

Some observations on the masking effects of Mach bands

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There are 8 cycle/deg ripples or oscillations in performance as a function of location near Mach bands in experiments measuring Mach bands' masking effects on random polarity signal bars. The oscillations with increments are 180° out of phase with those for decrements. The oscillations, much larger than the measurement error, appear to relate to the weighting function of the spatial-frequency-tuned channel detecting the broad-band signals. The ripples disappear with step maskers and become much smaller at durations below 25 ms, implying either that the site of masking has changed or that the weighting function and hence spatial-frequency tuning is slow to develop. © 2007 Optical Society of America

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1. INTRODUCTION

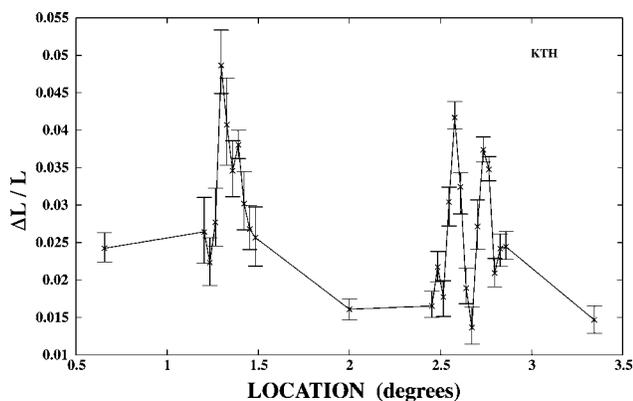
One stimulus that produces Mach bands consists of a region of uniform low luminance (the dark plateau) connected to a region of higher luminance (the bright plateau) by a luminance gradient (the ramp) that increases linearly from the lower to the higher luminance region. Mach bands appear as dark and bright bands at the transition from the dark plateau to the ramp and from the ramp to the bright plateau, respectively [1]. Measuring the masking effect of stimuli that produce Mach bands is complicated by the fact that the shapes of the Mach bands are visibly distorted by the signals to be detected [2–4]. When the signals are luminance increments located within the Mach bands, the distortion takes the form of a widening of the dark band and a narrowing of the bright band; signals that are decrements in luminance produce the opposite effect—narrowing the dark Mach band and widening the bright one. Evidence for the effect is also seen in the results of one observer in the earliest masking study of Mach bands [5].

The distortion cue is subtle but affects the shape of the psychometric functions fitted to detection performance in two-alternative forced-choice experiments. Fortunately, the opposing effects of increments and decrements mean that the distortion of the psychometric functions is removed by randomizing the polarity of the signal within blocks of trials. In this case, observers are unable to use differences in the width of the Mach bands as an indication of the interval containing the signal because, for signals in the bright band, say, a wider bright band in one interval could equally indicate an incremental signal in that interval or a decremental signal in the other interval. Randomizing the polarity appears to work, since the

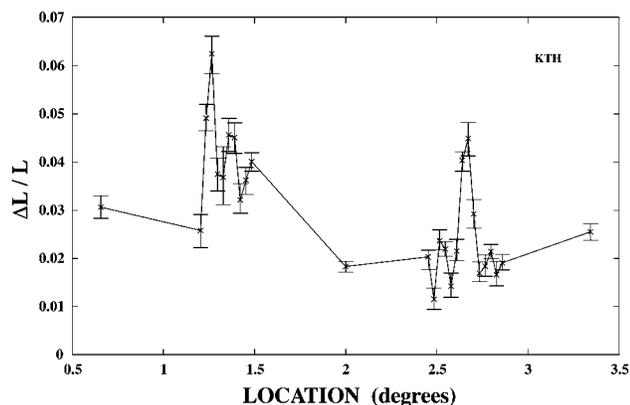
psychometric functions obtained with random polarity signals, when plotted on semilogarithmic coordinates, become approximately parallel for all locations across the masking stimulus, thus allowing a sensible threshold detection level to be defined [4].

An intriguing phenomenon is observed in the random polarity experiments, however, when performance on trials with increments and decrements are analyzed separately: in the vicinity of the Mach bands, there are large ripples or oscillations in performance as a function of location across the Mach-band masking stimulus. Figure 1 (after Figs. 6(a) and 7(a) of [4]) shows $\Delta L/L$ —the magnitude of the just-noticeable luminance change (at 75% correct in a two-alternative forced-choice experiment for one observer) divided by the masking luminance as a function of location along the ramp. (Strictly, the magnitude of the just-noticeable decrement should be subtracted from the denominator, but the effect of this manipulation is negligible.) The signals were $4^\circ \times 0.9'$ horizontal bars and were as likely to be increments as decrements; the change from the dark plateau to the ramp occurred at 1.3° , and the transition from the ramp to the bright plateau was at 2.6° .

Figure 1(a) shows the results for increments, Fig. 1(b), the results for decrements. The ripples as a function of location are clearly visible. The error bars indicate ± 1 standard deviation in the observer's 75% correct threshold and were extracted from psychometric functions fitted by using the techniques of Wichmann and Hill [6,7]. The ripples for both increments and decrements are large relative to the error bars, and they are approximately 180° out of phase. The frequency of the ripples is difficult to determine with any precision because the ripple ampli-



(a)



(b)

Fig. 1. For a single observer, the threshold luminance change (corresponding to 75% correct) divided by the masking luminance as a function of location. The results were extracted from an experiment in which the polarity of the signal was randomized. (a) data for increments, (b) data for decrements. The background was a horizontally orientated stimulus producing a dark Mach band near the stimulus inflection point at 1.3° and a bright Mach band near the stimulus inflection point at 2.6°. The signal to be detected was a 0.9' horizontal bar. The vertical lines indicate ± 1 standard deviation.

tude varies along the ramp and the ripples are limited in spatial extent—both factors that broaden their spectra. However, in both cases their frequency is between 5 and 10 cycles/deg.

One possible explanation of the ripples is that they represent alternating excitatory and inhibitory regions of the spatial weighting functions that determine the spatial-frequency and orientation-tuned channels through which spatial variations in luminance are sometimes thought to be detected [8–16].

