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Flicker Brightness Enhancement and Visual Nonlinearity*

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The purpose of this study was to investigate the nonlinear mechanism underlying brightness enhancement, in which a flickering stimulus appears brighter than a steady stimulus of equal mean luminance. The flickering and matching stimuli were temporally alternated. Both were cosine windowed to minimize the potential effects of temporal transients. Subjects adjusted the amplitude of the matching stimulus to match it in brightness to the flickering stimulus. The temporal frequency, modulation, and waveform of the flickering stimulus were varied. With sinusoidal flicker, brightness enhancement increased with increasing modulation at all frequencies, peaking at about 16 Hz at full modulation. The results were modeled by a broad temporal filter followed by a single accelerating nonlinearity. The derived temporal sensitivity of the early filter inferred from brightness enhancement decreased more slowly at high frequencies than the filter(s) inferred from flicker modulation thresholds. With low frequency sawtooth flicker, brightness enhancement was phase-dependent at low, but not at high modulations, suggesting that multiple neural mechanisms may also be involved in addition to an early nonlinearity. Copyright © 1996 Elsevier Science Ltd.

Brightness enhancement Flicker threshold Temporal characteristics Nonlinearity Sandwich model

INTRODUCTION

Flickering lights appear brighter than steady lights of equal mean luminance (Brücke, 1864; Bartley, 1938, 1951, 1961; Bartley *et al.*, 1957; Bleck & Craig, 1965; Ball & Bartley, 1966; Horst & Muis, 1969; Nilsson, 1972), an effect named brightness enhancement or the Brücke–Bartley effect. The existence of brightness enhancement requires a nonlinearity somewhere in the visual system, but this nonlinearity has not been fully characterized. The presence of a nonlinearity can be used to investigate stages of visual processing prior to the nonlinearity (Burton, 1973; Makous, 1987; Burns *et al.*, 1992). In the present study, we exploited the nonlinearity leading to brightness enhancement to investigate early temporal processing. Specifically, we measured the apparent brightness of flickering lights that varied in modulation, temporal frequency, and temporal waveform. We then analyzed the brightness results using a "sandwich" model (Spekreijse & Reits, 1982), in which there is a nonlinear stage sandwiched between two linear filters. To the extent that the model applies, the filter properties of the first linear stage can be deduced. As an example, consider the use of stimuli that generate distortion products of a fixed frequency. Such products must be generated at the nonlinearity, and, being fixed, must sustain constant attenuation by all subsequent stages. This approach has been used previously to study spatial vision (Burton, 1973; Williams, 1985; MacLeod *et al.*, 1992), temporal vision (MacLeod, 1991; Burns *et al.*, 1992; MacLeod & He, 1993; Hammett & Smith, 1994), and color vision (Stockman & MacLeod, 1986; Stockman *et al.*, 1993; Chang *et al.*, 1993). We now adopt a similar approach to analyze suprathreshold brightness enhancement.

To test whether the early temporal filter deduced from brightness enhancement is consistent with threshold estimates of the temporal sensitivity of the visual system, we also measured flicker modulation thresholds under the same conditions in the present study. Flicker threshold responses have been extensively studied, both within the framework of linear systems analysis (e.g. Levinson, 1966; Kelly, 1969, 1971; Veringa, 1970; Rashbass, 1976; Tyler & Hamer, 1990), and within the framework of parallel visual pathways (Mandler & Makous, 1984; Hess & Snowden, 1992; Hammett & Smith, 1992; Qi *et al.*, 1993). However, brightness enhancement as a nonlinear and suprathreshold phenomenon has not been similarly analyzed, and it is not known whether single or multiple pathways are involved in this effect.

The present study uses a sandwich model consisting of a single pathway (see General Discussion) to characterize the linear filtering characteristics of the visual system

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prior to brightness enhancement. We then compare the filtering characteristics inferred from brightness enhancement to the filtering characteristics derived from the measurement of flicker thresholds. The comparison of the filter estimates allows us to make inferences concerning the relative sequence in visual processing of the two processes, since cascading filters (except for compensation or differentiation) increase the slope of high frequency attenuation (Levinson, 1968; Kelly *et al.*, 1976). While temporal sensitivity determined from psychophysical measurements of flicker detection thresholds falls off rapidly at high temporal frequencies (DeLange, 1958; Kelly, 1961), the derived sensitivity based on measurements from the outer retina falls off more slowly (Baron & Boynton, 1975; Baron, 1977; Kelly *et al.*, 1976; Burns *et al.*, 1990; Toi & Riva, 1994), suggesting that there is at least one additional stage of high-frequency attenuation after the photoreceptors or outer retina that reduces psychophysical sensitivity. If the mechanism responsible for brightness enhancement occurs distal to such an additional stage in visual processing, then the high-frequency slope of the linear filter derived from brightness enhancement should be shallower than that derived from threshold measures.

An additional issue in such a comparison is that, according to Brindley's classification (Brindley, 1960), flicker thresholds and brightness belong to different classes of observations. Flicker thresholds are essentially Class A observations, in that at threshold different flickering stimuli are indistinguishable. Brightness matches, on the other hand, are Class B observations, since flickering stimuli of equal apparent brightness may remain distinguishable based on other visual attributes. Hence one may argue that the two measures are not comparable without an explicit linking hypothesis. In performing the brightness matches we assume that the observer abstracts the brightness attribute of the stimulus and the matching standard, while ignoring other perceptual attributes such as flicker. Our model describes this abstraction process (see Results and model). We also report control conditions in which we tested separately the observer's ability to use brightness as opposed to flicker information (see General Discussion).

