

Flicker Fusion Phenomena

Rapid flicker is attenuated many times over by repeated temporal summation before it is "seen."

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That a flickering light may appear steady if the flicker is sufficiently rapid is common knowledge, and is the basis for the acceptance of most fluorescent lights, motion-picture projectors, and television displays. But just why flicker fuses is, and has been, the subject of a surprisingly large number of investigations over the past 200 years. In recent years Fourier methods of analysis have been applied to the problem (1), with promising success. In this article I attempt, without going into mathematical detail (2), to demonstrate the power of these methods and to show how they have suggested previously unobserved flicker phenomena.

Ives (3) applied Fourier analysis to flicker 45 years ago. In those days the flicker stimulus was often generated by a sectored disk placed before a steady light. Use of this disk together with a little additional optical apparatus produced the result that some area viewed by the subject was alternately bright and dark (an effect hereafter called "on-off flicker" in this article). The experimentally controllable variables were three: the intensity of the steady light; the flicker frequency (dependent on the speed of rotation of the disk); and the ratio of "on" to "off" time (dependent on the ratio of the sizes of the transparent and opaque sectors). Luminance of the viewed target thus was a rectangular function of time—a complicated function for purposes

of analysis. Even from the viewpoint of psychophysics there is at least one parameter more important than any of the above three—namely, the average luminance, for the average luminance determines the viewer's level of adaptation. Ives considered the fluctuating luminance of the stimulus to be separable into various components—one, a steady component consisting of the time-average of the luminance, and the others, a set of sinusoidally varying components. He showed that, for a given average luminance, the fusion frequency for various wave forms depended primarily on the amplitude of the fundamental sinusoidal component of the flicker wave form, for frequencies above about 10 hertz (4). The exact dependence of threshold amplitude on frequency was not thoroughly investigated until deLange (5) succeeded in producing both square and sinusoidal stimulus wave forms at *constant average luminance*.

Sinusoidal luminance modulation is illustrated in Fig. 1. Several means of obtaining this type of luminance control are referred to below. For the present it is sufficient to note that the average luminance, \bar{L} , and the amplitude of the luminance modulation, L_o , were independently controlled. Since negative luminance is an impossibility, L_o cannot exceed \bar{L} . This limit suggests that the amplitude L_o may well be expressed as a fraction or per-

centage of \bar{L} . For a given average luminance \bar{L} , deLange plotted the threshold modulation ratio $L_o:\bar{L}$, as a function of frequency, on logarithmic scales in accordance with engineering practice. A low threshold ratio implies high visual flicker sensitivity, and vice versa. DeLange took flicker sensitivity as the object of primary interest and plotted modulation ratio *increasing downward*, so that high points on the plot would represent high flicker sensitivity and low points would represent low sensitivity. Such curves of visual flicker sensitivity as a function of frequency have come to be known as "deLange curves." Their most important aspect, for the purposes of this discussion, is the extreme steepness with which sensitivity drops for frequencies above 15 hertz. (The reader will find examples of deLange curves toward the end of this article.) In electronics, a circuit which has the property of responding uniformly from direct current to some critical frequency and then losing sensitivity is called a low-pass filter. But the mind is not a radio, and I shall take pains to avoid implying the existence of resistors, capacitors, and so on, anywhere in the visual system. Still, whatever physiological process is envisioned, it must have the properties of a steep-cutoff low-pass filter.

Ives (3) also proposed a photoreceptor process which leads to quite rapid falloff of sensitivity at high frequencies. The proposed process consists of photoionization followed by diffusion of the ions down the length of the receptor to a synaptic region. Even if all the ions are formed instantaneously by a flash, some will reach the synapse ahead of others. With flicker, the spread in delay of arrival of the ions leads to "smoothing" of this ionic response to the stimulus wave form. The response wave form rises and falls nearly sinusoidally around an average value. This average value equals the

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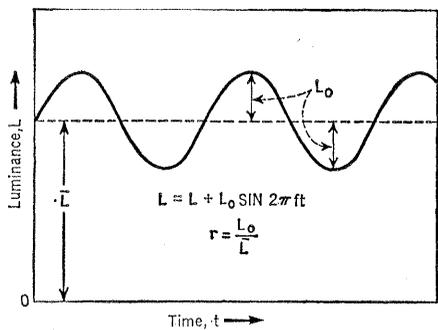


Fig. 1. Sinusoidal luminance modulation. See text for explanation of the symbols.

response to the average of the stimulus luminance. The amplitude of the sinusoidal component of the response falls rapidly with frequency above 15 hertz or so, while the average value of the response remains independent of frequency. The diffusion model, then, leads directly to the required high-frequency behavior of flicker sensitivity. It also makes clear the relatedness of steep high-frequency cutoff, near-sinusoidal response, and temporal dispersion of the response to a short flash.

