of a closed contour in the field of view. The visual equivalent of impending collision was isolated and compared with its sequential inversion. Infant and adult rhesus monkeys manifested persistent avoidance responses to "looming" but not to the inverse. This visual stimulus alone is a strong exciter of avoidance, and the response appears early in life.

The ability to avoid biologically dangerous situations is of ultimate importance to the survival of animals. The avoidance of dangers implies the ability to discriminate between stimuli signifying potential injury and stimuli signifying harmless or beneficial situations. Such stimuli are often optical, and they involve distance perception.

Walk, Gibson, and Tighe (*1*) investigated the "higher-order" visual stimulus reaching the ocular system from a drop-off of the ground—a danger for terrestrial animals. They used a "visual cliff" providing the optical input arising from a falling-off place. Avoidance of the cliff was studied with dark-reared and light-reared rats, and later studies by Gibson and Walk included other animals and human infants (*2*).

Our study is one of a series of cross-species investigations aimed at discovering visual stimuli sufficient for initiating avoidance and escape responses in animals at a given stage of development. The stimuli used are abstractions of those found in a natural environment.

The rapid approach of a solid body is also a natural source of danger for most animals. The optical stimulus arising from the approach of, or approach to, a body indicates an impending collision. One of us (J.G.) has previously proposed that the expansion of a closed contour in the field of view is specific to relative approach (*3*). Symmetrical expansion of any silhouette means a collision course, and when magnification comes to fill the entire 180° frontal field of view, a collision occurs. This optical stimulus may be called "looming." It is hypothesized to be a spatiotemporal stimulus, characterizing *any* case of impending collision with an environmental object. The mathematical properties of this stimulus have been described in recent studies relating to the prediction of time-to-collision by a human observer (*4*).

We have tested the effectiveness of this stimulus with rhesus monkeys, using an apparatus designed to provide the optical equivalent of an impending collision. A silhouette was made to undergo magnification or the reverse. A 25-watt, concentrated-arc, point-source lamp at the end of a 3-foot track projects the shadow of an object moving along the track onto a 6-foot square translucent screen. As the object is moved along the track perpendicular to the screen by an electric motor, the shadow expands or contracts geometrically.

In the particular study we are describing, the shadow was cast by a 1⅛-inch rubber ball. This resulted in a visual experience, for a human observer, of a dark circular object approaching or receding in a large luminous field at a constant high rate of speed. It was clearly a three-dimensional perception (*5*), not an experience in two dimensions. For purposes of control, this could be compared with a simple lightening or darkening of the screen produced by raising or lowering a shutter just in front of the lamp. This did not yield a three-dimensional perception for a human observer. The measured brightness of the unshadowed portion of the screen was 0.85 ft-lam, and the brightness of the shadow was 0.035 ft-lam, a ratio of about 24 : 1. The animal's cage faced the screen at a position 5 feet in front of it, the lamp being 5 feet behind it. The animals were observed from behind curtains on either side of the screen. The room was dimly illuminated.

Twenty-three monkeys, including eight infants 5 to 8 months of age and 15 adolescent or adult animals, were used (*6*). The trials were spaced approximately 45 seconds apart. The stimulus-event was produced only when the animal was facing the screen. Two hidden observers independently judged the animals' behavior as "abrupt retreat," or one of several other categories of response.

The four stimuli used were expansion of circle, contraction of circle, darkening of screen and lightening of screen. The conditions are sequential inversions of each other. The four conditions were given in a counterbalanced order to four animals on successive days, and one order each to the remainder of the animals.

It was found that the observers' judgments were in agreement in 98 percent of the trials. Responses were counted only when there was agreement.

The four stimuli resulted in two

markedly different kinds of response, one avoidant and one not. Six of the eight infants and 13 of the 15 adults withdrew abruptly or "ducked" in response to the stimulus of looming. These responses usually involved the animal's springing or leaping to the rear of the cage, often bumping sharply against the back. In the younger animals, alarm calls sometimes accompanied these responses. Other responses—especially typical of the less active animals—involved a sharp withdrawal of the head and upper part of the body: a "ducking" response akin to the reactions of a baseball player to a "beanball." The failures were probably due to the animal's looking away just at the onset of the temporal stimulus.

The inverse stimulus, that of contraction, led to exploratory responses in 19 of the 23 animals. These involved the animal's remaining at the front of the cage and looking "interestedly" at the contracting circle. In no case did an animal retract, duck, or flinch in response to this stimulus.

