Response of visual mechanisms to stimulus onsets and offsets

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Transient and sustained visual mechanisms were studied with single, *flickering* bars of various widths. Wide bars were largely detected on the basis of temporal luminance *transients* whereas thin bars were detected on the basis of the sustained *contrast*. A rapidly flickering uniform field selectively masked wide flickering bars, which suggests that different mechanisms detect wide versus thin flickering bars. For coarse spatial patterns, stimulus onsets were slightly more visible than stimulus offsets, and the response to onsets and offsets approximately summated.

INTRODUCTION

Transient visual mechanisms presumably signal motion or sudden changes in luminance and contrast[1-7]; they are more sensitive to lower spatial frequencies and higher temporal frequencies than sustained mechanisms.[2,3] The latter presumably signal information about the spatial details of patterns.

In the present study single flickering bars of different widths are used to attempt to separate transient and sustained mechanisms. (The reasons for using single bars will be considered in a subsequent part of the Introduction.) Wide bars contain more energy at low spatial frequencies than do thin bars. Since the transient mechanisms are more sensitive to low spatial frequencies, they might be used in detecting wide flickering bars. Thin bars at appropriate flicker rates, however, might be detected with sustained mechanisms. Figure 1 shows the basic stimulus, which illustrates the principle of the experiment. Luminance profiles are shown for various vertical, flickering bars. Figures 1(a) and 1(b) show, respectively, a light bar and a dark bar that are flickering on and off. These bars will be called *on-off bars*. Figure 1(c) shows a bar that flickers between light and dark about the mean luminance. This will be called a *reversing light-dark bar* (or "counterphase" bar). *All* three types of bars (when on) have the *same contrast* (contrast is defined in Methods). However, the reversing light-dark bar produces temporal luminance changes that are twice the size of the changes produced by the on-off bars. Thus if *wide* bars are detected by the transient mechanisms, the three types of wide bars would be at threshold when the bars produce equal transients, and hence the threshold *contrast* ratio for on-off versus reversing light-dark bars would be 2:1. Thin bars, however, may preferentially stimulate sustained mechanisms—the thresholds may be determined by the contrast of the patterns and not by the temporal luminance changes. Thus for *thin* bars, the threshold contrast ratio for on-off versus reversing light-dark bars may be approximately 1:1.

Kulikowski and Tolhurst[2] hypothesize that coarse and fine sinusoidal gratings are detected with transient and sustained mechanisms, respectively. They observed that for coarse gratings (below ~2 cycles/deg), the contrast threshold of reversing (counterphase) gratings was one-half the threshold of on-off gratings (in which the light and dark bars were, respectively, increments above and below the mean luminance of the field). For fine gratings (above 6 cycles/deg), contrast thresholds were similar for counterphase gratings and on-off gratings. The temporal modulation was square-wave at 3.5 or 8 Hz.

Arend,[8] however, argues that the results may *not* show distinct mechanisms if significant eye movements are present. Kulikowski and Tolhurst [Ref. 2 and personal communication] used the method of adjustment without a fixation point. Eye movements might cause retinal points to be stimulated sequentially by light and dark bars of the fine on-off gratings. The resultant stimulation might be similar to that produced by having the eyes still but the grating reversing in contrast (counterphase grating). Thus *both* high spatial frequency gratings might partially act like counterphase gratings due to eye movements. For coarse gratings, the size of eye movements may be too small relative to the grating bar width to produce these effects. Thus the different results for coarse and fine patterns could be due to eye movements.