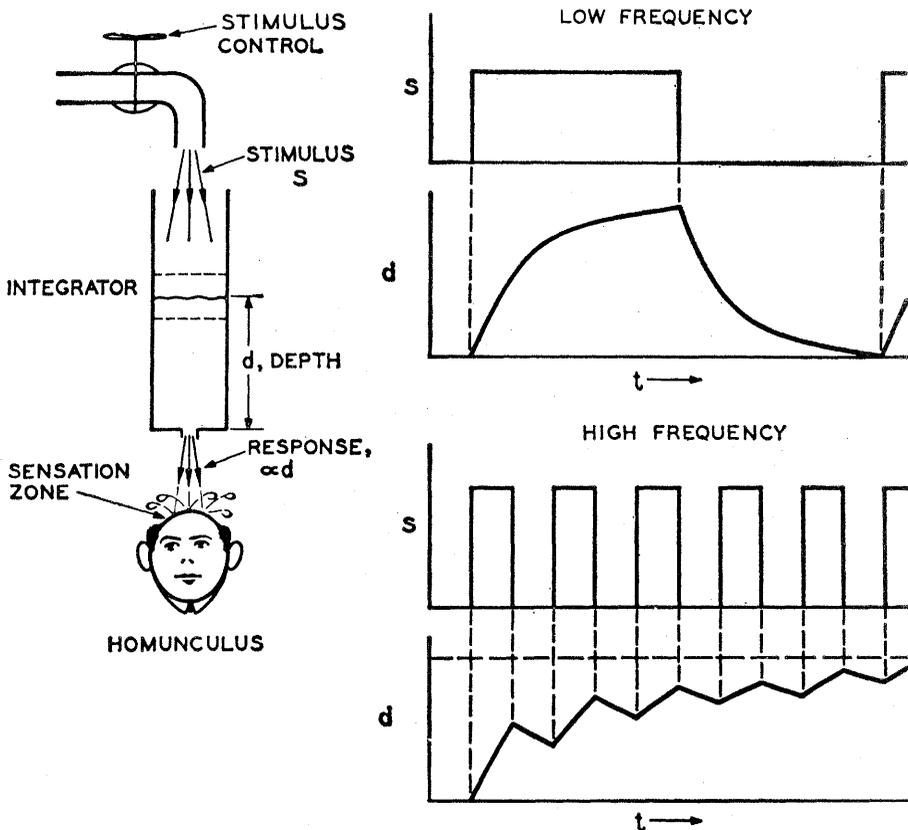


Fig. 2. Temporal integration and its effect on frequency sensitivity. Stimulus intensity s and depth d correspond to luminance L and photoproduct concentration P in the text. The accumulated depth, d , depends both on s and on the leakage, which in turn depends on d . The "homunculus," blind to the stimulus itself, senses only the leakage in response to the depth d . Thus a graph of the depth is an indication of what is "seen."

Nevertheless, Ives's work was largely ignored for over 30 years. Hecht and Verrijp (6) proposed a photochemical basis for flicker fusion 10 years after publication of Ives's work. Apparently they were dissatisfied with photoionization as a basis for a model. At constant average luminance and high frequencies their model, unlike Ives's, predicts flicker sensitivity to be inversely proportional to frequency, as pointed out by deLange (5). Sensitivity drops much more rapidly than that. It is not clear why anyone should take lightly the relation between flicker sensitivity and frequency, at constant average luminance, but Hecht was by no means the last to do so. Studies are still published in which flicker sensitivity as a function of various wave forms is carefully measured. But the frequency and amplitude of the fundamental component (let alone higher harmonics) are ignored. The result is confusion (see 7).

The relation between flicker sensitivity and frequency has a central place in the rest of this article. On the basis of this relation, and of an assumed

model, several predictions have been made and tested experimentally. Some readers will find the experiments more interesting than the rationale. They are invited to skip the discussion of the model and proceed at once to the section on psychophysical tests of the model. However, I doubt that much understanding can be gained without considering the model, if not before, then at least after, consideration of the tests.

A Model

In avoiding a purely mathematical discussion (8), a model is useful. Mindful of the fate of Ives's proposal, I shall use a clearly irrelevant but, I hope, entertaining model, to emphasize the fact that no specific physiological process is implied—ionic, electronic, enzymatic, or whatever. Only the temporal behavior of some unknown product in the visual system is relevant. Just where the process occurs is also unimportant, but it may most readily be imagined to be a receptor process. If one chooses to think of the model as applicable to more central locales, then it is important to remember that interactions between visual channels which represent different elements of visual space are ignored.

Suppose, then, that light falling on a retinal receptor causes a product to accumulate, in the manner of the water accumulating in the cylinder of Fig. 2. Photoproduct concentration responds by controlling subsequent sensation, just as the depth of the water determines the sensation of the homunculus. Of course, photoproduct must decay as well as accumulate, or the world would indeed "get brighter all the time"; the analog to decay is a leak in the water cylinder. No assumption need be made as to how the accumulated photoproduct is sensed, but the sensation must increase with increase in photoproduct. In the analog, for the sake of diagrammatic simplicity, we consider the leakage response and sensation to be combined, taking advantage of the fact that leakage rate must also increase with increase in depth. The homunculus senses only the depth of the water, in effect, and is "blind" to the faucet itself, just as we see only via our visual systems.

The concreteness of the model of Fig. 2 may help generate an intuitive grasp of the time course of visual re-

sponse. More explicitly, the rate of increase of photoproduct concentration

$$dP/dt = aL - f(P), \quad (1)$$

where a is a constant, L is the stimulus luminance, and $f(P)$ is the photoproduct decay term, a function about which we need only the assumption that it increases with increasing P (9, 10). For a suddenly applied, then steady, L , the term dP/dt will be high at first (equal to aL) and then will decrease to zero as $f(P)$ approaches aL , as in the low-frequency curves of Fig. 2. The concentration, P , will therefore rise rapidly from zero, then level off. When the light is turned off,

$$dP/dt = -f(P) \quad (2)$$

applies, giving the decay curve in the "off" interval.

In general, P lags behind the changes in L . For high-frequency flicker turned on at $t = 0$ (Fig. 2, lower right), P follows a time course which fluctuates around the values corresponding to the turning on of the average of the luminance, \bar{L} , at $t = 0$. Given enough time ["enough" being determined by the loss function $f(P)$], the ultimate value of P will be given approximately by

$$f(\bar{P}) = a\bar{L}. \quad (3)$$

The small change in P around \bar{P} in a short interval, Δt , is found from Eq. 1 by considering L as made up of two parts—its average, \bar{L} , and the momentary departure from \bar{L} , ΔL :

$$\begin{aligned} \Delta P &= \int_0^{\Delta t} [a(\bar{L} + \Delta L) - f(P)] dt \\ &\approx a \int_0^{\Delta t} \Delta L dt \end{aligned} \quad (4)$$

Here we have taken

$$a\bar{L} - f(P) \ll a\Delta L.$$

In the short time Δt , P cannot have changed much from \bar{P} , to which Eq. 3 applies.

Equations 3 and 4 are rich in psychophysical meaning. At least four points may be noted.