The present study consisted of two experiments. In Experiment 1 we measured the brightness of sinusoidally flickering stimuli of various temporal frequencies and modulation depths by matching them to a raised luminance cosine. In applying the sandwich model, we assumed that an initial linear filter is followed by a static nonlinearity of an accelerating nature to account for brightness enhancement. The use of sinusoidal stimuli simplifies the analysis, since the initial linear stage of filtering passes such stimuli without any waveform distortion, and permits a simple characterization of the nonlinear response to variations in stimulus modulation. Previous studies of brightness enhancement typically employed fully modulated rectangular flicker as the stimulus, which contains higher frequency harmonic components that may have contributed to brightness. As brightness enhancement must involve a nonlinearity, both the magnitudes and phases of the harmonic components in the rectangular stimulus may affect brightness in an unknown manner. Consequently, responses to such a complex stimulus do not easily lend themselves to analysis. With the aid of the sandwich model and the results of Experiment 1, however, responses to complex stimuli, such as sawtooth flicker, can be qualitatively predicted. In Experiment 2 we tested such a prediction against the brightness enhancement results obtained with the sawtooth flicker.

METHODS

Subjects

The four authors served as subjects. Complete sets of data were obtained from three subjects (SW, SB, and AR), all had corrected normal vision, with no evidence of ocular disease. The fourth author (AE) is a high myope, whose confirmatory data were similar to SW and SB, indicating that the differences among subjects did not arise from the degree of myopia causing a change in retinal area across subjects.

Apparatus

The stimuli were generated in a Maxwellian-view optical system with a 594 nm He–Ne laser as the light source. This wavelength is within the region of minimum chromatic brightness (i.e. the brightness associated with saturated hues: see Burns *et al.*, 1982), and minimum flicker-induced hue shifts (Nilsson, 1972). The laser beam illuminated a rapidly rotating motor shaft coated with a diffuser to eliminate speckle (Burns *et al.*, 1991). The stimulus field was 10 deg in diameter, with the central 2 deg blocked to reduce spatial inhomogeneity in flicker perception, as shown in Fig. 1(left). Within the annulus the stimulus field was spatially uniform; outside it the field was dark. The temporal profile of the annulus is shown in Fig. 1(right). The mean retinal illuminance of the flickering light was 4.25 log td.

The temporal modulation of the stimulus was controlled by a programmable function generator (Qua-Tech) with a 12 bit D/A converter and a multiplier. The output of the multiplier was converted by a voltage controlled oscillator to a pulse frequency that drove the acousto-optic modulator. Each pulse was 2 μsec in duration. The mean luminance was set such that average pulse frequency was ~100 kHz. Thus at a modulation of 0.99 the minimum pulse rate during a waveform was ~1 kHz. The final light output was linearly related to the input over a 1000:1 range.

Stimuli and procedures

Brightness Matching to a Raised Cosine. In this study we employed a temporal comparison paradigm, since pilot studies indicated that side-by-side comparison of the flicker and the matching stimuli did not provide stable measures of brightness. Not only did flicker induction strongly affect the matching field, but subjects also

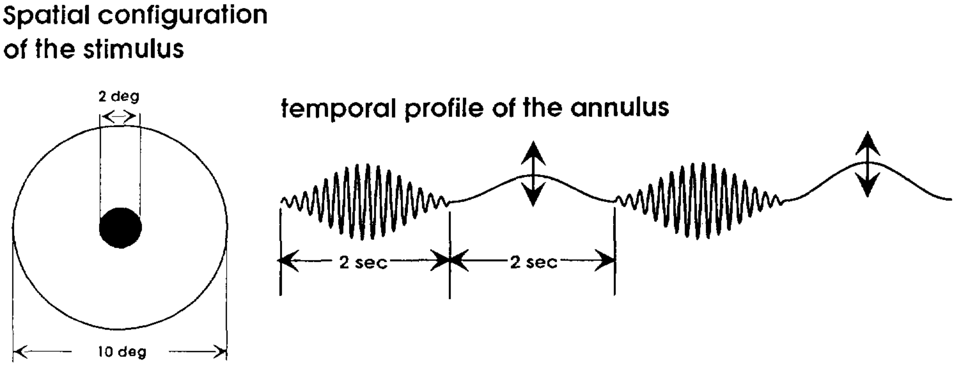

FIGURE 1. Schematic diagram of the spatial (left) and temporal configurations (right) of the stimuli. The field size was 10 deg in diameter, with the central 2 deg blocked. The test and matching stimuli were temporally alternated. The test stimuli were sine-wave (or sawtooth, in Experiment 2) flicker, windowed by a raised cosine of 2 sec duration. The matching stimulus was the raised cosine alone, also of 2 sec duration, and its peak amplitude was controlled by the subject. The two intervals were continuously alternated until the subject indicated a match.

tended to move their eyes back and forth between the two fields, making the adaptation state unstable.

With the temporal comparison paradigm, the subject was instructed to fixate the dark center of the field. The flicker and the matching stimuli were alternated in the annulus. The temporal waveform of the flicker was either sine-wave (for Experiment 1) or sawtooth (for Experiment 2). The modulation of the flicker was multiplied by a raised cosine, centered in the stimulus interval of 2 sec period (interval 1). The mean luminance of the flicker stimulus remained constant at 4.25 log td. In the 2 sec matching period (interval 2), a raised luminance cosine (the matching stimulus), similarly centered in this interval, was added to the mean luminance and the amplitude of the cosine was separately controlled by the position of an adjustable pot*. The matching stimulus was allowed to increase or decrease around the mean luminance level; thus a negative cosine was possible if a flicker-induced darkening occurred in the other interval. The two intervals were alternated with no temporal separation between them, and the whole 4 sec cycle was repeated continuously. In pilot experiments we found that the 2 sec period for flicker presentation was important, because the perception of brightness varies with time. If it is too short (e.g. 1 sec, which we attempted), brightness enhancement does not stabilize, especially for low frequency stimuli. If it is too long, the perceived brightness of the flicker is variable, presumably because of slow adaptation or changes in criterion. In addition, if one does not window the stimuli, but alternates them abruptly, transient effects prevent a stable brightness percept (Smith, 1970). The specific timing we adopted for our paradigm was found to yield reliable measures of brightness across sessions for a wide range of stimulus frequencies and modulations in the preliminary tests. However the pilot results were generally consistent with the findings described below, except for being more variable (see Design below).