This problem of eye movements is partially obviated by using single bars rather than gratings, for with a single light bar or dark bar, the bar of opposite lightness is not present, and thus eye movements cannot cause sequential stimulation of light and dark bars. In using the method of adjustment with a fixation point, there will be many occasions on which a reversing light-dark bar will stimulate given retinal points with twice the luminance fluctuation as that produced by an *equivalent contrast*, on-off light bar or dark bar. Although the eyes may move slightly, detection will be largely controlled by this *strong* stimulation, given the reasonable assumption of a relatively steep psychometric function. If the threshold is determined by the size of the temporal luminance transient, then the contrast threshold ratio of on-off versus reversing bars will be approximately 2:1. The effects of eye movements and probability summation on detection may cause this ratio to be slightly smaller than 2:1 for thin bars. However if sustained mechanisms are used in detecting thin bars, the threshold ratio for on-off and reversing thin bars may be approximately 1:1.

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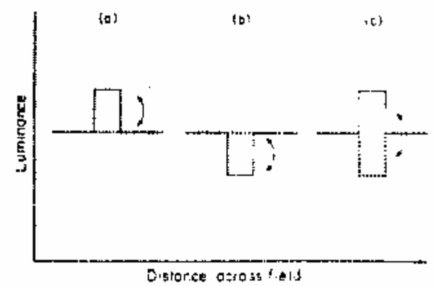

FIG. 1. Luminance profiles of vertical, flickering bars: (a) and (b) show light and dark bars that periodically flicker on and off as indicated by arrows; (c) shows a reversing light-dark bar that periodically reverses luminance. All three types of bars have approximately the same contrast (Methods), but the reversing bar produces a luminance change that is twice the size of the change produced by the other two types of bars.

The effects of on- versus off-transients are also examined. As discussed above, the threshold of coarse, counterphase gratings are about one-half those of similar on-off gratings.[2] A counterphase grating that reverses contrast at a slow rate (e.g., 2 Hz, square-wave modulation) can be plausibly thought of as a superposition of a grating turning off in one phase and a grating turning on in the opposite phase. The 2:1 threshold ratio for coarse, on-off and counterphase gratings thus suggests that offsets and onsets are about equally effective and *summate* physiologically. However, Breitmeyer and Julesz[4] observed that sharp on-transients improved the visibility of coarse gratings, whereas sharp off-transients had *no* effect. Due to the apparent discrepancy between these results, on- and off-transients are further examined with coarse gratings.

I. METHODS

A. Apparatus and stimuli

Vertically-oriented bars or gratings were displayed on a Tektronix 602 oscilloscope with white (P-4) phosphor. The mean field luminance is given in the figure legends. The stimulus field was 9° dia (unless noted) with a dark surround and small, central fixation point. Single bars were centered on the fixation point. The x-axis sweep repeated every 4.7 ms. The z-axis signals were produced with Wavetek 146 and 186 function generators, which produced amplitude-modulated signals. Patterns with very sharp onsets or offsets (less than 1 ms) were produced with auxiliary timers (for results in Figs. 6–7).

The contrast of the patterns is defined by,

$$(L_{\max}\text{-}L_{\min})2L_{\text{mean}},$$

where L is the luminance of a point on the display. This definition has been used by other investigators for gratings[9] and single bars.[10] Thus, the contrast of a bar that reverses in luminance is specified by the contrast of either the light bar or the dark bar component. For example, the on-off and reversing light-dark bars in Figure 1 have equal contrast. The mean luminance of the field was approximately constant during all presentations.

The patterns were sinusoidal gratings, square bars, or cosine bars. A light cosine bar, for example, was one cycle of a cosine grating extending from −180 to +180° phase angle (specifies bar width). The *entire* cycle was an increment above the mean luminance of the display, as shown in the inset of Fig. 3. A dark cosine bar was a decrement of the luminance.

B. Procedure

The observer fixated the center point on the display with his favored eye, which was well refracted. When a thin, reversing light-dark bar is presented, eye movements will reduce the illuminance fluctuation at given retinal points. However, with good fixation, there will be many occasions in which given retinal points would receive the full illuminance fluctuation. The observer could use these occasions to set the threshold; therefore the method of adjustment was used in the initial experiments (see Introduction).