Darkening led to a few slight flinching responses, but these were much milder than those observed in the looming condition, and occurred only when the darkening followed a looming trial. This finding suggests that darkening per se is not sufficient to produce a withdrawal response but that it may evoke a partial withdrawal response through learning or sensitization. The condition of lightening produced exploratory responses similar to those observed with the stimulus of contraction.

The infants' behavior did not differ significantly from that of the adults. The fact that the infants responded like the adults indicates that if past experience with collisions is critical in the development of such discriminations, it is operative at a very early age. Combining the responses of all animals, we found that the difference in response to the expansion and contraction conditions was statistically significant ($P < .01$).

Two of the animals tested previously were exposed to a succession of 15 looming trials spaced about 10 seconds apart. No evidence of habituation or extinction was found in this series.

We conclude tentatively that looming is a sufficient stimulus for withdrawal responses in rhesus monkeys. A temporally reversed but otherwise identical stimulus has an entirely different effect, and the component of darkening in the stimulus does not account for its effectiveness. The essential component must be the expansion. Preliminary informal observations indicate that the event remains effective over a range of speeds, the limits of which are yet to be determined, and also that a variety of patterns or forms undergoing expansion are equally effective.

From this series of studies it seems that an abstract optical representation of a rapidly approaching object elicits marked avoidance responses in rhesus monkeys. This visual stimulus ordinarily means a danger in the environment (*7*).

WILLIAM SCHIFF
JAMES A. CAVINESS
JAMES J. GIBSON
Department of Psychology, Cornell University, Ithaca, New York

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Fourier Treatment of Some Experiments in Visual Flicker

Abstract. This report analyzes some experiments in visual flicker recently described by Forsyth and Brown. The assumption that only the first Fourier component of their stimuli is at the flicker threshold, the other components being below threshold, provides a model that accurately predicts their data. Hence, contrary to the conclusions drawn by Forsyth and Brown, no new nonlinear property of the visual system has been demonstrated.

Some interesting experiments in visual flicker were recently reported by Forsyth and Brown (*1*). These authors periodically alternated two trains of rectangular visual stimuli with identical time-average luminances, each with a light-dark ratio of 1.00. Although each train of identical pulses had appeared fused when presented separately, periodic alternation of the two trains resulted in the appearance of flicker for sufficiently great differences between the durations of the pulses in the two trains.

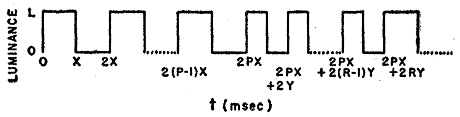

Fig. 1. Stimulus wave form used in the experiments under discussion. Symbols are defined in the text.

Figure 1 shows the stimulus wave form used: t is time, L is the peak luminance of each pulse, X is the duration of a single pulse in the first train of P pulses, Y is the duration of a single pulse in the second train of R pulses, and a cycle, which recurs regularly, is $T = 2PX + 2RY$ seconds long. While critical flicker frequency is normally about 53 cy/sec at the intensity which they used, flicker was observed by their subjects when one of the trains had a repetition rate as high as 500 cy/sec while the second train was set either above 625 cy/sec or below 355 cy/sec. As their main conclusions, Forsyth and Brown state that "changes of temporal pattern, rather than frequency, are responsible" for their results, and that a particular model (*2, 3*) is not adequate to deal with their data.

While the data merit further attention, the conclusions drawn by these authors are incorrect. I shall try to clarify the issues involved and will show that the model referred to does in fact very accurately predict Forsyth and Brown's results.

The model under discussion (*2, 3*) essentially involves the following:

1) Some mathematical theorems which state that any physically realizable repetitive wave form (thus, any repetitive visual stimulus) can be analyzed into an orthogonal set of sinusoidal frequency components by Fourier series techniques. (Hence any interpretation of the data under discussion in terms of changes in stimulus temporal pattern is *not* empirically isolable from its counterpart in the frequency domain.)

2) Experimental results which show that the visual system is differentially sensitive to different frequencies of sinusoidal intensity modulation. This function has been measured by determining the amplitude necessary for the appearance of flicker at different frequencies (*3*).

3) The assumption that each Fourier frequency component of any stimulus wave form may be placed into one of two categories on the basis of its appearance when presented as an individual stimulus against a steady background with luminance $L/2$: it would appear fused or it would appear to flicker. The model was concerned with