1) Averages and changes are treated separately. For psychophysics this means that average luminance and fluctuation in luminance should be treated as two separate variables. This is contrary to the traditional procedure in flicker fusion studies, in which, for example, on-off flicker is presented at

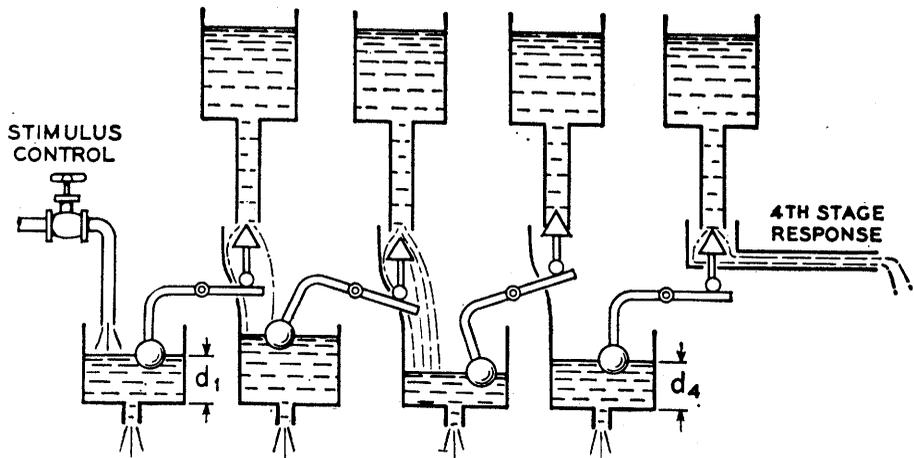


Fig. 3. A hydraulic system in which the response depends on four successive stages of "leaky" integration. Here leakage is not used as the response, as it is in Fig. 2; the depth in each stage controls the flow from a hypothetical infinite reservoir of some material. High frequency fluctuations in the fourth output are reduced as the fourth power of the frequency.

various "on" luminance levels, average and change thus being varied together. Adaptation, being slow, is determined by the average luminance. The effect is that each fusion frequency is found at a different adaptation level. But there is an additional infinity of possible fusion frequencies at any one adaptation level, corresponding to the infinity of possible values of ΔL between 0 and 100 percent of \bar{L} . The dependence of flicker sensitivity on frequency, without change of adaptation level, should be investigated first. Once that dependence is understood, it may be reasonable to go on to study the dependence on adaptation level. Certainly it is more difficult to attempt to study the dependence on both simultaneously. It was deLange who first designed a systematic experiment in which the separability of \bar{L} and ΔL was taken into account (5).

2) The transient events connected with the onset of stimulation have been deliberately set aside in making the assumption that the visual response, P , has more or less reached its stable value, \bar{P} . Experiments must be designed accordingly—that is, designed either to reveal transient effects or to reveal behavior in a more-or-less stable state, without confounding the two.

3) Eq. 4 also implies low-pass filtering, for, if ΔL alternates between two fixed values, say $\pm L_0$, around a maintained \bar{L} , then

$$\Delta P \approx \pm aL_0 \Delta t.$$

[This corresponds to the ultimate condition of the response (Fig. 2, lower

right, curve d).] Since ΔP is proportional to Δt , it is inversely proportional to the frequency, $1/2\Delta t$. Thus, the amplitude of the response, ΔP , or the sensitivity on the accumulator model, drops as frequency rises, for sufficiently high frequencies.

4) The corollary of point 3 is that the model of Fig. 2 is inconsistent with Ives's and deLange's results. Sensitivity drops much more rapidly with frequency than the model implies.

The failure of the "hydraulic" model is easily corrected, not by discarding the model but by applying it several times in succession. In Fig. 3 the hydraulic analogy is retained to show how the response of the first stage might control the input to the second, and so on, through four stages. A high-frequency square-wave stimulus leads to a triangular wave input to the second stage, as discussed above, with amplitude inversely proportional to the frequency. The output of the second stage has a curvilinear wave form, with amplitude inversely proportional to the square of the frequency, and so on. After the fourth stage the output is essentially sinusoidal and drops in amplitude with the fourth power of the frequency. There is little point in deriving, here, the mathematical bases for these assertions; they follow directly from successive applications of Eq. 4, with the output from the previous stage substituted for ΔL . Of course there are more elegant ways of deriving the results, but they do not differ in principle from repeated integration.

Psychophysical evidence suggests

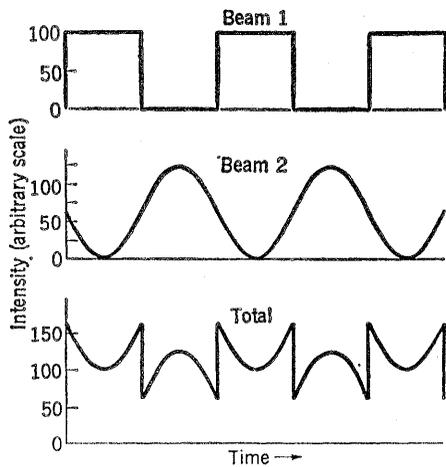


Fig. 4. Removal of the fundamental component of a square wave by means of two beams of light (12). If the frequency is 10 hertz or higher the flicker disappears, provided the amplitude and phase of the two flickers are precisely related.

(11) that the total number of stages of integration in the human visual system may be as high as ten. Since each stage merely increases the slope of the sensitivity-frequency curve, the evidence gives no information as to the nature of the stages; that is, it is impossible to tell whether the attenuation of sensitivity is due to peripheral or to central processes. However, Fuortes and Hodgkin (10) have found it necessary to assume ten stages in a model, similar to the one described, for the time-behavior of the receptors in *Limulus*. It may be that all the attenuation is retinal, but this possi-

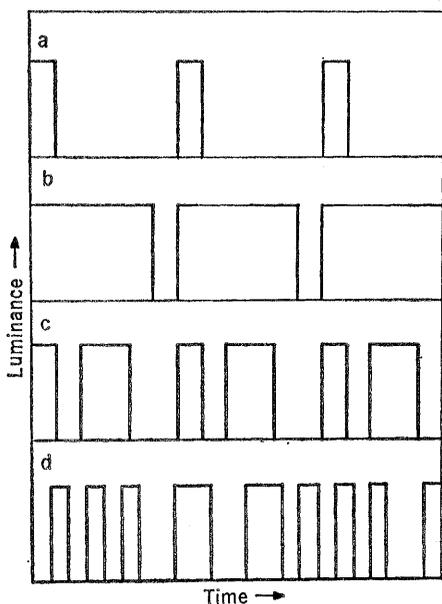


Fig. 5. Some flicker wave forms in which the fundamental component has been shown to determine flicker visibility (13).

bility is more likely to be verifiable by physiological than by psychophysical experiments.