For Experiment 1, we used flicker frequencies of 6, 12, 16, 20, 24, 28, 32, 36, and 40 Hz. The modulations were 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 0.99 (nominally, 1.0). Within each session, we ran one or two frequencies, with all modulations of the same frequency blocked together to avoid cross-frequency interactions (see below). The 11 modulations for each frequency were randomly ordered within the session. The subject's task was to adjust the luminance amplitude of the matching stimulus until the brightness of the two intervals appeared identical, at which point he/she pressed a button to have the value recorded. Five consecutive matches were made for each condition. The subject adapted to each new modulation for 20–30 sec before making the five matches. When there were two frequencies in one session, the subject also adapted to the new frequency for at least 30 sec when the frequency was changed. For each subject, brightness measurements at each frequency were determined in at least three separate sessions, on different days and with different sequences of modulations. The results for each condition were then averaged.

Metric for Brightness Enhancement. In this study brightness enhancement was defined in relative terms as:

$$\text{Brightness enhancement} = (L_c - L_f)/L_f \qquad (1)$$

where L_c is the peak luminance of the matching stimulus (interval 2), and L_f is the mean luminance of the flicker (interval 1), which was always 4.25 log td. Brightness enhancement is a positive value when the flickering light appears brighter than the mean luminance, i.e. the subject requires $L_c > L_f$ for a match, and is zero when the flickering light appears to have the same brightness as the mean luminance, i.e. when L_c equals L_f.

Brightness enhancement might also be defined relative to the overall mean which includes the amplitude of the matching stimulus, since this could contribute to the average adaptation state. Thus, at the match the average

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*Pilot data were also collected using a nulling paradigm, varying either the depth of a luminance decrement superimposed on a fixed modulation flicker, or the modulation of the flickering stimulus required to null a fixed luminance decrement. Neither of these attempts produced results as reproducible as those from the method described above.

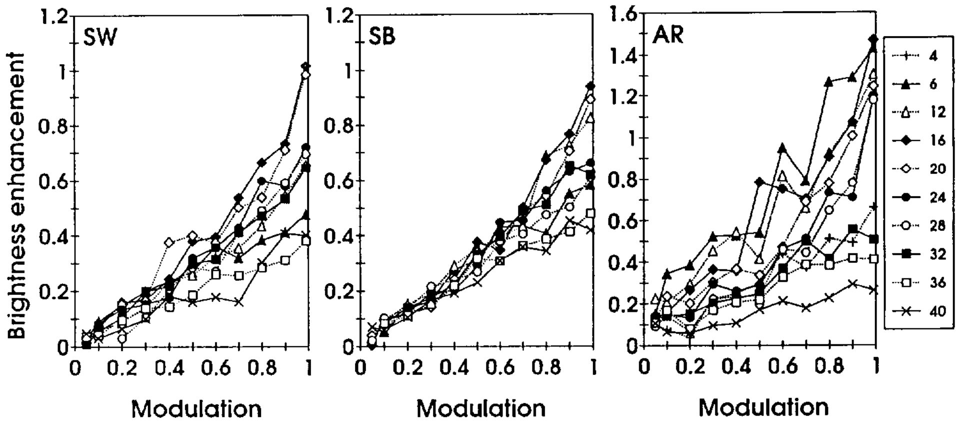

FIGURE 2. Brightness enhancement as a function of modulation depth of the flickering stimuli for a series of different temporal frequencies. Brightness enhancement was defined as $(L_c - L_f)/L_f$, where L_c is the peak luminance of the matching stimulus, and L_f is the mean luminance of the flicker (4.25 log td). SW, SB and AR are the three main subjects.

adaptation state can be characterized by $(3/4)L_f + (1/4)L_c$, as the matching stimulus (the raised cosine) is present for half the time and adds $L_c/2$ to L_f during this time. However, incorporating the raised cosine into the mean level cannot alter the nature of our results, since it reduces both the modulation of the flicker and brightness enhancement by a constant proportion. As a result, the overall relation between modulation and brightness enhancement would remain the same.

Measurements of Flicker Detection Thresholds. Flicker thresholds were measured for each subject using the same stimulus configuration. The measurements were made using a two-alternative forced-choice staircase procedure, with a flickering stimulus in one interval and a steady field of equal mean luminance (4.25 log td) in the other. The subject's task was to indicate which interval contained the flicker. The modulation was decreased following two consecutive correct judgments, or increased by the same amount following one incorrect judgment. The step size was initially set to 0.2 log units, but was decreased to 0.1 and 0.07 log units following the second and fourth reversal, respectively. In each trial there were four interleaved staircases (for four frequencies) predetermined to go through 12 reversals each. The mean of the last ten reversals for each frequency was taken as one measurement. Thirteen frequencies ranging from 4 to 56 Hz, in 4 Hz steps, were tested. Each frequency was tested three to five times on different days for each subject. Results presented are the medians of the three to five thresholds.

Design

Both Experiments 1 and 2 were run with a blocked-frequency design, in which frequency was fixed for a session. This design was adopted after extensive pilot research as described below:

1. We obtained a data set with nine frequencies, each with four modulations, from two subjects (SW and AR) with a randomized design, in which both modulation and frequency were varied from trial to trial. The curves of brightness against modulation obtained with this design were variable, indicating cross-frequency adaptation effects. However, when plotted against frequency, the data from both subjects were similar to the data shown below (Fig. 3), peaking at the same frequency with similar amplitudes, and dropping off slowly towards 40 Hz.
2. Data were obtained from one subject (SW) with a blocked-modulation design. Eleven frequencies were randomized from trial to trial and all frequencies were tested in the same session at a fixed modulation of 0.2. The peak frequency and amplitude were similar to the results presented below at the same modulation. We did not retain this design because between-session variability might alter the relation between brightness enhancement and modulation, which was of major interest in this study.
3. We also obtained a data set with a two-alternative forced-choice procedure, in which we presented either a 25 Hz or a 40 Hz standard stimulus in one interval and a comparison stimulus of variable frequency in the other. Different comparison stimuli which matched the same L_c in Experiment 1 (and thus could match each other by interpolation in Fig. 2) typically matched the standard stimulus which also matched the same L_c ('transitivity'). Violations of transitivity were small and did not change the ordinal relations among the data, even though the conditions of adaptation were now very different, with flicker present in both intervals, rather than in only the test interval as in the main experiment.

