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*).

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7. This research was supported in part by contract 401(14) with the Office of Naval Research.

5 March 1962

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.

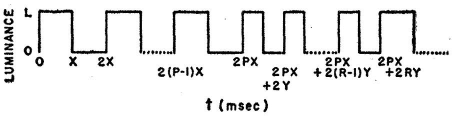

Fig. 1. Stimulus wave form used in the experiments under discussion. Symbols are defined in the text.

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

data in which it was reasonable to expect that at the fusion point for the entire stimulus, each of the Fourier frequencies in the stimulus except the fundamental was varying with an amplitude below the threshold for flicker. Hence, assuming the Talbot-Plateau law to hold, all of these components would appear as a steady brightness whose value is identical to the brightness of a steady light with the same time-average luminance. It will be shown below that this assumption is reasonable in the present case.

In order to relate the data to the model, it is necessary that the stimulus time function, $f(t)$, be Fourier analyzed. The Fourier series expansion of $f(t)$ may be written as:

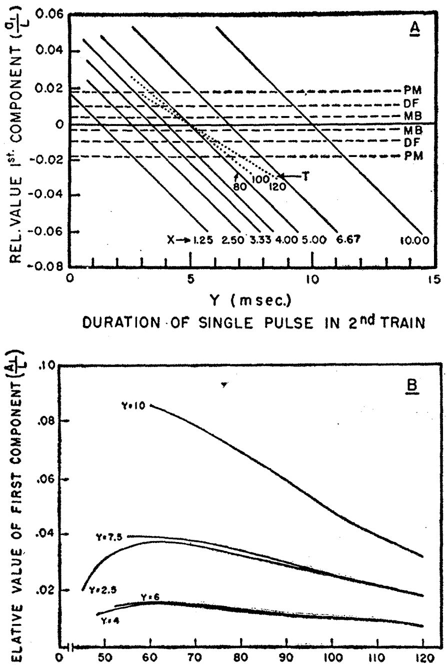

Fig. 2. *A*, Relative value of first Fourier component (f_1=12.5 cy/sec) as a function of duration of a pulse in the second train (Y) when length of first and second trains are equal and length of a cycle is 80 msec (solid lines). The parameter (X) of the family is the duration of a pulse in the first train. The relative amplitude $A_1/L = |a_1|/L$. The dashed lines have ordinate values equal to the predicted amplitude criterion at fusion for each subject. Also shown for X=5 msec (and equal train duration) are single members of the families for T=100 and T=120 msec (dotted lines); together with the solid line for T=80 which intersects them at the point (Y=5, a_1/L=0) these show the change in slope of the families with change in T. *B*, Relative amplitude of the first component (A_1/L) as a function of duration of a single cycle (T) with duration of single pulse in second train (Y) as parameter; X and P are fixed at 5 msec and 4 pulses respectively, and R=(T−40)/Y. Note that T<80 msec was not used in the experiments under discussion.

$$f(t) = \frac{L}{2} + \sum_{n=1}^{\infty}\left[a_n \cos\frac{2\pi nt}{T} + b_n \sin\frac{2\pi nt}{T}\right] \tag{1}$$

in which

$$a_n = \frac{L}{\pi n}\left[\frac{\sin\frac{2\pi nPX}{T}\cos\frac{\pi nX(2P-1)}{T}}{\cos\frac{\pi nX}{T}} + \frac{\sin\frac{2\pi nRY}{T}\cos\frac{\pi n\,[4PX+(2R-1)Y]}{T}}{\cos\frac{\pi nY}{T}}\right] \tag{2}$$

and

$$b_n = \frac{L}{\pi n}\left[\frac{\sin\frac{2\pi nPX}{T}\sin\frac{\pi nX(2P-1)}{T}}{\cos\frac{\pi nX}{T}} + \frac{\sin\frac{2\pi nRY}{T}\sin\frac{\pi n\,[4PX+(2R-1)Y]}{T}}{\cos\frac{\pi nY}{T}}\right] \tag{3}$$

Forsyth and Brown only used values of $P \geqq 3 \leqq R$, and values of $2PX \geqq 40$ msec $\leqq 2RY$; exact values for P and R were not given. The Fourier composition of the stimulus is influenced by these values, as will be shown shortly. However, a simple analysis can be performed which makes exact knowledge of values of P and R unnecessary though nevertheless desirable.