The present paper describes several experimental examinations of the ripples: first, an attempt to change their frequency by changing the center frequency of the signals to be detected, second by using a luminance step rather than the Mach-band masking stimulus, and finally by changing the stimulus duration.

2. METHODS

Each trial of the two-alternative forced-choice masking experiments had two observation intervals separated by a

uniform field of approximately 800 ms duration. The masking stimulus, usually a luminance ramp for producing Mach bands, varied vertically but was constant in the horizontal direction. [The stimuli were horizontally orientated so that changes in luminance were made at the line rate of the display and not at its pixel rate, thus avoiding the stimulus (slew-rate) dependent distortions that would otherwise occur.] The masker was present in both observation intervals and subtended $4^\circ \times 4^\circ$ of visual angle.

The signal to be detected was one of several different horizontally orientated “bars”, all subtending 4° horizontally. One such bar had a rectangular vertical profile subtending 0.9' vertically. This signal occupied a broad band of spatial frequencies. The vertical cross-sectional luminance profile of the other incremental bar is shown in the top panel on the left in Fig. 2; the absolute value of its power spectrum is shown on the right. The decremental bars (not shown) had the same envelope with a negative cosinusoidal carrier. The vertical luminance profiles consisted of a 5 cycle/deg cosine (or negative cosine), centered in a Gaussian envelope where the σ of the Gaussian envelope was 0.1°. This manipulation narrows the bandwidth of the signal and changes its center frequency. Changing the polarity of the carrier produced no difference in the power spectrum of the signals. Except during the observation intervals, the central $4^\circ \times 4^\circ$ of the screen was a uniform field at the 78 cd/m² mean luminance.

We were minded also to use a signal centered on 15 cycles/deg but, as can be seen in the lower panels of Fig. 2, a 15 cycles/deg carrier inside the same 0.1° Gaussian envelope produces large decrements as well as the central increment so that the spatial specificity of the signal is destroyed; the observers might use the flanking decrements, the central increment, or different combinations of all three to reach their decisions. It would be easy to make a 15 cycle/deg signal more spatially localized by narrowing the Gaussian envelope to produce small flanking decrements like those for the 5 cycle/deg grating, but that manipulation broadens the spatial-frequency spectrum at visible spatial frequencies almost to the width of the spectrum of the rectangular bar. Consequently, only the 5 cycle/deg signal was useful.

The observers were dark adapted for a few minutes before each session. The signal on every trial was either an increment or, with equal probability, a decrement in luminance. In each block of trials, the incremental and decremental signals had the same magnitude. Before each observation interval the location at which the signal might lie was indicated by horizontal red arrows at either side of the masking stimulus. Beside each arrow was a small red numeral indicating whether the observer was viewing interval 1 or interval 2. The arrows were present for 600 ms, ending 200 ms before the trial began; only the shafts of the arrows were present during the observation intervals. The masker and signals were gated on and off rectangularly in time. For the narrowband signals, the signal duration was always 500 ms. With the broadband signals, measurements were made with stimuli of different durations.

Both observation intervals contained the masker and were thus identical in form except that, in one, the signal was added to the masker. On each trial the signal was as

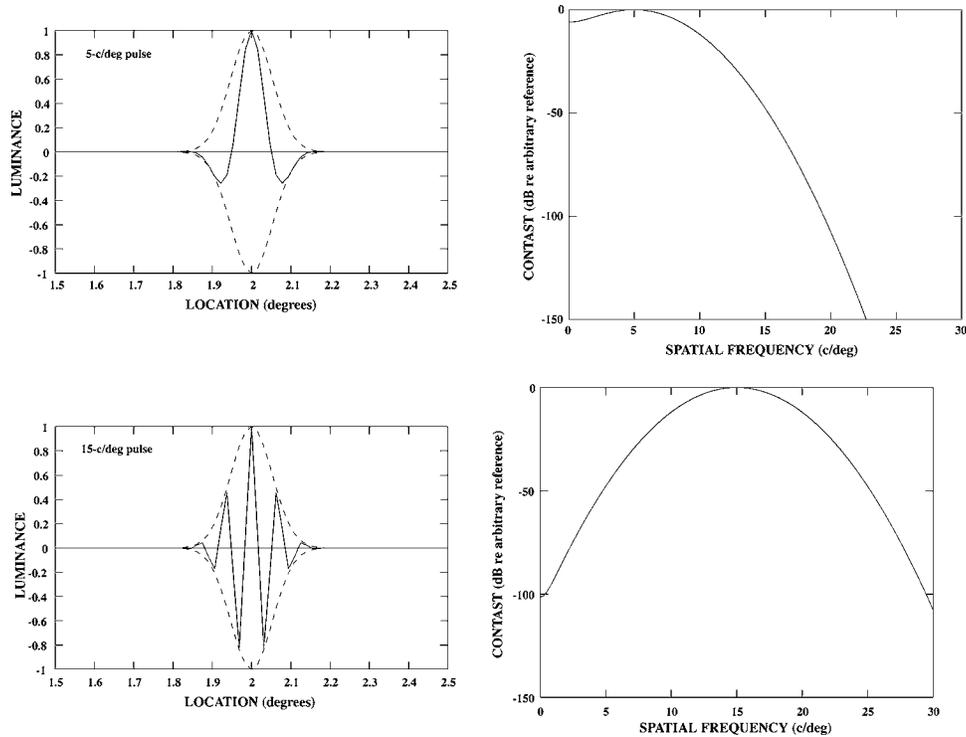


Fig. 2. Cross-sectional luminance profile of narrow-band signal bars (in the left-hand panels) and their spectra the top pair is for an (incremental) 5 cycles/deg cosine carrier within an approximately Gaussian envelope with a σ of about $6'$. In the lower pair the carrier is 15 cycles/deg within the same Gaussian envelope. Decremental signals were produced by changing the sign of the carrier and without affecting the spectra.

likely to be in the first as in the second observation interval, and, when the signal occurred, it was always at the location indicated by the arrows. After pressing a button to indicate the interval they judged to have contained the signal, the observers were informed which interval had been correct by a large red numeral ("1" or "2") shown at the bottom of the display: they were not informed whether the signal had been an increment or a decrement in luminance.