In summary, these pilot studies suggested that cross-frequency adaptation within a randomized design increased the variability in the data, but did not alter the overall pattern of results shown below. The blocked-frequency design that we adopted minimized cross-frequency adaptation and was readily performed by the subjects. The results of the pilot experiments indicate that the relation between brightness enhancement and frequency measured in Experiment 1 are not arising from prolonged temporal adaptation to particular frequencies.

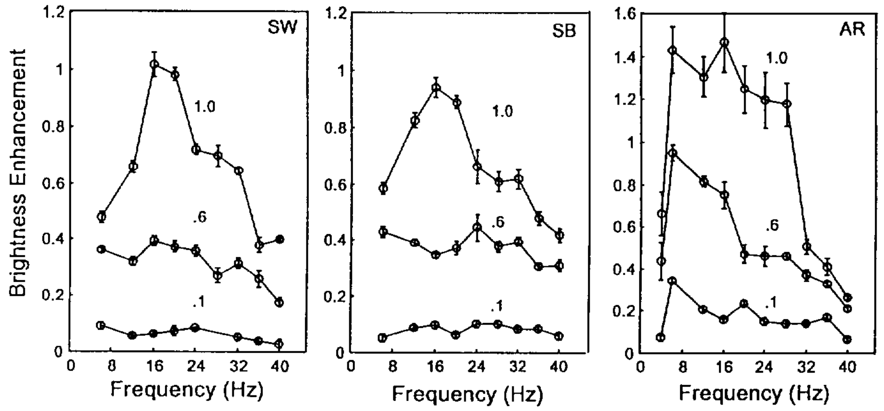

FIGURE 3. Brightness enhancement as a function of frequency, for three representative modulations (0.1, 0.6, and 1.0). SW, SB and AR are the three main subjects. Error bars represent mean ± SE around each data point, where SE is the standard error of the

RESULTS AND MODEL

Results: Experiment 1

Reliable brightness enhancement was found for all subjects, as shown in Fig. 2 (for three subjects, in separate panels). The effect increased systematically with modulation at all frequencies, although there were considerable individual differences in the amount of brightness enhancement. At high modulations (>0.4), brightness enhancement accelerated with increasing modulation in a frequency-specific manner. The brightness enhancement vs modulation curves from subject AR were less smooth, reflecting his larger standard errors (which are shown in Fig. 3). Results from subject AE (not shown) showed somewhat less brightness enhancement than those from the other subjects, but were in qualitative agreement with those from SW and SB.

Figure 3 replots the data from Fig. 2 obtained at modulations of 0.1, 0.6, and 1.0 as a function of stimulus frequency. Brightness enhancement increased with increasing modulation at all frequencies, peaking around 16 Hz at high modulations. The standard error of the mean was generally greater for stimuli at higher modulations, but was not frequency dependent.

The measured flicker thresholds were similar to previously published measurements [e.g. Kelly (1961) see Discussion]. Sensitivity was generally band-pass, with a peak at 16 Hz for all subjects, and decreased rapidly with increasing frequency.

A qualitative model for brightness enhancement: experiment 1

To account for the results of Experiment 1 we employed a sandwich model consisting of an initial linear filter followed by a static nonlinearity. Effects of other linear stage(s) after the nonlinearity are not quantified by this technique (see below). Schematic illustrations of this model are shown in Fig. 4. The subject compared the brightness of two stimuli: a sine-wave flicker multiplied by a raised cosine, and a raised luminance cosine. The initial linear filter determines the amplitude and phase of the response to the flicker component, but there is no response at the frequency of the cosine at this stage. After the cosine-windowed sinusoid passes through this initial linear filter, the accelerating nonlinearity expands the upper portion of the wave, creating a distortion product at the cosine frequency (0.5 Hz).

We assume that a brightness match is made when the amplitude of the 0.5 Hz distortion component is equal to that of the 0.5 Hz matching stimulus. To illustrate, in Fig. 4 we schematically separated the effects created at the nonlinearity by filtering the output waveform into its low frequency component and its high frequency component (indicated with the open bracket in Fig. 4). The latter has a distorted waveform (sharper peaks) due to its higher harmonic content, but no assumption is made as to the exact shape of this component, since we assume that it

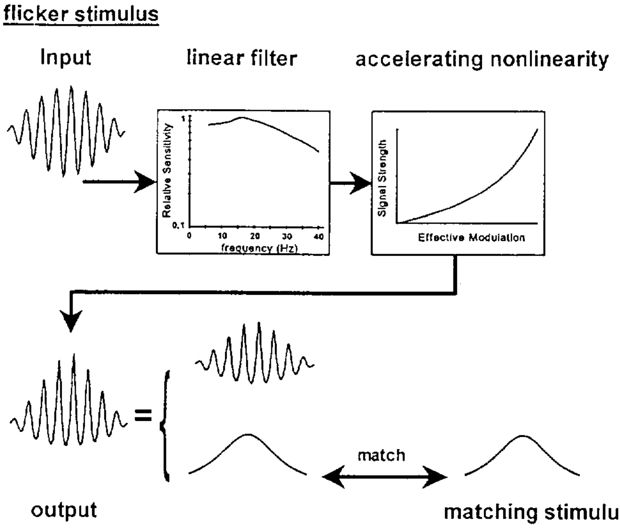

FIGURE 4. Illustration of a qualitative model for brightness enhancement. The input to the model is a cosine-windowed sinusoid. It first passes through a linear filter, which attenuates different frequencies differentially. The response of the linear filter is then used as the input to an accelerating nonlinearity. The output of the nonlinearity is shown in the (lower left). The effect of the nonlinearity is represented by a decomposition of the output into a high frequency flicker component and a low frequency distortion product. The subject makes the brightness matches based on the comparison between the distortion product and the similarly distorted matching stimulus.