Psychophysical experiments have been used to test the model in several ways, some of which are described below.

Psychophysical Tests of the Model

The n -stage model seems to predict that at high frequencies we see a sinusoidal wave form regardless of the stimulus wave form. This is readily understood in terms of Fourier harmonics. The steepness of the high-frequency cutoff of sensitivity weights the lowest-frequency or fundamental component most heavily. If this is indeed the case it should be possible to cancel out a square-wave stimulus by a sinusoidal one, as seen in Fig. 4.

Given the means of generating the wave forms shown (12), and of superposing them, it then becomes a matter of adjusting their relative amplitude and phase. As expected, the flicker disappears most completely when square waves and sine waves are exactly in opposite phase (as shown) and the amplitude of the sine wave is 1.27 (± 0.01) times that of the square wave. The ratio 1.27 is significant: the Fourier (sinusoidal) fundamental component of a square wave has, itself, $4/\pi$ (that is, 1.273) times the amplitude of the square wave. Thus the prediction that only the fundamental sinusoid is seen is borne out with an accuracy of 1 percent. Similar corroboration is obtained simply by comparing the threshold amplitudes of sine wave and square wave (5), but the precision of the comparison is lower than that of the null method described above.

The "percept" (or "sensation," or response) in rapid on-off flicker is that of the fundamental sinusoidal component. This statement has been verified repeatedly within the last several years, yet it seems to bear repeating. Figure 5 shows some of the wave forms which have been used. Unfortunately, the calculation of the amplitude of the fundamental was usually carried out subsequently by someone other than the experimenter (13). The data points needed for the most critical check of the calculations were therefore not always available. The result is that although 1-percent accuracy of verification was attainable in the case of the square wave, such accuracy was not

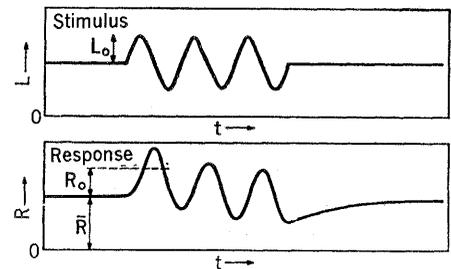


Fig. 6. (Top) Short-term sinusoidal modulation of otherwise steady light. L_0 is the amplitude of the sinusoid. (Bottom) Response of a low-pass filter consisting of a "leaky" integrative stage. R_0 is the amplitude of the sinusoidal component.

attainable for the wave forms of Fig. 5. The experiments have been reviewed by Brown (14). These remarks on the sinusoidal nature of the response are sufficient for the purposes of this discussion. It may be worth repeating that the response at frequencies below 10 hertz or so reproduces the stimulus wave form more faithfully than the response at higher frequencies—that is, the first few harmonics, as well as the fundamental, play a role.

The model predicts other phenomena besides the significance of the Fourier fundamental. Consider a light whose luminance can be varied as in Fig. 6 (top)—that is, kept steady until sinusoidal modulation of the luminance is turned on. For convenience, only three cycles are shown. In practice, modulation was turned on and off about once every 2 seconds. Suppose the frequency is well above that at which fusion occurs. Will the viewer see any change in brightness?

A "flash" is seen at the onset of modulation and at its termination, even though the modulation frequency is as high as 600 hertz! The two "pseudo-flashes" appear very much alike. What is being seen at these high frequencies? Consideration of the behavior of even a single stage of integration of the type pictured in Fig. 2 indicates the nature of the signal generated in the visual system. The response is shown schematically in Fig. 6 (bottom). If the luminance L has been steady for some time prior to modulation, the accumulated photoproduct P (corresponding to depth, d , of water in Fig. 2) will have reached an equilibrium value. When modulation is applied as shown, L rises and so also must P . The situation is best described by Eq. 4; that is, photoproduct increases while ΔL is positive, all through the first positive half-cycle. During the second half-

cycle L is below its average (or steady) value and P decreases, finally returning to approximately \bar{P} at the end of the full cycle. P will have been above \bar{P} throughout the cycle.

Thus, with the onset of modulation, P jumps to a new average value. However, the stimulus continues to oscillate about the same average, \bar{L} , and there still is a decay term, $f(P)$, now greater than $f(\bar{P})$. In time, the average will drop to its former value—that is, after a number of modulation cycles. While the sinusoidal fluctuations in P may be too fast for the rest of the visual system, the transient change in average value will last long enough to be seen. Additional stages reduce the slow transient response of the first stage less than they reduce its response to the modulation frequency. Figure 7 shows the response at each of four successive stages, simulated in terms of electricity rather than hydraulics. An electrical circuit whose behavior is an exact analog of Eq. 1 can be built much more readily than the hydraulic contraption of Fig. 2. It consists of a resistor and a capacitor. Voltage across the capacitor is the analog of photo-product concentration P , and is readily displayed on an oscilloscope and photographed. The record of the last stage (only four are shown in Fig. 7) represents “what is seen” at the onset and offset of high-frequency modulation. Note that this effect could hardly have been observed had the light been off altogether until flicker began, since the change from dark to light would swamp the pseudoflash.

Pseudoflashes at the onset (and termination) of modulation have been studied in detail. The experimental evidence corroborates the model.

Pseudoflashes look alike near threshold whether modulation begins on the increasing or on the decreasing phase, and whether modulation begins or ends. The low-pass filter model alone cannot account for the similarity, and it would be a digression to discuss how the sign of a flash may be lost. G. Sperling (15) has noted that brief increments and decrements in target luminance look alike, and are frequently confused.