Trials were presented in blocks of 55 with the first five trials for practice. The observers completed a block of trials at a given magnitude of signal contrast at a given location on the masking background. Then the signal magnitude was changed to produce psychometric functions giving the proportion of correct judgments as a function of the signal magnitude, usually for at least five signal levels. The position of the signal was then changed. Psychometric functions at about 35 locations across the masking stimulus were obtained. The experiments were then repeated with the locations in reverse order to give 100 observations for each point on each psychometric function for each condition for each observer.

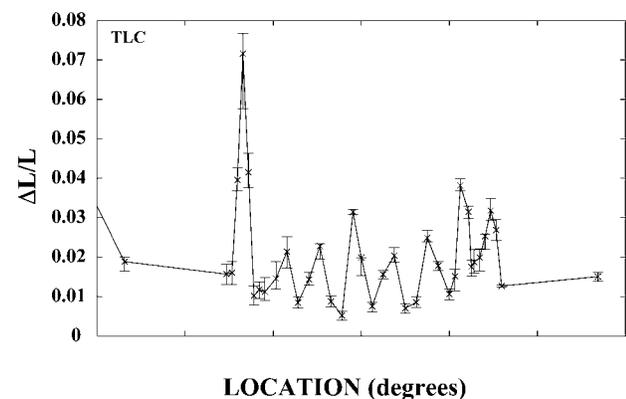
The stimuli were displayed on a Mitsubishi FR8905SKHKL color monitor at a frame rate of 152 Hz (noninterleaved). The monitor screen subtended $6.8^\circ \times 5.5^\circ$ at the viewing distance of 2 m. The dynamic range of the (carefully linearized) display was extended by connecting two 8 bit digital-to-analog converters through a passive attenuator to the green gun of the display, as described by Pelli and Zhang [17], to approximate 12 bit precision in the representation of luminance [4]. Apart from the signal location indicators, the screen was uniformly

dark except for the region subtending $4^\circ \times 4^\circ$, which contained the stimuli. The vertical cross-sectional luminance profile of the Mach-band masker comprised a luminance ramp connecting dark and bright plateaus of constant luminance. The ramp and each of the plateaus subtended $4^\circ \times 1.33^\circ$ of visual angle. The mean luminance of the display was 78 cd/m^2 , measured with a Gamma Scientific photometric telescope calibrated against a beta radiation source. The bright plateau at the bottom of the display had a luminance of 117 cd/m^2 , and the dark plateau at the top, 39 cd/m^2 ; the luminance profile of the ramp connecting the plateaus was linear.

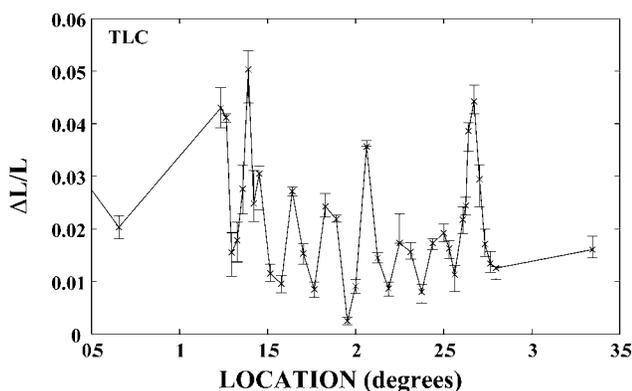
3. RESULTS AND DISCUSSION

A. Narrowband Signal

Consider first the results with the relatively narrowband signal centered on 5 cycle/deg. Because the psychometric functions are approximately parallel on semilogarithmic coordinates, it suffices to consider only one performance level; we use the conventional 75% correct level. Figures 3 and 4 show, separately for two observers (authors), the signal magnitude corresponding to 75% correct as a function of location in the vicinity of the bright Mach band. Figures 3(a) and 4(a) show the results for increments; 3(b) and 4(b), the results for decrements. The ripples in performance are clearly visible and have approximately the center frequency of the signal (5 cycle/deg); the ripples with increments are approximately 180° out of phase from those obtained with decrements and extend large



(a)



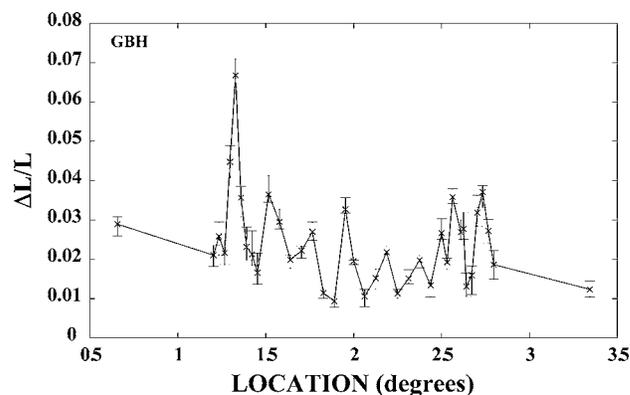
(b)

Fig. 3. In the same format as Fig. 1, the increments (upper panel) and decrements (lower panel) corresponding to 75% correct for observer TLC. The signal to be detected was the 5 cycles/deg bar. The vertical lines indicate ± 1 standard deviation.

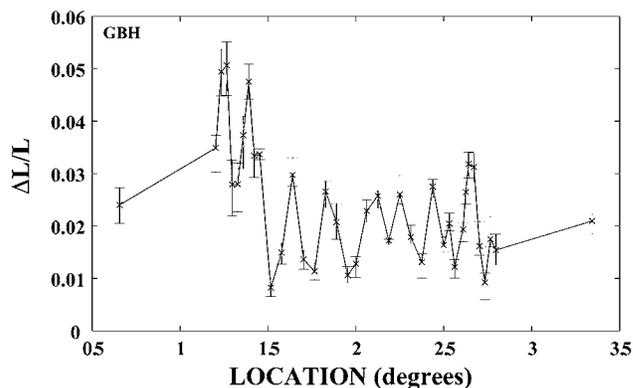
distances from the bands. To determine the spatial frequency and phase of the ripples, we measured the correlation between the data and elements of an array of sinusoids of different spatial frequency and phase. The sinusoids were adjusted to have approximately the same mean value as the data. The data are, of course, noisy, and the ripples are of limited extent and not equal in magnitude. The latter two factors broaden the spectra of the ripples, and all three factors reduce the correlation with extended sinusoids. However, Table 1 gives the frequency and phase of the sinusoids producing the biggest correlations for increments and decrements for both observers at both frequencies. The best frequencies are close to 5 cycle/deg, and the best phase for increments is approximately 180° from the best phase for decrements.