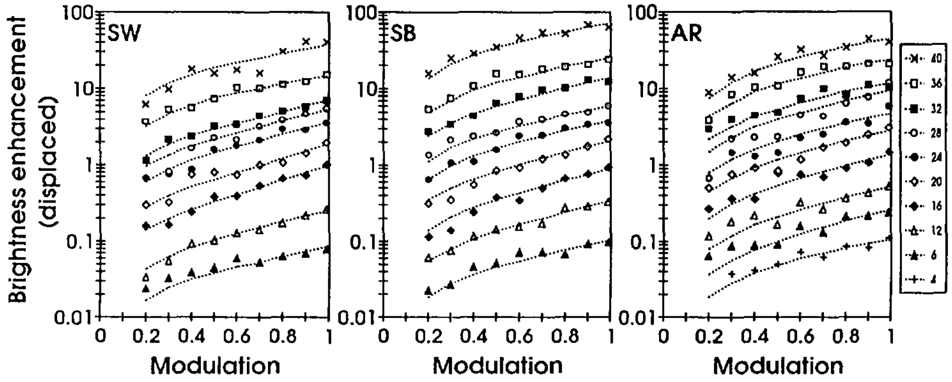

FIGURE 5. Comparison of the template fits and the brightness enhancement data of Fig. 2. Only data points obtained at modulations ≥ 0.2 were included in the fits. The template is a third order polynomial constrained to pass through the origin. The coefficients of the polynomial and the attenuation at each frequency are simultaneously optimized by a simplex algorithm. The template and the data at different frequencies are vertically displaced for clarity.

does not contribute to the brightness matches in our experimental paradigm. The low frequency component, on the other hand, is a distortion product that arises from the nonlinear interaction between the flicker and the cosine window, and has the same fundamental frequency as the cosine window (0.5 Hz). The response to the matching stimulus also contains primarily a low frequency (0.5 Hz) component, with some distortion arising from higher harmonics. We assume that in our paradigm, the subjects made their matches by comparing the 0.5 Hz distortion product from interval 1 to the 0.5 Hz matching stimulus in interval 2. This corresponded to the subject's perceptual experience of tracking the envelope of the flickering stimulus and ignoring the sensation of flicker. As the matches were based on the 0.5 Hz components that were common to the two intervals, they should be identically affected by any further visual processing.* Had the duration of the cosine window been changed, the frequency of the distortion product would change accordingly.

Test of the model by a template fit: experiment 1

A testable prediction of the model is that, if a single initial filter accounts for all the frequency-dependent effects on brightness, then after compensating the data for the effects of this filter, all the brightness enhancement curves should follow a fixed template when plotted on a log scale. This assumption was tested by applying a single template fit to each subject's brightness enhancement data, allowing only for variable attenuation along the modulation axis. The fitted curves and data are compared in Fig. 5.

Since we have no theoretical reason to presume the shape of the nonlinear template for brightness enhancement, we used a third order polynomial constrained to pass through the origin. (That is, no brightness enhancement at zero modulation.) Data points at 0.05 and 0.1 modulations were excluded from the fits because brightness enhancement was not reliably different from 0 at such low modulations, and thus the data at these modulations were proportionately more variable. A simplex algorithm was used to simultaneously optimize the following parameters: the three coefficients of the polynomial, and the amount of attenuation at each frequency. The fits and the data points are compared in Fig. 5, for three subjects, with brightness enhancement at each frequency plotted on a log scale and vertically shifted for clarity. A single, frequency-independent template accounts for 97% of the variance in two subjects and 93% in the third. Thus, we conclude that brightness enhancement can be adequately modeled by a single accelerating nonlinearity preceded by a linear temporal filter.

Experiment 2: sawtooth flicker

Previous research on brightness enhancement often used square-wave stimuli or rectangular stimuli with variable pulse width (e.g. Bartley, 1938; Bartley, 1961), both of which have a complex temporal frequency spectrum. If the harmonic components in a complex stimulus contribute to brightness in proportion to their Fourier amplitudes, then the results obtained using such a complex stimulus should be related to our results from Experiment 1 by a simple amplitude summation. However, while this may be the case for flicker thresholds, at which the temporal waveform effect has been mostly attributed to the first harmonic due to the low sensitivity to high frequencies (e.g. DeLange, 1954; Levinson, 1959; Kelly, 1964), it is known that suprathreshold data on flicker matching (Veringa, 1958; Forsyth & Brown, 1959) cannot be explained by the response to each component frequency alone (Brown, 1962). In addition, in a recent study it was found that sine-wave flicker produced greater brightness enhancement than square-wave flicker at 1 Hz, but less brightness

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*Note that an exact linking hypothesis for the brightness match is not required. For concreteness, we have assumed that the subject matched amplitudes of the two 0.5 Hz components, but other strategies may also have been used, such as a power detector or an integrator. As long as the matching strategy is based on sustained responses, our model still applies.

enhancement at 3 Hz and higher frequencies (Rüttiger *et al.*, 1994). This waveform effect is inconsistent with a simple amplitude summation. To account for such effects, it is necessary to understand how the harmonics in a complex stimulus contribute to brightness.

One possibility is that the brightness contribution by higher harmonics depends on both amplitude and phase. However, any phase effect cannot be seen from the results of Experiment 1, as brightness enhancement was measured by matching sine-wave flickering stimuli to a luminance cosine. In modeling the results we considered only the amplitude attenuation characteristics of the initial linear filter. To investigate whether the higher harmonics contribute to brightness enhancement in a phase-dependent manner, we measured brightness enhancement using both slow-on and slow-off sawtooth stimuli (Krauskopf, 1980) in Experiment 2.

The Fourier series for the two types of sawtooth stimuli are given by:

$$F(t) = I_0 * [1 + m * \sin(2 * \pi * f1 * t + \phi) + m/2 * \sin(2 * \pi * 2f1 * t + \phi) + \ldots] \quad (1)$$

where I_0 is the mean luminance, m is the modulation, $f1$ is the fundamental frequency, and ϕ equals π for the slow-on sawteeth and 0 for the slow-off sawteeth. Thus, the two types of sawtooth flicker have identical amplitude spectra, but differ in phase.