Yet positive and negative pseudoflashes can be distinguished—and even measured, as follows. If a real flash from an additional source is added at the time of onset of modulation it is found that its intensity can be adjusted to cancel out the observed pseudo-

flash. This is possible only if modulation begins in the decreasing phase. Similarly, if the real flash is timed to coincide with the end of modulation, it can be adjusted to cancel out the termination pseudoflash only if modulation ends on the termination of a negative half-cycle. Thus, the sign of the pseudoflash can be determined, and, for those cases where cancellation can be obtained, the intensity of the pseudoflash can be measured in terms of the intensity of the canceling real flash.

What is the relationship between the threshold modulation amplitude, L_o , for flicker and for pseudoflashes? Figure 8 presents a typical answer. The flicker threshold curve (circles) is a “deLange curve” (5); modulation amplitude L_o is plotted as a percentage, r , of the average luminance \bar{L} . Values along the ordinate give r on a logarithmic

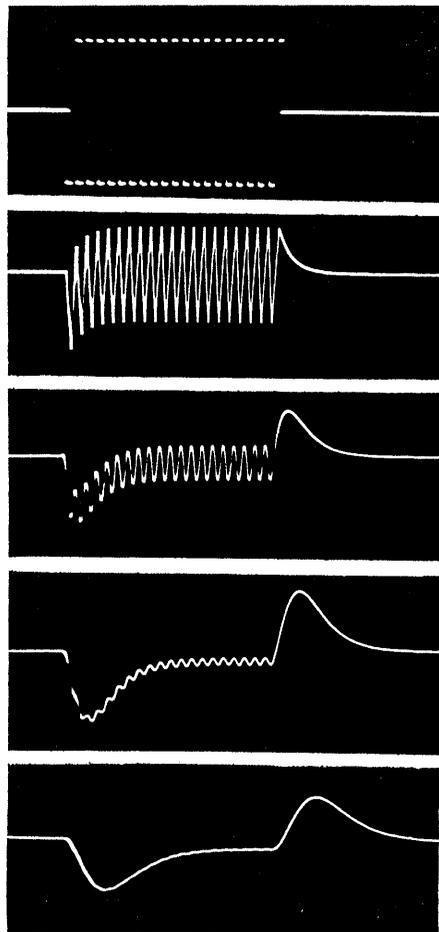


Fig. 7. Responses of each of the four stages of an electronic low-pass filter. The short-term input square wave, onset downward, is shown at the top; the responses are shown in succession, reading downward. Relative to the “onset” and “offset” transients, the response to the high-frequency modulation itself rapidly disappears.

mic scale, increasing downward, so that the height of the ordinate may represent visual sensitivity. Values along the abscissa represent frequency, also on a logarithmic scale. In this instance the modulation was sinusoidal, as in Fig. 6, but continuous. The curve is similar to those obtained by deLange (5) and Kelly (7). When modulation is begun abruptly, as in Fig. 6, the threshold modulation amplitude for the onset pseudoflash is proportional to frequency (Fig. 8, squares).

These curves may be compared with the expected behavior of a model of n stages of “leaky” integration, as pictured in Fig. 3. Equation 4 is applied to each stage. The product P of one stage is taken as the stimulus, L , for the next stage. Then for $\Delta L = L_o \sin 2\pi ft$ in the first instance, the amplitude of the final sinusoidal response is

$$R = k L_o [1 + (2\pi f\tau)^2]^{-n/2}. \quad (5)$$

Here, f is the modulation frequency, t is time, k is an overall proportionality constant, and τ is an exponential decay time constant, assumed to be the same for each stage. Equation 5 is a more exact form of the statement, made above, that visual response falls off as the n th power of flicker frequency. It is more exact in that the equation holds for an n -stage low-pass filter down to low frequencies.

In order to compare Eq. 5 with the experimental results, the assumption is made that at threshold the value of R is always the same. If this particular response is labeled R_T , Eq. 5 may be rewritten to show the expected relation between the ratio r and the frequency f :

$$r = \frac{R_T}{kL} [1 + (2\pi f\tau)^2]^{n/2}.$$

Here k and R_T , being internal unobservable quantities, may be absorbed along with the constant average luminance \bar{L} into a single constant K :

$$r = K[1 + (2\pi f\tau)^2]^{n/2} \quad (6)$$

Comparison of Eq. 6 with the deLange curve of Fig. 8 (r , it should be remembered, increases downward) shows a critical departure at low frequencies. In Eq. 6 the decrease of r with decreasing f is essentially monotonic, whereas the experimental curve has a peak near 10 hertz. This discrepancy at low frequencies is to be expected. There is no dearth of psychophysical evidence (16) of inhibitory interaction

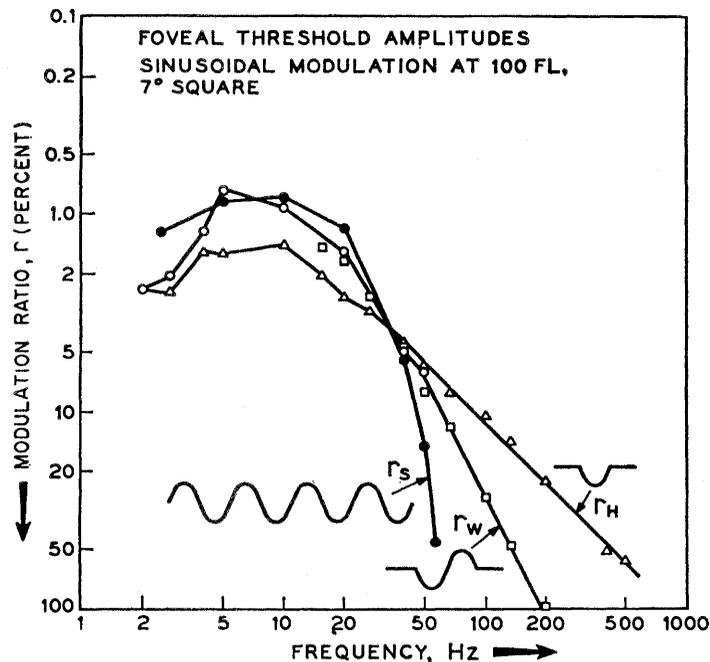
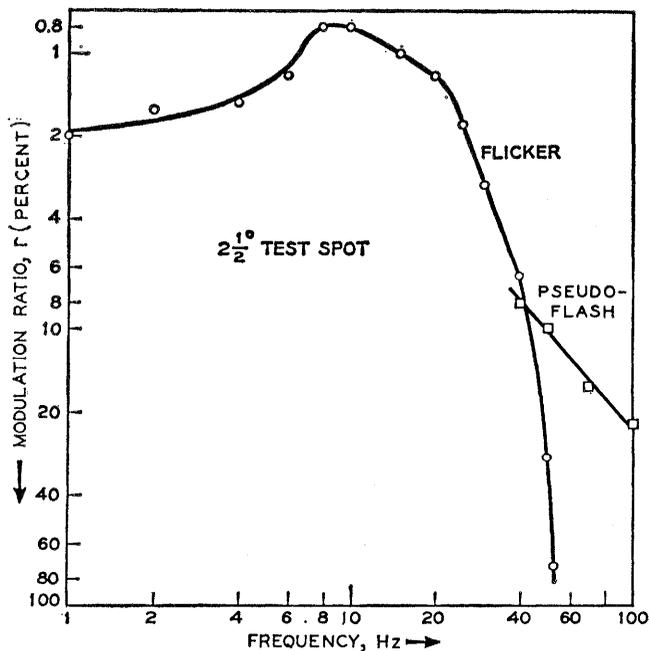