B. Step Masking Stimulus

Figures 5 and 6 show the same observers' performance near a luminance step in the center of the display, 2° from the top of the display. The step jumped from 39 cd/m² on a dark plateau occupying the upper half of the display to 117 cd/m² on a plateau occupying the lower half; thus the change was the same size as the total change in the Mach-band-generating stimulus. The signal was the 5 cycle/deg bar of random polarity, and the 75% correct



(a)



(b)

Fig. 4. As in Fig. 3 but for observer GBH.

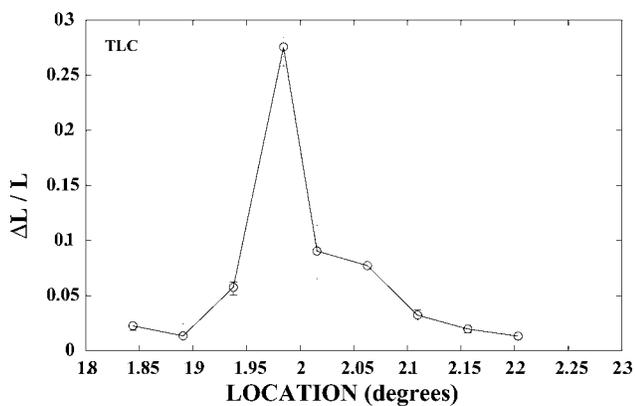
signal levels are again plotted as a function of location in the vicinity of the step. The top panels show the results for increments; the bottom panel, the results for decrements. (Note the change to a much finer scale on the abscissae and the factor of two difference on the ordinates for the two observers.)

The ripples are no longer present for either observer when the masking stimulus is a step. The masking produced by increments and decrements is almost identical; the maximum masking for both increments and decrements for GBH occurs at the step, and for TLC the maximum for increments is shifted by only about 0.04° toward the darker part of the display relative to the maximum masking for decrements. Plotted as $\Delta L/L$ against location, the masking is roughly symmetrical about the step,

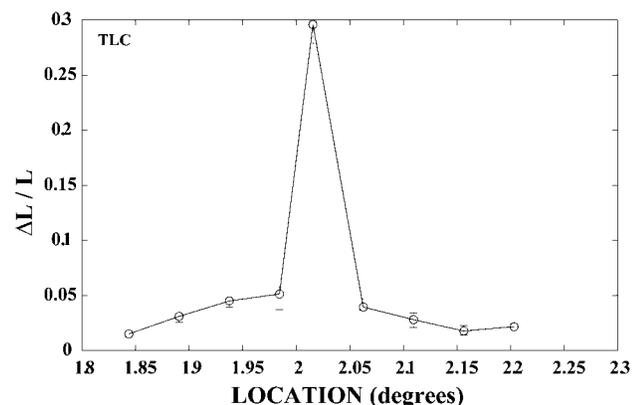
Table 1. Estimates of the Frequency (cycles/deg) and Phase (deg) of Performance Ripples versus Location for Luminance Increment (incs) and Decrements (decs)^a

Observer	Frequency (cycles/deg)	Phase (deg)
TLCincs	4.8	168
TLCdecs	4.8	0
GBHincs	4.9	192
GBHdecs	4.9	0

^aFor two observers, TLC and GBH. The incremental and decremental signals were randomly interleaved but analyzed separately.



(a)



(b)

Fig. 5. As in Fig. 3 but with a masking stimulus that was a step in luminance from the luminance of the lower plateau to that of the upper plateau. The step occurred at 2°.

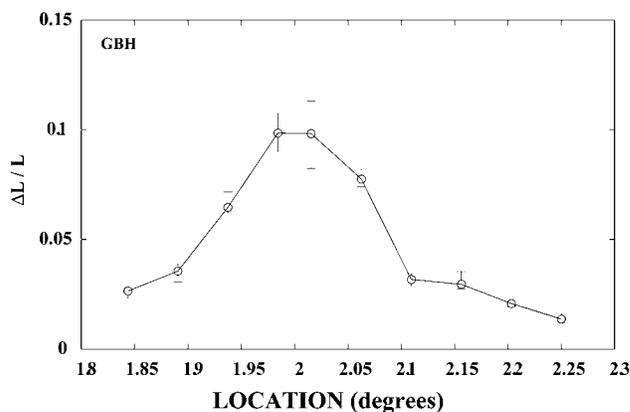
but plotted as ΔL against location, most of the masking would appear to occur on the brighter side as has been previously reported [3,18].

The disappearance of the ripples with the step masking stimulus is difficult to explain but clearly shows that the ripples are a property of the visual system's response to the Mach-band stimulus and not some obscure artifact of the equipment generating the stimulus.

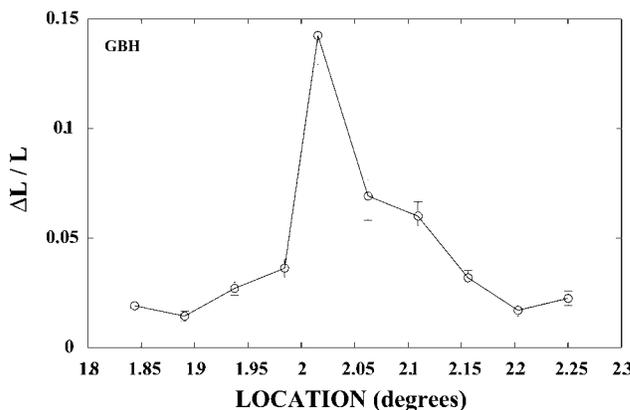
C. Effect of Stimulus Duration

Figures 7–11 summarize the effect of duration on masking by Mach-band stimuli when the signal to be detected is a 0.9' bar. The masking stimulus and the signal, when present, had the same duration and were turned on abruptly. Each figure shows separately for two observers (both authors) the signal magnitude corresponding to 75% correct as a function of location. Figures 7 and 8 show the results for 200 ms stimuli, Figs. 9–11 the results for 25 ms stimuli.