However, a signal detection method, described elsewhere,[11] was used for most experiments. Each run was 100 trials in which a single pattern was presented with equal probability at four contrast levels (including blanks). The observer initiated the trial with a switch. He rated the visibility of the pattern and was given feedback about the contrast level. The detection parameter d' was determined for each contrast level and was based on 2–5 runs.

II. RESULTS

A. On-off and reversing light-dark

Figure 2 shows thresholds for square bars of different widths that turned on and off or reversed in luminance with a 3.5-Hz square-wave modulation. The on-off bars were light or dark. The contrast threshold ratio for *wide* on-off and reversing bars approaches two. For the thinnest bars the ratio is considerably less than two (approximately 1.15).

Figure 3 shows similar measurements for cosine bars with a 2.0-Hz square-wave modulation. When the observer closed a switch the bar appeared for two cycles of temporal modulation. The threshold ratio approached two for the widest bar and was smaller for the thinnest bar (approximately 1.33). Similar results, which are not shown, were obtained with observer CFS.

B. Reversing light-dark bars masked with uniform flicker.

Coarse and fine bars may preferentially stimulate transient and sustained mechanisms, respectively. This idea is further

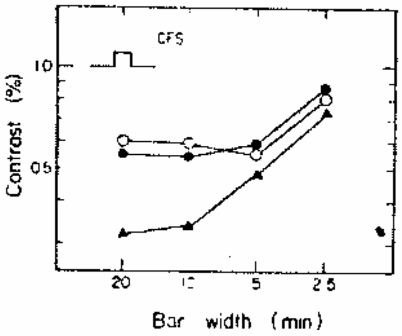

FIG. 2. Contrast thresholds for a single square bar (inset) as a function of bar width. The bar is continuously modulated with a 3.5-Hz square-wave so as to turn on and off or reverse in luminance (as shown in Fig. 1). Light, on-off bars (open circles); dark, on-off bars (closed circles); reversing, light-dark bars (triangles). Standard error, 1%–13% of settings. Mean luminance is 55 cd/m². Field is 9° diam throughout, unless noted.

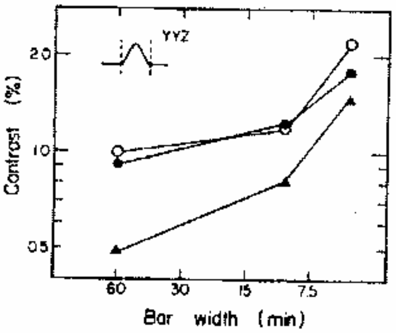

FIG. 3. Contrast thresholds for a single cosine bar of various widths (indicated by dotted lines in inset). Bar is modulated with 2.0-Hz square-wave so as to turn on and off or reverse in luminance. Each presentation was two cycles of modulation. Bright, on-off bars (open circles); dark, on-off bars (closed circles); reversing light-dark bars (triangles). Standard error, 3–7% of settings. Mean luminance 19 cd/m².

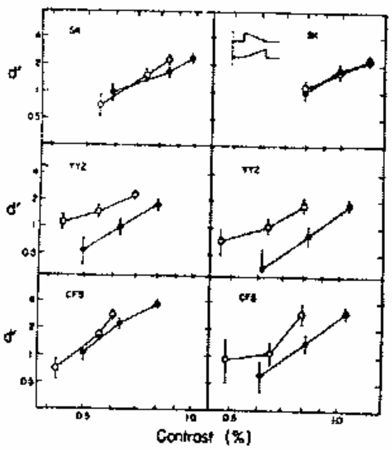

FIG. 5. Detectability of 1.0 cycle/deg sinusoid gratings with sharp onsets (open circles) or sharp offsets (closed circles). Temporal patterns shown in inset—dotted line indicates when observer initiates trial. The inset shows how the *contrast* of the pattern changes with time. Temporal ramps of 0.5 and 1.0 s were used for observer SK and observers YYZ and CFS, respectively. Mean luminance was 55 and 6 cd/m² for left and right columns, respectively. Each curve in left and right columns is based on about four and two runs, respectively.

tested by measuring thresholds for flickering bars in the presence of a mask that is spatially uniform and *rapidly* flickering. Transient mechanisms may be strongly affected by the rapid flicker, whereas sustained mechanisms may be rather insensitive to the mask. Differential masking of coarse and thin bars would indicate *different* underlying mechanisms.