Fig. 8 (left). Modulation amplitude thresholds for continuous flicker and for pseudoflashes at onset of modulation. Values on the ordinate are the ratio, r , of modulation amplitude, L_o , to the average luminance, \bar{L} . Fig. 9 (right). Modulation amplitude thresholds for continuous flicker (r_s), for half-sinusoids (r_H), and for whole sinusoids (r_w).

between spatially adjacent visual channels (whether at the receptor level or at the level of more central processes). Further, Fuortes and Hodgkin (10) have found strong loss of sensitivity within a receptor of *Limulus* with increase of output. Both the spatial interaction and the intrareceptor effects are most marked at low frequencies. Thus our model may represent only a single channel of the visual system, and that only at high frequencies.

At high frequencies, Eq. 6 becomes

$$r = K(2\pi f\tau)^n,$$

which, on a logarithmic plot, is a straight line of slope n . Most deLange curves approach linearity at high frequencies. The linear slopes set lower bounds on n . Values as high as 10 have been estimated (11), but the accuracy is poor, since only the last two experimental points are generally usable. Points representing results obtained at lower frequencies may be contaminated by the effect of the low-frequency inhibition mentioned above. It would be desirable to have an independent measure of n , one precise enough to show whether it is indeed an integer and a constant one, as the model assumes. This is a difficult problem, not yet solved to my knowledge.

At any rate, it seems that experimental results will bear most closely on theory if they are obtained with stimuli

of the highest possible frequency. Pseudoflashes have been seen at frequencies up to 600 hertz. Let us consider them a little further. The n -stage model implies that, when f is high enough, the threshold pseudoflash modulation amplitude r_p is

$$r_p = K\sqrt{2\pi(n-1)} \cdot 2\pi f\tau. \quad (7)$$

The 45-degree slope and linearity of the pseudoflash data in Fig. 8 indicate that the frequencies are probably high enough for the theory to be applicable. However, it is not possible to see the pseudoflashes when visible flicker is present, so the data stop where the curves cross. It would be valuable to pursue this curve into the lower-frequency region.

Theory helps here, in that the threshold for a real flash consisting of a single half-sinusoid, r_H , is predicted to occur at half the threshold amplitude for a pseudoflash; that is,

$$r_H = K\sqrt{2\pi(n-1)} \cdot \pi f\tau. \quad (8)$$

Our experimental results seem to give the ratio r_p/r_H as 1.95:1 rather than 2:1, but the departure is within the limits of experimental error. Perception of a half-sinusoid is not confused by flicker, since there is none, so experimental values for r_H were measured at frequencies down to 2 hertz. They are shown in Fig. 9. The deLange

curve for continuous sinusoidal modulation, labeled r_s , is included for reference. The proportionality of r_H and f is again clear. In fact, the linear part of the r_H curve may be drawn with a straight edge held at 45 degrees to the axes, and shifted to fit the data. This relation is known as Bloch's law of temporal summation.

Figure 9 is the experimental answer to the question of the relative visibility of continuous flicker and pseudoflashes. The thresholds for pseudoflashes may be found by multiplying those for half-sinusoids, r_H , by 2, unless one doubts the theoretical relationship. There is, in fact, very little to be learned from pseudoflashes that cannot more readily be learned from half-sinusoids.

Two interesting aspects of the r_H curve should be mentioned, although detailed discussion would be a digression.

1) Use of the r_H curve should be compared with other techniques of obtaining what is called the "critical duration." In experiments on critical duration a "square" decrement or increment of luminance is used rather than a sinusoidal one. The 45-degree slope between decrement amplitude and duration is found, of course, just as in Fig. 9 (duration and frequency being reciprocally related, one is the negative of the other on a logarithmic scale). But the low-frequency (long-

duration) data differ. I suggest that the differences bear on the rather interesting question of just how temporal changes in luminance are detected. Probably neither square nor sinusoidal modulation is most revealing. There should be an optimum decrement or increment wave form, related to what is known as the impulse response of the visual system. A search for this may be rewarding.

2) At low frequencies r_H is approximately twice r_S (a relationship not to be confused with the 2:1 ratio of r_p to r_H). This relationship, too, should bear strongly on the nature of luminance-change detection, but is also outside the scope of the low-pass filter model.