Figures 7 and 8 show that at 200 ms, the ripples remain. The data are noisier than with the long-duration stimuli of Fig. 1, and the Weber fraction $\Delta L/L$ has increased, but the ripples remain roughly the same size. At 25 ms (Figs. 9 and 10) the Weber fraction has increased



(a)



(b)

Fig. 6. As in Fig. 5 but for observer GBH.

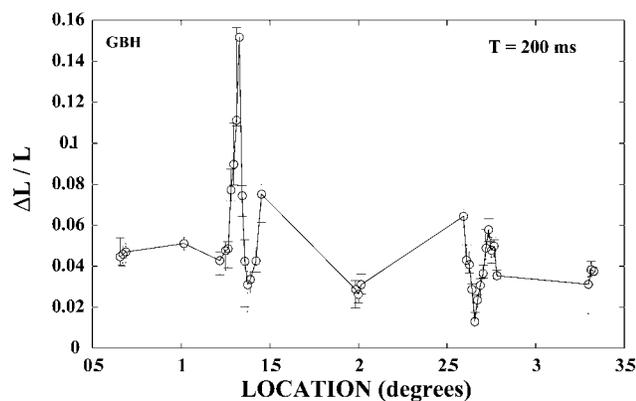
further, particularly on the dark plateau for GBH. Although Weber's law holds for DAC, it no longer holds for GBH, for which $\Delta L/L$ is twice the size on the dark as on the bright plateau.

The masking effects on decrements and increments even for 25 ms stimuli differ: decrements require more magnitude in order to be detected in the vicinity of the edge of the bright plateau than on it and less magnitude to be detected in the vicinity of the edge of the dark plateau than on it. Thus the masking effect of the Mach-band stimulus on decrements follows the perceptual appearance of Mach bands. Increments follow the inverse pattern and require less magnitude to be detected in the vicinity of the edge of the bright plateau than on it and more magnitude to be detected in the vicinity of the edge of the dark plateau than on it. The complementary effects appear clearly in Fig. 11, where the results for 25 ms increments and decrements for the observers' 75% contours are shown on the same graph.

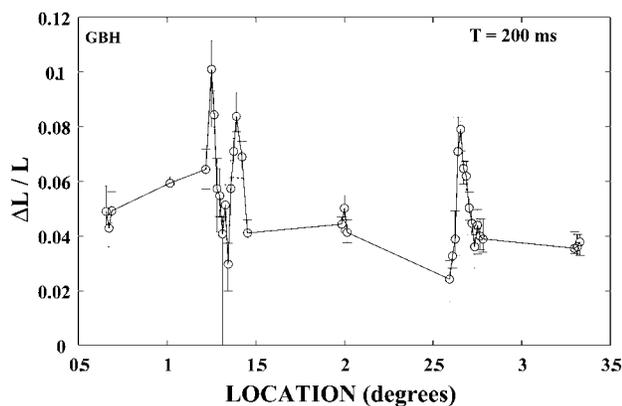
However, the most striking result is that the ripples are very much reduced with 25 ms stimuli.

4. GENERAL DISCUSSION

The easiest interpretation of the ripples is that they reflect the spatial characteristics of the spatial-frequency-



(a)

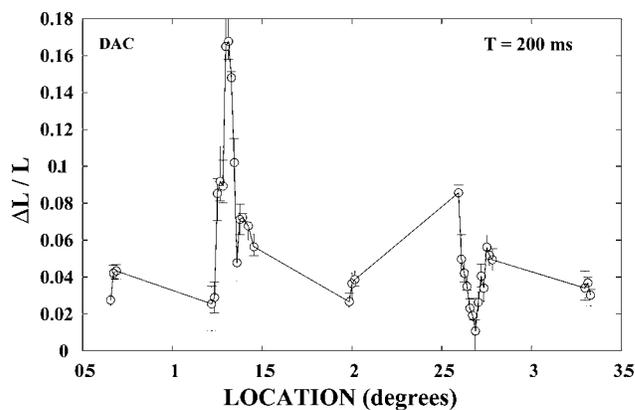


(b)

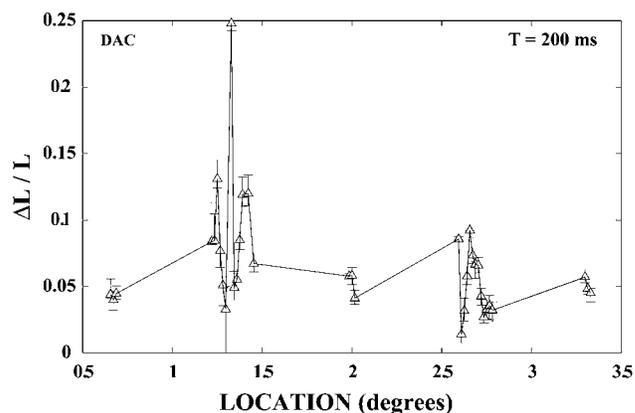
Fig. 7. For GBH, the threshold luminance change (corresponding to 75% correct) divided by the masking luminance as a function of location across the Mach-band stimulus. The signal to be detected was a 0.9' horizontal bar, and the results were extracted from an experiment in which the polarity of the signal was randomized. (a) data for increments; (b) data for decrements. Vertical lines indicate ± 1 standard deviation. The stimulus duration was 200 ms.

tuned channels through which the signals are thought to be detected [8–13,19]. The channel characteristics are usually measured in the spatial-frequency domain and are partially specified by their spatial-frequency tuning; their spatial phase characteristics, on which the form of their spatial-weighting characteristic depends, is usually unspecified [20]. The properties of behavioral channels are sometimes identified with those of orientation- and spatial-frequency-tuned cortical neurons, but the spatial-phase characteristics of the latter are also rarely determined [15]. However, a few general features of the spatial characteristics of a channel can be summarized: if the channel weighting function has alternating positive and negative regions, they will usually ripple at the center frequency of the channel, and the spatial extent of the ripples will decrease as the bandwidth of the channel increases [21].