Our simple model can predict a phase-dependent effect by assuming that the initial stage produces either a phase lag or a time delay, as well as an amplitude attenuation of the high frequency components in the sawtooth stimuli. Thus, after passing through the initial filter the slow-on sawteeth will have sharper positive peaks and shallower negative troughs, and the slow-off sawteeth will have the opposite. The sharp peaks of the slow-on sawteeth will fall on a higher portion of the accelerating nonlinear curve, resulting in greater brightness enhancement. In addition, the difference in brightness between the two sawteeth will increase monotonically with increasing modulation. Below we test this prediction.

The methods and the procedures were the same as in Experiment 1. Sawtooth flicker of fundamental frequencies of 6 and 12 Hz was tested for subjects SW, SB, and AR, and also 4 Hz for AR, and 16 and 20 Hz for SW. The modulations for the sawtooth stimuli were 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and nominally 1.0, corresponding to modulations of 0.03–0.64 for the fundamental component. Within each session, we typically ran two frequencies, each with a randomly chosen sawtooth polarity. As in Experiment 1, we blocked all modulations of the same frequency together to avoid cross-frequency interactions (see above). The 11 modulations for each frequency with the same polarity were randomly ordered. For each subject, brightness measurements at each frequency and each polarity were determined in at least three separate sessions, on different days and with different sequences of modulations. The results for each condition were then averaged.

Results: Experiment 2

We found that slow-on sawtooth stimuli appeared brighter than slow-off sawtooth stimuli at low modulations and low frequencies, which we call the polarity effect. Figure 6 shows brightness enhancement data measured at a fundamental frequency of 12 Hz, for both slow-on and slow-off sawteeth, for two subjects (SW and SB). The data from Experiment 1 for sine-wave flicker at 12 Hz are replotted for comparison.

For the two subjects in Fig. 6, the polarity effect was measured at modulations < 0.5. At a modulation of 0.25 this difference in brightness enhancement is significant ($t = 8.17$ and 6.52 for SW and SB, both with $P < 0.001$). The sine-wave flicker produced an intermediate amount of brightness enhancement. Similar results were obtained for SW and SB at a fundamental frequency of 6 Hz. (Data not shown. At a modulation of 0.25, $t = 387.0$ and 7.29 for SW and SB, $P < 0.001$.) Results at 16 and 20 Hz for SW showed no polarity effect and did not differ from the sine-wave data obtained at the same fundamental frequencies ($P > 0.1$). This suggests that only the higher harmonics in a low frequency, low modulation stimulus contribute to brightness enhancement in a phase-dependent manner. Subject AR produced a polarity effect at 4 Hz ($t = 6.7$, $P < 0.001$, at a modulation of

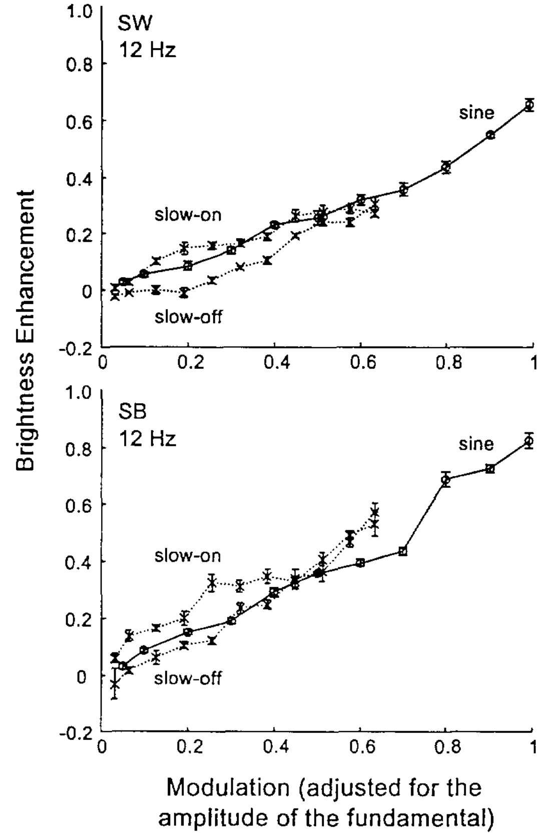

FIGURE 6. Brightness enhancement for sawtooth flicker of both directions as a function of the modulation adjusted for the fundamental (12 Hz). The sine-wave data at 12 Hz are replotted for comparison (solid curve). Results for SW and SB. Error bars represent mean ± SE around each data point, where SE is the standard error of the mean.

0.25), but not at 6 and 12 Hz. Both 6 and 12 Hz sawteeth were brighter for AR than corresponding sinusoidal stimuli at modulations higher than 0.3. (Data not shown. At a modulation of 0.5, $t = 5.31$ and 7.26 for 6 and 12 Hz, $P < 0.001$, by an ANOVA with planned comparisons between averaged sawteeth and sine-wave data.)

GENERAL DISCUSSION

Relation of brightness to threshold

The measured brightness of flickering lights peaks at around 16 Hz and declines at higher frequencies (Fig. 3). As mentioned in the Introduction, one purpose of this study was to determine whether this temporal characteristic of brightness enhancement is related to the threshold sensitivity to flicker. We first tested whether re-scaling modulation to units relative to flicker thresholds can account for brightness enhancement in a frequency-independent manner. Two types of re-scaling were attempted. First, we plotted brightness enhancement against m/T_f, where m is the actual modulation and T_f is the threshold modulation at that particular frequency. If, for instance, all lights at modulations twice their respective thresholds were equally bright, this manipulation should superimpose the data at different frequencies. It did not. In all three subjects, scaling the data according to the individual thresholds measured at each frequency overcorrected the brightness enhancement data, resulting in greater brightness enhancement at both low (6 and 12 Hz) and high frequencies (36 and 40 Hz) than at 16 Hz. Second, in spatial processing, it has been suggested (Kulikowski, 1976) that subtraction of the threshold contrast from the actual contrast for each frequency accounts for brightness. However, as the threshold modulations were small, scaling the data in this way made no appreciable difference in the relation between brightness enhancement, modulation, and temporal frequency. Thus, we concluded that the frequency-dependent relations of brightness enhancement to modulation cannot be simply attributed to the change in flicker thresholds with temporal frequency.