Finally, theory also predicts that at high frequencies for a single *whole* sinusoid the threshold modulation amplitude

$$r_w = \frac{(n-1)^{n/2}}{\sqrt{2\pi}(\sqrt{n-1})^{n-2} \exp\sqrt{n-1}} (2\pi f\tau)^2 \quad (9)$$

Thus the r_w curve should have a slope of 2. A straight line of this slope has been drawn among the high-frequency data points, with adequate fit. If we divide the two sides of Eq. 9 by corresponding sides of Eq. 8, the unobservables in K , including the threshold criterion R_T , drop out, and we obtain

$$\frac{r_w}{r_H} = \frac{(n-1)^{(n-1)/2}}{(\sqrt{n-1})^{n-2} \exp\sqrt{n-1}} 2 \frac{f_w^2 \tau}{f_H}$$

where f_w and f_H are the frequencies at which r_w and r_H are determined. This suggests a measurement which is independent of the subject's threshold criterion. A particularly simple technique would be to set r_w and r_H both at 127 percent—that is, to use square waves (and so come full circle, so to speak) and find the corresponding f_w and f_H . The ratio

$$\frac{f_H}{f_w^2} = \frac{2(n-1)^{(n-1)/2} \tau}{(\sqrt{n-1})^{n-2} \exp\sqrt{n-1}} \quad (10)$$

is a characteristic time proportional to τ . If the coefficient in n may be assumed constant, then differences in the ratio (Eq. 10) represent differences in τ . This measurement seems independent of threshold criterion. Differences between subjects and under various experimental conditions must represent real differences in speed of response. This statement seems to be true for any model which displays the required low-pass behavior (8). Other models

might require other functions of n and τ in Eqs. 8 and 9, but the roles of R_T and f need not be affected. Thus, the time f_H/f_w^2 represents an inherent property of the visual system. It has the advantage over the flicker fusion frequency of an on-off square wave of being independent of the subject's threshold criterion. As a characteristic time it is superior to critical duration, which suffers from difficulties of definition, whereas f_H/f_w^2 is unambiguous and very precisely measurable.

Comments

Much of this article is concerned with a multistage linear low-pass filter. This is not necessarily to imply that physiologists must expect to find n successive processes underlying the temporal properties of vision. That even a one-stage statistical model can lead to the same results has been shown (17). Also, diffusion of photoproduct from a point of origin to a point of detection is a process which displays similar attenuation properties, as was long ago pointed out by Ives (3). At this speculative stage in our investigations, diffusion seems an unlikely process because of the losses it entails, whereas receptors seem capable of responding to single photons with considerable amplification of energy. To discriminate between diffusion and other processes, additional information, such as phase-delay information, would be helpful. Phase delays are best measured physiologically, not psychophysically.

These basically different alternatives are mentioned, not to exhaust the subject, but to open it. Other possibilities have been suggested by Jones, Green and Pinter (18), by Troelstra (19), and by DeVoe (20). A somewhat different approach, based on the idea that visual inputs are summated periodically, as in the exposures of a motion-picture camera (21), has unfortunately not been elaborated and examined for relevance to the experiments described here. This "psychological moment" approach would seem to require a 45-degree slope of the deLange curves in the high-frequency region, and would be ruled out on this basis. On the other hand, there is no apparent reason why it should not apply to low-frequency phenomena—those "passed" by the low-pass filter.

Another approach which seems rele-

vant to low- but not high-frequency flicker is that of Bartley (22), also discussed by Brown (14). This theory is concerned with neural "on" and "off" responses to flicker. As such, it strongly implies a cycle-by-cycle response process and would seem to be incapable of predicting pseudoflashes. On the other hand, it may be successful in accounting for such effects as the low-frequency portion of the r_H and r_S curves.

The low-frequency portion of the r_w curve is also of interest in this connection. At frequencies near 10 hertz the thresholds for an indefinite number of sinusoids and for a single sinusoid are apparently equal. A cycle-by-cycle theory might work here.

Approaches based on the assumed involvement of central processes may very well bear on the "flicker detector," which can only "see" what the low-pass filter has passed on. They may also help explain why the sign of a pseudoflash cannot be directly perceived.

The physiologically derived model of Fuortes and Hodgkin (10) is also applicable to the low-frequency region. The Fuortes-Hodgkin model makes a of Eq. 1 (applicable to ten stages) a function of the final response of the low-pass filter. At low frequencies the response is sensitive enough to the stimulus wave form so that a cannot be considered constant. In this situation Fourier methods are a poor approximation—the system is "nonlinear"—and numerical computation is required to solve the differential equations. So far as I know, the differential equations have not been solved for such data as those of Fig. 9.

There are thus many relevant possibilities for use of low-frequency data, and several types of low-pass filter model for the high frequencies are still in the running.

The temporal phenomena which result from the limited time resolution of the visual system have their analogs in the spatial domain, owing to the limited resolving power of the eye. The equivalent of the deLange curves has been found (23), and indeed Fourier methods are widely accepted in optics generally (24). The analog of pseudoflashes has also been found, somewhat indirectly (25). No one has yet measured the spatial analog of the suggested characteristic time of Eq. 10. Its relation to the spatial impulse response function should be of some interest.

Summary

The high-frequency temporal behavior of the human visual system has been shown to have some of the properties of a linear low-pass filter. For such a system it is appropriate to consider a repetitive stimulus as having separable Fourier harmonic components. The direct-current component or average luminance is important in that it sets the adaptation level. It is therefore convenient to keep it constant when varying other stimulus parameters, such as frequency or wave form. Of the alternating-current components, only the fundamental is important at high frequencies, the higher harmonics being relatively more attenuated.

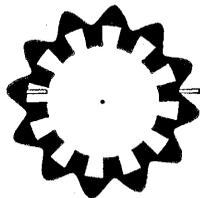
Any linear low-pass filter system responds in a predictable way to sinusoidal stimulation, whether continuous or of short duration. In the case of the visual system, predictable behavior is found at high frequencies, and it leads to discovery of hitherto unobserved pseudoflash and real flash phenomena. Measurement of a new characteristic time is suggested.

At low frequencies the use of half- and whole-sinusoidal flashes leads to the discovery of some interesting relations with flicker thresholds, but these remain for future discussion.

References and Notes

1. For a thorough and lucid review of flicker studies up to 1963 see J. L. Brown, in *Vision and Visual Perception*, C. H. Graham, Ed. (Wiley, New York, 1965), pp. 251-320.
2. A concise, readable summary is that of R. D. Stuart, *An Introduction to Fourier Analysis* (Wiley, New York, 1961).
3. H. E. Ives, *J. Opt. Soc. Amer.* **6**, 343 (1922).
4. P. W. Cobb, *ibid.* **24**, 91 (1934). Cobb qualified Ives's work in two ways, although he definitely supported the main ideas: (i) he pointed out that the fundamental alone does not determine fusion at low frequencies; (ii) he offered a modification of Ives's hypothetical model of the visual process. These qualifications have been taken by some as an invalidation of Ives's results generally.