Reversing (2.0-Hz), spatial cosine bars were presented alone or with a mask that was a sinusoidal fluctuation of the display luminance at 20 Hz and 26% modulation. Observers adapted to the mask for 5 min before measurements were made. For observer CFS, the mask elevated the threshold of the widest bar (60 min arc) by 120 ± 6%, where the uncertainty is one S.E.; the elevation for the thinnest bar (5 min arc) was only 10 ± 3%. Figure 4 shows similar results obtained with the signal detection method. The selectivity of masking suggests that the wide and thin, reversing light-dark bars are detected with different mechanisms.

C. On- versus off-transients

The high visibility of coarse, reversing patterns suggests that on- and off-transients are both effective and summate (Introduction). The effects of on- and off-transients therefore were measured with various patterns.

Figure 5 shows results for a 1.0 cycle/deg sinusoidal grating obtained at luminances of 55 and 6 cd/m²—left and right columns, respectively. For the on-transient, the grating was turned on linearly for 22 ms and off linearly for 1.0 s (inset); for the off-transient, the temporal pattern was reversed. The inset shows the relative contrast of the grating as a function of time. For observer SK, the temporal patterns were one-half this duration. For this observer, sharp onsets and offsets were about equally effective; for the other two observers, onsets were more effective.

Figure 6 shows results for a coarser grating of 0.5 cycle/deg. The temporal patterns were segments of a 4-s sinusoid as shown in the inset; the dotted lines indicate when the observer initiated the trial. Sharp onsets were slightly more effective than sharp offsets, and both onsets and offsets were more effective than gradual changes.

Figure 7 shows results for a still coarser grating of 0.2 cycle/deg with the same temporal patterns shown in Fig. 6. Sharp onsets and offsets were about equally effective and more effective than gradual changes.

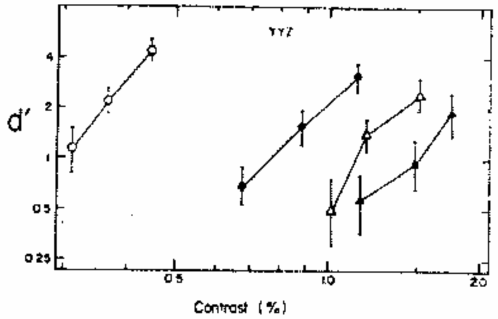

FIG. 4. Detectability *d'* and ±1 S.E., for a reversing light-dark cosine bar (Fig. 3) measured with (closed symbols) and without (open symbols) a mask consisting of a sinusoidal fluctuation of the field luminance of 20 Hz and 26% modulation. Wide test bar of 60 min arc (circles) and thin bar of 5 min arc (triangles) were used. Each curve is based on two runs. Mean luminance is 19 cd/m².

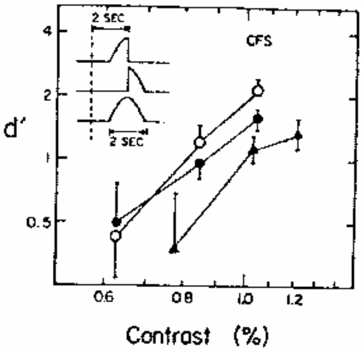

FIG. 6. Detectability of 0.5 cycle/deg sinusoidal gratings with sharp onsets (open circles), sharp offsets (closed circles), or gradual changes (triangles). Dark bar of grating is centered on fixation point. Temporal patterns are shown in inset—quarter or half cycles of sinusoid. Each curve is based on two runs. Mean luminance is 19 cd/m².