Another approach which allows us to compare brightness enhancement and temporal sensitivity is to deduce the temporal filtering properties that contribute to each criterion. This is straightforward for the threshold data. However, brightness enhancement varies with modulation nonlinearly, so at different modulations the relation between brightness enhancement and frequency varies (Fig. 3). Thus, a metric of brightness enhancement is needed that accounts for the nonlinear relation between brightness and modulation. To the extent that the sandwich model adequately describes brightness enhancement (Fig. 5), the amplitude attenuation characteristic of the first linear filter estimated from the brightness enhancement data provides such a metric. In Fig. 7 we plot the amplitude attenuation coefficients derived from the template fits against frequency (solid triangles), and compare them to the measured flicker thresholds (open triangles). For subjects SW and SB (Fig. 7), the derived filter for brightness was band-pass but broadly tuned, with a peak sensitivity at 16 Hz, and at higher frequencies decreased more slowly with increasing frequency than the threshold measurements. For subject AR, the derived filter for brightness showed a peak at 6 Hz, which attenuated slowly to 28 Hz then dropped rapidly at higher frequencies. In general, the brightness at high frequencies is relatively less for AR than for the other two subjects, mostly due to a large reduction in brightness for this subject at 40 Hz. If we excluded this point, we found that AR's derived sensitivity for brightness decreased by 0.35 log units while his threshold sensitivity decreased by 0.49 log units from 16 to 36 Hz. SW and SB showed a larger difference within the same frequency range (0.26 vs 0.50 log units for SW, and 0.17 vs 0.52 log units for SB, for brightness and thresholds, respectively).

Thus, although there are considerable individual variations, all three subjects have a broader temporal filter for brightness enhancement than for flicker thresh-

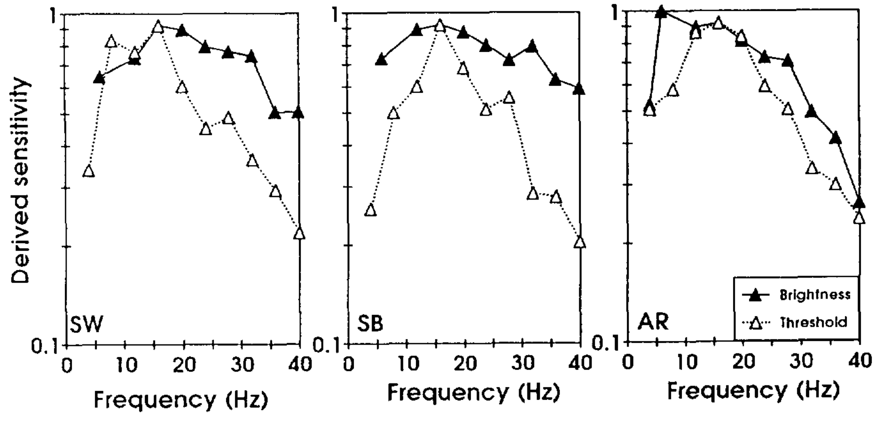

FIGURE 7. Comparison of the attenuation characteristics estimated from the brightness enhancement data and from the flicker thresholds. The attenuations for brightness were obtained from the template fit to the data shown in Fig. 5. The threshold measures are the medians of the individual runs. SW, SB and AR are the three main subjects. Both brightness and threshold estimates were normalized at 16 Hz.

olds. From this comparison we infer that we are able to measure the properties of an early visual filter using brightness enhancement, and that the steeper high-frequency slope of the temporal filter estimated from flicker thresholds reflects the cascading of additional (and later) stages of processing (see Introduction). This inference is possible because flicker sensitivity at different frequencies is determined by the filtering characteristics of the entire visual system, and the small amplitude of the flicker stimulus at threshold is minimally affected by nonlinearities due to small signal linearity.

Although the data clearly support the hypothesis that the early visual process measured with brightness enhancement is broadly tuned to temporal frequencies, it is possible that these derived attenuation characteristics do not entirely reflect the mechanism underlying brightness enhancement. Indeed, brightness matches might be biased by the concurrent flicker. As brightness enhancement is caused by flicker, it is not possible to isolate the two percepts entirely. In the model, we assumed that brightness matches depend only on the 0.5 Hz component (Fig. 4), not on the fast flicker component. Two observations supported this assumption. First, subjects reported that they perceived a slow brightness variation while making the brightness matches. Second, in a pilot experiment, using Design No. 3 (see above), we asked subjects to match comparison stimuli of different frequencies (5–55 Hz) to a standard stimulus (25 or 40 Hz) either in perceived flicker modulation or in perceived brightness. We found that they were able to reliably make distinct brightness matches or flicker modulation matches at modulations ≥ 0.3. Indeed, for comparison stimuli at frequencies away from the peak (16 Hz for SW and SB, 6 Hz forAR), more modulation was needed to make a flicker modulation match than to make a brightness match, again indicating that the temporal response of the mechanism underlying brightness enhancement is broader than that underlying flicker perception. As the template fit to brightness data in Experiment 1 was based on data at modulations ≥ 0.2 (Fig. 5), we conclude that bias by perceived flicker is unlikely to have a major influence on the shape of the derived temporal filter (Fig. 7).

Sawtooth flicker

The results from Experiment 2 show that at 6 and 12 Hz the two sawteeth, which have identical amplitude spectra, produce different amount of brightness enhancement. In addition, the data from both sawtooth polarities differ from those obtained using the sine-wave stimuli at the same fundamental frequencies. Thus, not only do the higher harmonics in the low frequency sawtooth stimuli contribute to brightness, but also they must contribute in a phase-dependent manner.

However, the predictions we made based on our model, which incorporates either a phase lag or a time delay in the first stage of linear filtering, are also inconsistent with the results of Experiment 2. As mentioned earlier, the model predicts that the difference between the two sawteeth would be amplified with increasing modulation. The results show that the difference in brightness between the two sawteeth is largest at low modulations (Fig. 6). This challenges any model incorporating a single, static nonlinearity.