The left-hand panel of Fig. 12 shows the spatial weighting function of a channel tuned to 5 cycle/deg based on behavioral data [13,20,22] and assuming cosine phase characteristics that produce a weighting function that is symmetrical about its positive peak. The corresponding spatial-frequency-tuning characteristic, shown in the



(a)



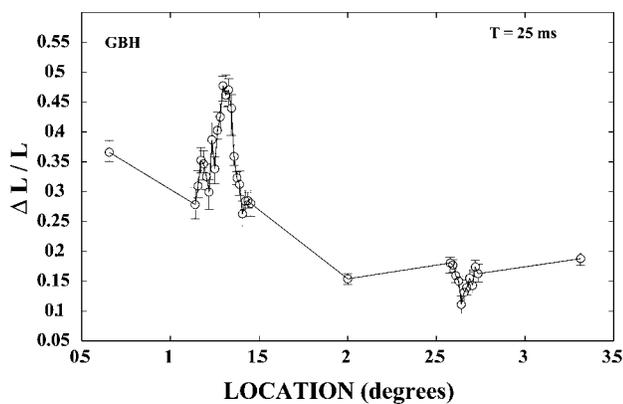
(b)

Fig. 8. As in Fig. 7 but for observer DAC.

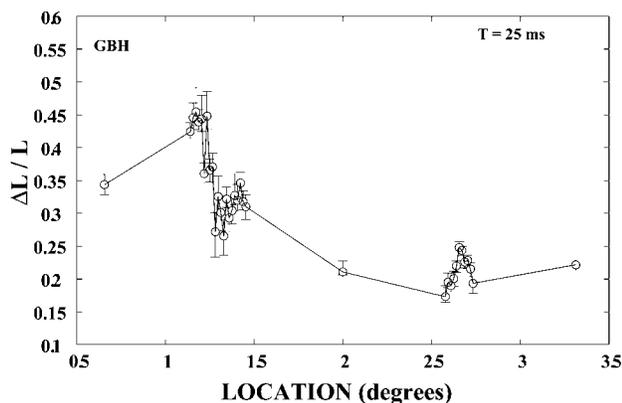
right-hand panel of Fig. 12 is asymmetrical with a 14 dB/octave low-frequency skirt and an 8 dB/octave high-frequency skirt. We cannot say whether it is the ripples seen in the weighting function that are related to the ripples produced in response to a particular polarity signal or whether it is a complimentary filter centered on a negative peak; if this is indeed the explanation, then incremental and decremental signals are processed by complementary weighting functions, since the ripples they produce are 180° out of phase.

If the ripples represent the operation of spatial-frequency-tuned channels, the disappearance of the ripples for the 25 ms stimuli implies that at 25 ms, either the site of masking has changed or the behavioral channels have yet to form—their formation and indeed their characteristics may be determined by the stimuli [20,23].

The different shapes for increments and decrements with the 25 ms stimuli also have implications: the data for decrements follow the appearance of Mach bands, implying, as Mach inferred, a weighting function with an excitatory center and flanking inhibitory surround reminiscent of on-centered cells. The complementary results with increments suggest off-centered cells. This line of argument, together with the lack of ripples, implies that masking at short durations is determined by the tuning characteristics of mechanisms at lower levels in the visual system and that spatial-frequency-tuned channels may be cortical, where more and deeper oscillations in the



(a)



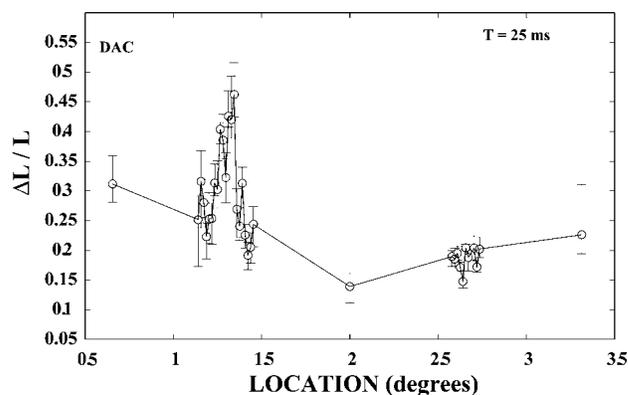
(b)

Fig. 9. As in Fig. 7 but for stimulus duration of 25 ms.

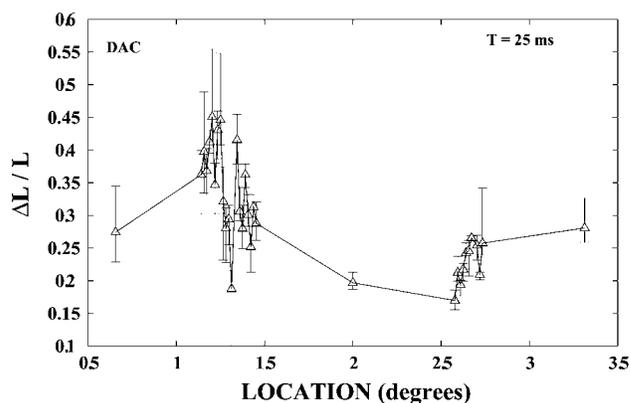
cross section of the spatial weighting functions produce narrower spatial-frequency tuning and, presumably, ripples in the masking functions. At longer durations the masking appears to occur at cortical levels where there are more narrowly tuned mechanisms that, as a consequence of their relatively narrow tuning, have more extensive ripples in their spatial weighting functions.

We can see no easy explanation why the ripples should disappear at a step; for most observers Mach bands are not seen at a step either. Yet explanations based on the linear operation of weighting functions require Mach bands to be greater at a step than at ramps between the same luminance levels. It is hardly an explanation to suggest a different processor, but that seems the only reasonable possibility. In particular, if the spatial-frequency channels that are observed neurophysiologically occur merely when certain stimuli drive them, then the lack of ripples in the masking produced by a step implies that a step stimulus does not create spatial-frequency-tuned channels [20].