First, consider the case in which $2PX = 2RY$ for each value of X and Y. For this case, $b_1 \equiv 0$, and the amplitude of the first component is

$$A_1 = (a_1^2 + b_1^2)^{\frac{1}{2}} = \left|a_1\right| = \left|\frac{L}{\pi}\left[\tan\frac{\pi X}{T} - \tan\frac{\pi Y}{T}\right]\right| \tag{4}$$

(It might be noted that for this case, $a_n \equiv b_n \equiv 0$ for all even values of n.) If T is fixed also, it is clear from Eq. 4 that a parallel family of curves will result when a_1/L is plotted against Y with X as parameter; further, within the region of present interest the a_1/L values deviate by less than .001 at any point from a linear relationship with Y. In Fig. 2*A* the solid lines represent part of the family that results when T is set at 80 msec. The slope of the linear portion of the a_1/L versus Y function decreases toward zero as T increases, however, as may be seen in Fig. 2*A* where, with X fixed at 5 msec, a_1/L is plotted against Y for T at 100 and 120 msec (dotted lines) as well as for T at 80 msec (solid line); each dotted line is a member of a family such as the set of solid lines.

We now assume that in order for a subject to see flicker the first component must have an amplitude at or greater than some criterion value. This determines a horizontal line in Fig. 2*A* for $X > Y$ which lies at the positive criterion value of a_1/L and cuts each solid line at a point whose abscissa value is the lower limiting Y value for fusion; similarly, for $X < Y$ the horizontal line lies at the negative criterion value of a_1/L and cuts each solid line at a point whose abscissa value is the upper limiting Y value for fusion. If the lower limiting values of Y are plotted against X a straight line results; similarly for the upper limiting Y values. The dashed lines in Fig. 2*A* indicate the criteria for Forsyth and Brown's three subjects (*4*), and each resulting straight line determined by the points at which a dashed line crosses the family is fitted to the data in Fig. 3. When $X = Y$, the first component, f_1, has a frequency of $1/2X$ and an amplitude of $2L/\pi$. The values of percentage ripple ratio (100 times criterion amplitude of first component divided by time-average stimulus luminance) are 0.68, 1.82, and 3.93 for the three subjects. These are close to (although the latter two are slightly higher than) the values at 12.5 cy/sec which de Lange (*3*) found for stimulus intensities that yield ripple ratios of 127 percent for a sinusoid of about 53 cy/sec as does the stimulus used in Forsyth and Brown's experiments when $X = Y$.

The choice of T = 80 msec was determined by the fact that Forsyth and Brown maintained $2PX \geqq 40$ msec $\leqq 2RY$. It is worth noting that if any value of T other than 80 msec was assumed to have been used in the experiments, a different threshold value of a_1/L would have been found; *however, the same predicted curves in Fig. 3 would have resulted.*

In fact, only part of the family for T = 80 msec is shown in Fig. 2*A*. Also, the entire family for T = 80 msec involves only those values of X and Y for which P and R are integers; further, since experimentally $P \geqq 3 \leqq R$, the part of the family in Fig. 2*A* applicable to the data involves only $X \leqq 6\frac{2}{3}$ msec $\geqq Y$. For other values of X and Y a

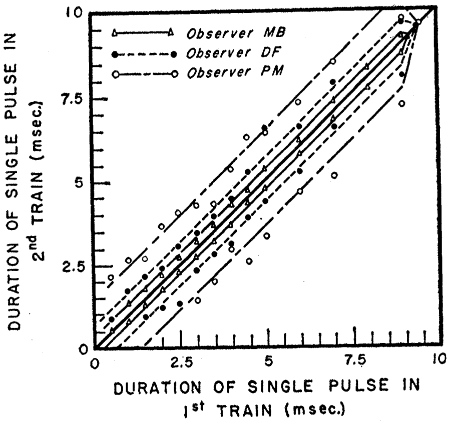

Fig. 3. Duration of a pulse in the second train (Y) as a function of duration of a pulse in first train (X) for fusion. Points represent thresholds from Forsyth and Brown's experiment. Straight lines on both sides of diagonal are predicted values of Y at fusion. (In Forsyth and Brown's report $2X$ and $2Y$ were plotted on the axes.)

rigorous treatment involves exact knowledge of P and R and requires using other families as well. For example, for $X = 8\frac{1}{3}$ msec, the smallest value of $2PX \geqq 40$ msec is 50; hence, the family for $T = 100$ could be used at $X = 8\frac{1}{3}$ msec. As can be determined from Fig. 2A the slope of the a_1/L versus Y function with $T = 100$ is only slightly different than for the $T = 80$ msec family, and if we assumed the same criterion amplitude at $T = 100$ as at $T = 80$, the predicted points would be changed by an amount that is well within the noise level of the present type of experiment. However, as T is changed, $f_1 = 1/T$ is changed, and as shown by de Lange's data (*3*), the criterion amplitude would also be changed. These variations are, however, also not large in the region of present interest. They would introduce only further slight changes in prediction.