It has been reported that adaptation to a slow-on or a slow-off sawtooth stimulus differentially raises the detection thresholds for decrements or increments, respectively (Krauskopf, 1980). Detection thresholds without adaptation are also slightly lower for slow-on than for slow-off sawteeth, with the difference increasing with luminance (Bowen *et al.*, 1989; Bowen *et al.*, 1992). In addition, Arnold and Anstis (1993) have found that the dimming aftereffect produced by slow-on sawtooth stimuli was stronger than the brightening aftereffect produced by slow-off sawtooth stimuli. This asymmetry in the effectiveness of sawtooth stimuli in producing the aftereffects is in the same direction as that in producing brightness enhancement in our Experiment 2. However, the aftereffect asymmetry also increased with modulation, while our asymmetry disappeared at high modulations. The selective adaptation and the asymmetry in both detection thresholds and aftereffects were all attributed to separate ON and OFF pathways, which have different sensitivities. Since we cannot model our sawtooth brightness results with a single, static nonlinearity, possible alternatives would be either to include a dynamic nonlinearity, or to adopt a two-mechanism model. A two-mechanism model also finds support from physiological data (Schiller, 1982).

The above discussion only applies to slow sawtooth flicker. At fundamental frequencies ⩾ 16 Hz, the sawtooth data (from subject SW) showed no polarity effect, nor did the data differ from those obtained from the sinusoidal stimuli at the same fundamental frequencies. As the attenuation of brightness enhancement at both 24 and 32 Hz (the second harmonics of 12 and 16 Hz) is minor (Fig. 7), summation of amplitudes would predict more brightness for sawtooth than for sinusoidal flicker at both 12 and 16 Hz. Contribution from yet higher harmonics (such as the third, at 36 and 48 Hz) also would not explain the coincidence of the sawtooth and sinusoidal data at 16 Hz. Thus, the results for sawtooth flicker at 16 Hz or higher seem to be determined by the first harmonic component only.

Individual differences

The individual differences among our three main subjects are consistent across experiments. Firstly, the shape of the derived filters for brightness enhancement clearly differed among subjects (Fig. 7). For SW and SB, the brightness-derived filter peaked at 16 Hz and dropped off slowly at higher frequencies. AR's filter peaked much lower, at 6 Hz, and dropped off slowly up to 28 Hz and then more rapidly at higher frequencies. Partial data from subject AE also peaked between 12 and 16 Hz, with brightness enhancement decreasing slowly at high frequencies, similarly to the results from SW and SB.

In addition, the template fit to AR's data was worse, especially at 16 and 28 Hz (Fig. 5), indicating that the derived filter may not be as accurate for this subject as for SW and SB. Secondly, AR's results from Experiment 2 showed a sawtooth polarity effect at 4 Hz but not at 6 Hz or higher, whereas SW and SB showed a sawtooth polarity effect at 6 and 12 Hz (Fig. 6) but not at 16 Hz or higher. Thus, each subject shows a polarity effect only at frequencies below his or her frequency of peak brightness enhancement. As the polarity effect can only occur when the responses to higher harmonics are relatively large (i.e. not attenuated too much by the first linear filter), the fact that AR's first filter peaks at lower frequencies may account for the finding that this subject did not show the polarity effect at frequencies > 4 Hz.

Previous results on brightness enhancement and contrast modulation flicker

In the classic literature (for example, see Bartley, 1938), the Brücke–Bartley effect was sometimes measured by a drop in the luminance needed for the flicker to match the standard, yielding plots inverted relative to ours (Fig. 3). However, this does not alter the findings. For example, Bartley's results (1938) obtained with stimuli of rectangular waveforms showed that brightness enhancement peaks at about 8 or 9 Hz and declines slowly to zero at about 32 Hz. Both features of the data (the peak and slope of the decline) were stable across light-to-dark ratios from 1:8 (a brief pulse) to 1:1 (square wave), and across variations in maximum luminance from 4.5 to 400 cd/ft^2 (about 2.3–4.2 log td, near the level we employed). The initial linear filter deduced from our data (Fig. 7) predicts that brightness enhancement should peak at slightly lower frequencies for rectangular stimuli than for sinusoids due to the contributions from the higher harmonics. A qualitative comparison of our Fig. 3 to Bartley's data in the frequency region beyond the peak confirms this prediction. Our brightness enhancement for fully modulated sinusoids peaked at 16 Hz and dropped to half-maximum at 36 Hz, whereas his observer's brightness data peaked at 9 Hz and dropped to half-maximum at 18 Hz.

More precise predictions are not warranted, however, since results of Experiment 2 imply that a simple summation of component frequencies (with or without phase shifts) does not account for brightness enhancement. In addition, brightness enhancement disappeared at about 32 Hz in Bartley's data, which was close to the c.f.f. for his subjects, while our subjects were able to see flicker at 40 Hz and experienced some brightness enhancement even at this frequency, suggesting that the experimental conditions are not directly comparable.

Using a similar approach but much different stimuli, MacLeod and He (1993) investigated the brightness of the contrast modulation flicker generated by interference of ultra-fine gratings. The apparent modulation of the flicker was attributed to a distortion product that arises at an early nonlinear stage in visual processing. The temporal characteristics they measured appeared to be very similar to ours (see Fig. 4 in MacLeod & He, 1993). Indeed, the high frequency asymptote of their deduced early filter is shallow, and coincides closely with the average of our derived filters shown in Fig. 7. This supports our hypothesis that we are measuring the properties of an early temporal filter (since their spatial stimuli were above the resolution limit). This agreement between studies also implies that both techniques are measuring the same early filter in the visual system, even though the techniques themselves are very different.

CONCLUSIONS

1. Brightness enhancement to sinusoidal stimuli varying in frequency and modulation can be modeled by a broad temporal filter, followed by a single accelerating nonlinearity.
2. The amplitude attenuation of the inferred early filter has a shallower high-frequency asymptote than that determined from flicker thresholds.
3. When tested with sawtooth flicker, brightness enhancement is phase-dependent at low modulations for relatively low frequencies (Experiment 2). This suggests that the brightness enhancement nonlinearity is more complex than a single, static, accelerating nonlinearity.

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