The 25 ms masking function with decrements, which follow the appearance of Mach bands, appears to be processed in on channels and increments in off channels. Whether this is a reasonable suggestion depends on the form of the rate versus level functions for the two types of channel and on the rates determined by the background on the plateaus and near the bands [24].



(a)



(b)

Fig. 10. As in Fig. 8 but for stimulus duration of 25 ms.

Geometrical considerations of circularly symmetrical receptive fields that have an antagonistic surround roughly balancing the central region suggest that their response to narrow strips lying across their centers will be in the direction determined by the central region. Thus signals that are luminance increments lying across the centers of receptive fields will increase the response of on cells and decrease the response of off cells; strips of luminance decrement will have the opposite effect. For on cells, the response under the bright plateau will always be less than for on cells located with their central region just touching the edge of the bright plateau. On cells under the dark plateau will have a higher response than on cells located with their central region just touching the edge of the dark plateau. The opposite situation occurs with off cells.

To proceed further, assume that the response of both cells approaches some asymptotic upper rate limit and that the response of both types of cell to the brief 25 ms flash of the Mach-band stimulus is just below that saturation rate where the rate versus intensity function becomes negatively accelerated. In this operating regime, a masker location producing a greater response will produce more masking than a location producing a smaller response. This is because the curvature of the rate versus intensity function means that a bigger signal will be necessary to produce the same change in response as that

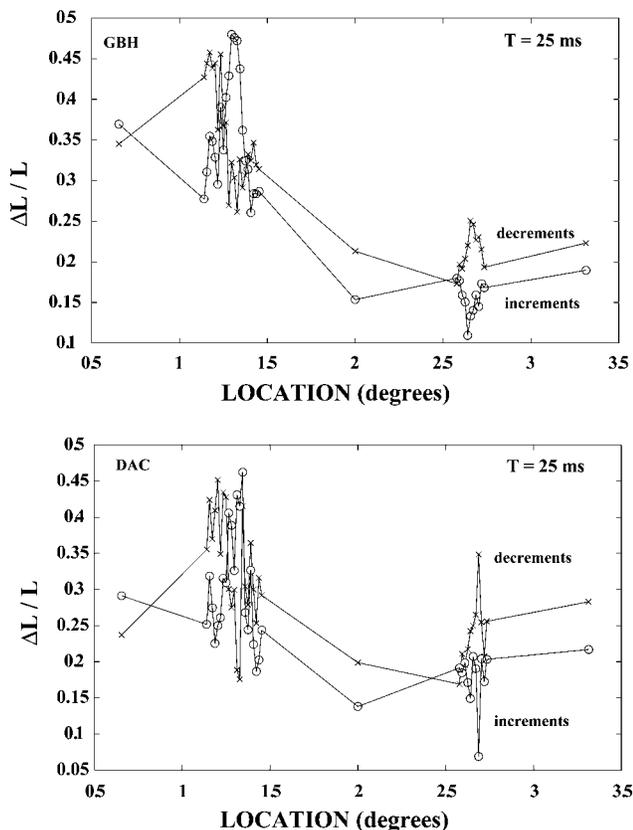


Fig. 11. Data for 25-ms increments and decrements on the same graph; upper panel, GBH; lower panel, DAC.

produced where the masker is less effective. On this line of argument, the behavior with increments fits the response of off cells and the behavior with decrements fits the response of on cells, just as we observe.

Further, in this near saturation region, the response of off cells to incremental signals will be greater than the response of on cells because the increments drive the response of off cells lower, away from the saturating level, and increments drive on cells further toward their saturation level. Thus it would be expected that off cells would dominate the behavioral response to increments.

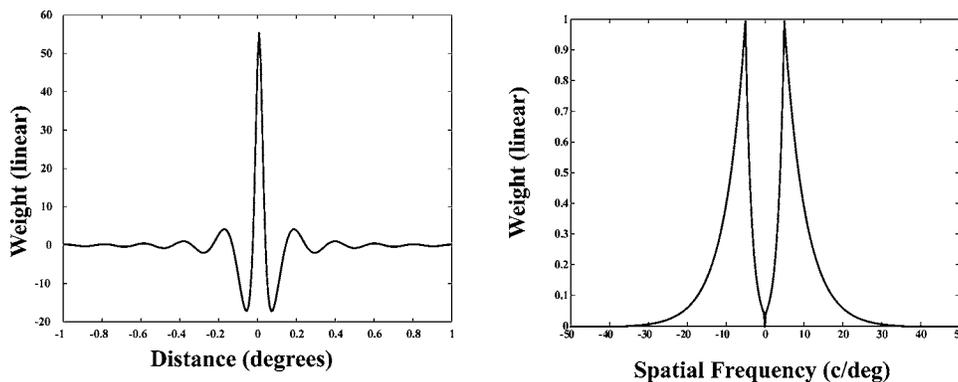


Fig. 12. Left-hand panel, the spatial weighting function of a channel tuned to 5 cycles/deg based on noise masking data and assuming cosine phase characteristics that produces a weighting function that is symmetrical about its positive peak. Right-hand panel, corresponding spatial-frequency tuning.

Similar arguments imply that on cells should dominate the behavioral response to decrements, but we are reluctant to speculate further in the absence of relevant physiological observations.

It is possible that the data at short durations arise because spatial-frequency tuning in cortical cells is slow to develop and not present for 25 ms stimuli. Increasingly, more is being discovered about the functional characteristics of the higher levels of the visual system [23,25]. However, there are some physiological data showing that spatial-frequency tuning is present at short durations in cortical cells and that it is only the spatial frequency to which they respond best that changes with duration [26]. On the other hand, there are data that show little orientation or spatial-frequency tuning in cortical cells at short durations [27–30].

5. SUMMARY

The masking effects of Mach bands on signals of random polarity are different, depending on whether the stimulus is an increment or a decrement. With signals of long duration, there are large ripples in the function relating the signal threshold magnitude to location. The ripples for increments and decrements have similar spatial frequencies but are approximately 180° out of phase. The spatial frequency of the ripples (about 8 cycle/deg with broad band signals) can be altered by manipulating the spatial-frequency content of the signals.