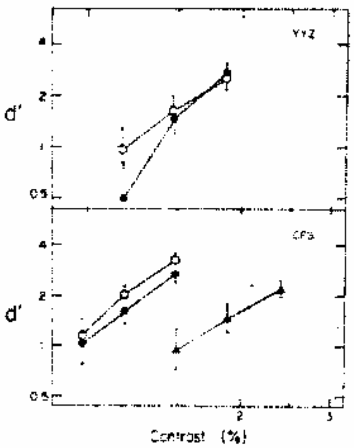

FIG. 7. Detectability of 0.2 cycle/deg sinusoidal gratings (15° field) with sharp onsets (open circles), sharp offsets (closed circles), or gradual changes (triangles). Dark bar of grating is centered on fixation point. Temporal patterns are the same as Figure 6. Each curve is based on two runs. Mean luminance is 19 cd/m ^{2}

III. DISCUSSION

A. On-off and reversing light-dark bars

At low flicker rates, the contrast threshold for a wide light or dark bar was about 1.8 times the threshold for a wide reversing light-dark bar (Figs. 2 and 3). This difference was considerably reduced for thin bars. Observers stated that the wide, reversing light-dark bars appeared spatially diffuse and flickering at threshold; the thin, reversing light-dark bars appeared as sharp, fine lines that appeared light or dark at threshold—flicker was not clearly seen. (At flicker rates considerably above 4 Hz, the *thin* reversing bars also appeared as spatially diffuse and flickering at threshold). The results for bars resemble the results of Kulikowski and Tolhurst[2] for gratings; however, the bar stimulus obviates the problem of eye movements considered in the Introduction. Using retinally stabilized gratings, Kulikowski[12] also obtained similar results; the results were unusual, however, in that the contrast thresholds were extremely high.

It may be questioned whether the low sensitivity to *thin*, reversing light-dark bars is due simply to a long integration time. If integration were very long, then the temporally reversing light and dark bars may summate *negatively*, and thus a reversing bar might even have a higher threshold than a light, on-off bar or a dark, on-off bar. (For example, if the reversing bar were retinally stabilized and reversed at a rapid rate, such as 60 Hz, the field would appear uniform.) However, the present results show no such negative summation. Some of the results were obtained with a 2.0-Hz square-wave modulation (Fig. 2). At this rate the integration time would have to be longer than 250 ms, or one-half temporal cycle, to obtain negative integration. Other results[5,7] show that the integration time is about one-half this value for relatively fine gratings of 6 and 10 cycles/deg. The integration time was assessed by measuring the function of exposure duration versus contrast to determine the "critical duration", or time at which the contrast threshold is largely independent of exposure duration. Measurements we made with a 5 cycle/deg grating (mean luminance, 55 cd/m^2) gave a critical duration of approximately 100 ms. A long integration time thus presumably does not account for the different results obtained with wide and thin bars.

The different results obtained with wide versus thin bars might be accounted for by postulating different detection mechanisms, viz, transient versus sustained. Alternatively, wide and thin bars might simply produce different responses in a *single* class of mechanisms. This latter hypothesis, however, is implausible, for a wide flickering bar (Fig. 4) was strongly affected by a rapidly flickering, uniform mask, whereas a thin flickering bar was little affected. This selective masking suggests that different mechanisms are used in detecting wide and thin flickering bars.

King-Smith and Kulikowski[3] also observed that the visibility of a wide flickering bar was strongly affected by a flickering uniform field. They used the method of subthreshold summation and adjusted the contrast of the test pattern so flicker *per se* (not only pattern) was just seen. A wide cosine bar (1 cycle of a cosine grating of 0.67 cycle/deg) which reversed luminance at 24 Hz was strongly affected by a subthreshold, uniform field that flickered at the same rate in-phase with the bar. A thin bar of 1.2 min arc flickering at 12 Hz was considerably less affected by a uniform field also flickering at 12 Hz. Thus both these results for subthreshold summation and our masking effects suggest that different mechanisms detect wide and thin flickering bars.