We have so far assumed $2PX = 2RY$. Forsyth and Brown's description suggests that they did not deviate widely from this condition. However, briefly consider what happens when $2PX \neq 2RY$. Assuming X and $2PX$ constant (for example, $X = 5$ and $2PX = 40$ msec as in Fig. 2B) we note that for a particular value of $2RY$ larger than 40 msec, A_1/L increases as Y deviates from X in either direction; also, for a particular value of Y, as R increases beyond the region in which $2RY = 40$, A_1/L decreases monotonically. For near-threshold values of Y (for example, 4 and 6 msec in Fig. 2B) this decrease is slow. Nevertheless, deviations from the condition $2PX = 2RY$ could be involved in the small differences between the data and predicted values. Since the experimenters did not use values of $2RY$ smaller than 40 msec, deviations from $2PX = 2RY$ would have resulted in a small systematic bias in the direction of larger differences between Y and X at threshold. Such a bias leads to predictions of higher criterion amplitudes for the first component than were in fact employed by the subject and is very probably the reason that two of the criterion amplitudes inferred above were slightly higher than those reported by de Lange.

The particular interest in Forsyth and Brown's results stems from the appearance of flicker when each of two alternating trains has a repetition rate far above the usual values of critical flicker frequency. The present treatment makes it clear that the observer in this situation discriminates variation of a single low frequency component against a background of high frequency components which are steady as far as the observer's visual system is concerned. While the highest repetition rate used within a single train was 1000 cy/sec, it can be predicted from Eq. 4 and Fig. 2A that there should be no upper limit whatever. For any value of P it should be possible to find small enough values of R so that the first component will be above the flicker threshold; for high P values (greater than 1000 or 2000 cy/sec), however, it is not expected that any values of R larger than P would result in the appearance of flicker.

Some earlier experiments of Brown and Forsyth (*5*) had been analyzed by Levinson (*6*). In these experiments, two trains, each with a single pulse of different duration were alternated and fusion contours plotted for the durations of the two pulses. The case treated in the present report is thus a general case of that situation and reduces to it when $P = R = 1$. While the present type of linear frequency analysis may be expected to hold for any stimulus in which the amplitudes of all but one of the frequency components are sufficiently below threshold, when two or more components are close to threshold it is not certain that simple superposition will be applicable; it has in fact been shown that it does not hold for one such set of conditions (*7*), (*8*).

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Organ Cultures of Newborn Rabbit Skin Affected by Rabbit Papilloma Virus

Abstract. Small fragments of newborn rabbit skin were exposed to papilloma virus and transferred to tissue culture. Control cultures were treated the same way, but without addition of the virus. These cultures were then followed for 4 weeks. During the first ten days, the number of epidermal elements declined gradually in both test and control cultures. From the 10th day on, however, a marked proliferation of the remaining epidermal cells was observed in cultures exposed to the virus, whereas no further changes were noticed in the control cultures.

Dawe and Law infected organ cultures of mouse salivary glands with polyoma virus and noticed a proliferation of the glandular epithelium in the infected cultures (*1*). Lasfargues and colleagues found evidence for the multiplication of the mouse mammary tumor virus in organ cultures of mouse mammary epithelium, but obtained no results with roller tube cultures of pure epithelial cells (*2*). The experiments described in this report (*3*) were designed to investigate the effect of the rabbit papilloma virus (Shope) on organ cultures of rabbit skin.

The skin of 1- to 5-day-old rabbits (*4*) was cut into small fragments about 3 mm^2. The fragments were dipped in a suspension of virus obtained from cell-free extracts from warts of cottontail rabbits (*5*), and previously tested for potency in the skin of domestic rabbits. The skin fragments were placed, keratin side up, in a semisolid medium consisting of medium 199 (*6*) with 0.5 percent