The ripples vanish at a luminance step. They also vanish at stimulus durations below 25 ms, implying that either the site of masking has changed or that the weighting function and hence spatial-frequency tuning is slow to develop.

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REFERENCES

1. E. Mach, "Über die Wirkung der räumlichen Verteilung des Lichtreizes auf die Netzhaut," in *Mach Bands: Quantitative Studies on Neural Networks in the Retina*, F. Ratliff, ed. (Holden-Day, 1965).
2. F. Ratliff, ed. in *Mach Bands: Quantitative Studies on Neural Networks in the Retina* (Holden-Day, 1965).
3. G. B. Henning, R. W. Millar, and N. J. Hill, "Detection of incremental and decremental bars at different locations across Mach bands and related stimuli," *J. Opt. Soc. Am. A* **17**, 1147–1159 (2001).
4. G. B. Henning, K. T. Hoddinott, Z. J. Wilson-Smith, and N. J. Hill, "Masking effect produced by Mach bands on the detection of narrow bars of random polarity," *J. Opt. Soc. Am. A* **21**, 1379–1387 (2004).
5. A. Fiorentini, M. Jeanne, and G. M. Toraldo di Francia, "Mésures photométrique visuelles sur un champ à gradient d'éclairement variable," *Opt. Acta* **10**, 209–216 (1955).
6. F. A. Wichmann and N. J. Hill, "The psychometric function: I. Fitting, sampling and goodness-of-fit," *Percept. Psychophys.* **63**, 1293–1313 (2001).
7. F. A. Wichmann and N. J. Hill, "The psychometric function: II. Bootstrap-based confidence intervals and sampling," *Percept. Psychophys.* **63**, 1314–1329 (2001).
8. F. W. Campbell and J. G. Robson, "Application of Fourier analysis to the visibility of gratings," *J. Physiol. (London)* **197**, 551–566 (1968).
9. C. Blakemore and F. W. Campbell, "On the existence of neurons in the human visual system selective to the orientation and size of retinal images," *J. Physiol. (London)* **203**, 237–260 (1969).
10. U. Greis and R. Röhler, "Untersuchungen der subjectiven Detailerkennbarkeit mit Hilfe der Ortsfrequenzfilterung," *Opt. Acta* **17**, 515–526 (1970).
11. B. E. Carter and G. B. Henning, "The detection of gratings in narrow-band visual noise," *J. Physiol. (London)* **219**, 355–365 (1971).
12. C. F. Stromeyer III, and B. Julesz, "Spatial-frequency masking in vision: critical bands and the spread of masking," *J. Opt. Soc. Am.* **62**, 1221–1232 (1972).
13. G. B. Henning, B. G. Hertz, and J. L. Hinton, "Effects of different hypothetical detection mechanisms on the shape of spatial-frequency filters inferred from masking experiments: I. Noise masks," *J. Opt. Soc. Am.* **71**, 574–581 (1981).
14. R. L. DeValois and K. K. DeValois, *Spatial Vision* (Oxford U. Press, 1988).
15. D. B. Hamilton, D. G. Albrecht, and W. S. Geisler, "Visual cortical receptive fields in monkey and cat: spatial and temporal phase transfer functions," *Vision Res.* **29**, 1285–1308 (1989).
16. N. van S. Graham, *Visual Pattern Analyzers* (Oxford U. Press, 1989).
17. D. Pelli and L. Zhang, "Accurate control of contrast on microcomputer displays," *Vision Res.* **31**, 1337–1350 (1991).
18. S. Novak and G. Sperling "Visual thresholds near a continuously visible or a briefly presented light-dark boundary," *J. Opt. Soc. Am.* **53**, 1–5 (1963).
19. G. B. Henning, "Spatial-frequency tuning as a function of temporal frequency and stimulus motion," *J. Opt. Soc. Am. A* **5**, 1362–1373 (1988).
20. G. B. Henning, A. M. Derington, and B. C. Madden, "Detectability of several ideal patterns," *J. Opt. Soc. Am.* **73**, 851–854 (1983).
21. A. Papoulos, *Systems and Transforms with Applications in Optics* (McGraw-Hill, 1968).
22. G. B. Henning, "Masking effect of low-frequency sinusoidal gratings on the detection of contrast modulation in high-frequency carriers," *J. Opt. Soc. Am. A* **21**, 486–490 (2004).
23. R. W. Guillery and S. M. Sherman, "Thalamic relay functions and their role in corticocortical communication: generalizations from the visual system," *Neuron* **33**, 163–175 (2002).
24. G. Sperling and Z.-L. Lu, "Unequal representation of black and white in human vision," *Invest. Ophthalmol. Visual Sci.* **40**, S200 (1999).
25. L. C. Sincich and J. C. Horton, "The circuitry of V1 and V2: integration of color, form, and motion," *Annu. Rev. Neurosci.* **28**, 303–326 (2005).
26. D. G. Albrecht, W. S. Geisler, R. A. Frazor, and A. M. Crane, "Visual cortex of monkeys and cats: temporal dynamics of the contrast response function," *J. Neurophysiol.* **88**, 888–913 (2002).
27. D. L. Ringach, M. J. Hawken, and R. M. Shapley, "Dynamics of orientation tuning in macaque primary visual cortex," *Nature* **387**, 281–283 (1997).
28. C. E. Bredfeldt and D. L. Ringach, "Dynamics of spatial frequency tuning in macaque V1," *J. Neurosci.* **22**, 1976–1984 (2002).
29. D. L. Ringach, C. E. Bredfeldt, R. M. Shapley, and M. J. Hawken, "Suppression of neural responses to non-optimal stimuli correlates with selectivity in macaque V1," *J. Neurophysiol.* **87**, 1018–1027 (2002).
30. D. Xing, D. L. Ringach, R. M. Shapley, and M. J. Hawken, "Correlation of local and global orientation and spatial frequency in Macaque V1," *J. Physiol. (London)* **557**, 923–933 (2004).