The different responses to wide and thin bars may be related to the difference in temporal impulse response of the underlying mechanisms, as suggested by other studies. The use of spatially coarse patterns[6,13,14,15] has generally yielded diphasic impulse responses and fine patterns has yielded monophasic responses.[6,16] For example, Watson and Nachmias,[6] using coarse sinusoidal gratings of 1.75 or 3.5 cycles/deg obtained summation between two opposite-phased gratings and inhibition between two same-phased gratings that were flashed at separations of 40–100 ms. At spatial frequencies above 7 cycles/deg, opposite-phased gratings did not summate. Coarse spatial patterns with sharp temporal transients appear to produce diphasic responses, whereas fine spatial patterns produce monophasic responses.

B. On- versus off-transients

A reversing bar [Fig. 1(c)] is composed of the superposition of an *on-off* light bar plus an *off-on* dark bar [Fig. 1(a), 1(b)]. Similarly a counterphase grating is the superposition of two on-off gratings with appropriate phases. The high visibility of coarse counterphase gratings and bars, discussed in the previous section, suggests that both sharp onsets and offsets affect visibility and the effects of onsets and offsets summate.

Breitmeyer and Julesz,[4] however, observed that sharp offsets did *not* affect the visibility of gratings below about 2 cycles/deg, for gratings with sharp offsets were not more visible than gratings that were turned gradually on and off. They observed that the contrast thresholds for gratings with sharp offsets were 50% and 65% higher than gratings with sharp onsets for two observers.

The present results show considerably smaller differences between sharp onsets and offsets. For gratings of 0.2 cycle/deg (Fig. 7), the sharp onsets were at most 5%–10% more visible than the sharp offsets and were about 70% more visible than gratings with gradual onsets and offsets. Tolhurst[5] obtained similar results with gratings of the same spatial frequency and a considerably smaller field (3.5° vs 15° for the present results). For gratings of 0.5 cycle/deg (Fig. 6), sharp onsets were also only about 10% more effective than sharp offsets. For gratings of 1.0 cycle/deg (Fig. 5) the results were mixed: one observer was equally sensitive to onsets and offsets, one observer showed a 30%–40% enhanced sensitivity to onsets, and the third observer was in between.

Evidence for the symmetry between onsets and offsets was obtained by Tolhurst[17] who measured subthreshold summation of a 4-ms and a 800-ms presentation of a grating of 2 cycle/deg. Detection was enhanced strongly and about *equally* either by presenting the brief-grating spatially in-phase with the long-duration grating at the onset of the latter grating or by presenting the brief-grating spatially in anti-phase at the offset of the long-duration grating. This suggests the on- and off-transients may *equally* enhance detection.

In general, the results show that sharp onsets may be slightly more effective than sharp offsets in enhancing the visibility of low spatial frequencies. This may be due to adaptation, as shown, for example in electrophysiological studies of ganglion cells. The response of both X and Y cells and sustained and transient cells decreases during the stimulus presentation.[18,19,20] However, adaptation may be negligible for the threshold stimuli of the present experiments. Any difference between the visibility of sharp onsets and offsets might also be explained by an asymmetric impulse response or by an impulse response that has both sustained and transient properties.

Note added in proof: Budrikis and Lukas recently reported [Z. L. Budrikis and F. X. J. Lukas, "Phase response of the visual system," Suppl. Invest. Ophthalmol. and Visual Sci. 18, 92 (1979)] that a low spatial frequency pattern with slow onset and sharp offset is not more visible than a pattern with slow onset and offset. Their stimuli, procedures (method of adjustment), and results are similar to those of Breitmeyer and Julesz, and are different from our finding that a sharp offset aids detection at low spatial frequencies.

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