5. H. deLange, *Dzn.*, *ibid.* **48**, 777 (1958); *ibid.* **51**, 415 (1961). Those seeking deLange's name in the index of *J. Opt. Soc. Amer.* will find it under "Dzn." Unfortunately the Dutch equivalent of our "Jr." is not well known in the United States. In Holland, one writes the abbreviation in three letters, "zn" for "zohn," preceded by the father's initial. I suspect that Dr. deLange has enjoyed his unlikely designation too much to correct it himself. I hope he will forgive my meddling: several requests for clarification have been directed to me.
6. S. Hecht and C. D. Verrijp, *J. Gen. Physiol.* **17**, 266 (1933).
7. D. H. Kelly, *J. Opt. Soc. Amer.* **51**, 422 (1961); *ibid.*, p. 747; *ibid.*, p. 917.
8. J. Z. Levinson, in preparation.
9. Both Ives and Hecht took a to be dependent on P . In this article only small variations in P are considered. Variations in a are neglected. For a recent study in which the dependence of a on P is taken into account, see Fuortes and Hodgkin (10).
10. M. G. F. Fuortes and A. L. Hodgkin, *J. Physiol. London* **172**, 239 (1964).
11. J. Levinson, *Science* **130**, 919 (1959); ——— and L. D. Harmon, *Kybernetik* **1**, 107 (1961); F. W. Campbell and J. G. Robson, *Doc. Ophthalmol.* **18**, 83 (1964).
12. A word about the generation of complex light wave forms. Electronic means are the most precise and versatile. Either simple or composite wave forms may be produced on a single light source; this obviates the need to mix, or match, separate sources. Circuits for use with an oscilloscope have been described by van der Gon, Strackee, and van der Tweel in *Phys. Med. Biol.* **3**, 164 (1958). For a discussion of fluorescent tubes, see G. Sperling, *J. Opt. Soc. Amer.* **55**, 541 (1965). H. S. McDonald described glow modulator circuits in a talk reported in *J. Opt. Soc. Amer.* **50**, 1138 (1960). Where electronic circuits are not available, an episotister may be used. Various wave forms may be generated by passing a beam of light of elongated cross section through an appropriate sector disk. The cross section may be obtained by focusing the image of a strip filament lamp on the disk. The disk may be of plexiglass, and have an appropriate pattern painted on the annulus. Sometimes two such patterns are combined on one disk, as shown below.
13. Forms a and b of Fig. 5, first dealt with by H. E. Ives [*J. Opt. Soc. Amer.* **6**, 254 (1922); *ibid.*, p. 343] were again studied by S. H. Bartley and J. M. Nelson [*ibid.* **50**, 241 (1960); *ibid.* **51**, 41, (1961)]. The results were analyzed by D. H. Kelly [*ibid.* **51**, 917 (1961)]. These wave forms illustrate on-off flicker with different ratios of "on" to "off" times but the same fundamental frequency. The illustrated instance is a special case, in that the amplitude of the fundamental component is the same in both a and b ; however, the average luminances differ. Wave form c was studied by C. R. Brown and D. M. Forsyth [*Science* **129**, 390 (1959)] and analyzed by Levinson [*ibid.* **130**, 919 (1959)]. It may be described as alternating fast and slow cycles of square on-off flicker. However, such a description misses the point: the fundamental cycle now includes both cycles. There is therefore a component of considerable amplitude at the frequency at which the composite wave form repeats itself. Wave form d was also studied by Forsyth and Brown [*ibid.* **134**, 612 (1961)]. Here several successive fast cycles alternate with several slow ones. Again, this establishes a fundamental cycle length equal to the total time between two identical sequences. In this instance, one "wave" includes three short on-off cycles and two long ones. The analysis was provided independently by Kelly and by Levinson for Forsyth and Brown [*ibid.* **135**, 794 (1962)] and was also given by L. Matin [*ibid.* **136**, 983 (1962)]. In every case, flicker threshold was determined primarily by the fundamental component.
14. J. L. Brown, in *Vision and Visual Perception*, C. H. Graham, Ed. (Wiley, New York, 1965).
15. G. Sperling, private communication.
16. D. H. Kelly, *Doc. Ophthalmol.* **18**, 16 (1964); J. Levinson, *ibid.*, p. 36; F. W. Campbell and D. G. Green, *J. Physiol.* **181**, 576 (1965); F. Ratliff, *Mach Bands* (Holden-Day, San Francisco, 1965).
17. J. Levinson, *J. Opt. Soc. Amer.* **56**, 95 (1966).
18. R. W. Jones, D. G. Green, R. B. Pinter, *Federation Proc.* **21**, 97 (1962).
19. A. Troelstra, *Non-linear Systems Analysis in Electroretinography* (Institute for Perception RVO-TNO, Soesterberg, Netherlands, 1964).
20. R. D. DeVoe, private communication.
21. C. T. White, *Psychol. Monographs* **77**, No. 575 (1963).
22. S. H. Bartley, *J. Exp. Psychol.* **21**, 678 (1937).
23. D. G. Green and F. W. Campbell, *J. Opt. Soc. Amer.* **55**, 1154 (1965).
24. E. H. Linfoot, *Fourier Methods in Optical Image Evaluation* (Focal Press, New York, 1964).
25. J. Palka, *Science* **149**, 551 (1965); H. B. Barlow, *ibid.*, p. 553.
26. I am indebted to my colleagues B. Julesz, L. D. Harmon, J. Krauskopf, L. S. Frishkopf, R. R. Capranica, G. Sperling, and D. H. Kelly for critical discussions. Mrs. A. B. Brown was a patient and persevering subject. J. Kohut and C. F. Matke were of inestimable help with the apparatus.



The rectangles show where each of the beams passes through its annulus. Opposed placement of the beams makes it possible to change the relative phase of the two wave forms by moving the disk up or down with respect to the fixed beams. To this end, the