

Correction. In the article "Direct observation of large chiral domains in chloroplast thylakoid membranes by differential polarization microscopy" by Laura Finzi, Carlos Bustamante, Gyözö Garab, and Ching-Bo Juang, which appeared

in number 22, November 1989, of *Proc. Natl. Acad. Sci. USA* (86, pp. 8748–8752), Fig. 2 was incompletely reproduced due to a printer's error; the more accurate Fig. 2 appears below.

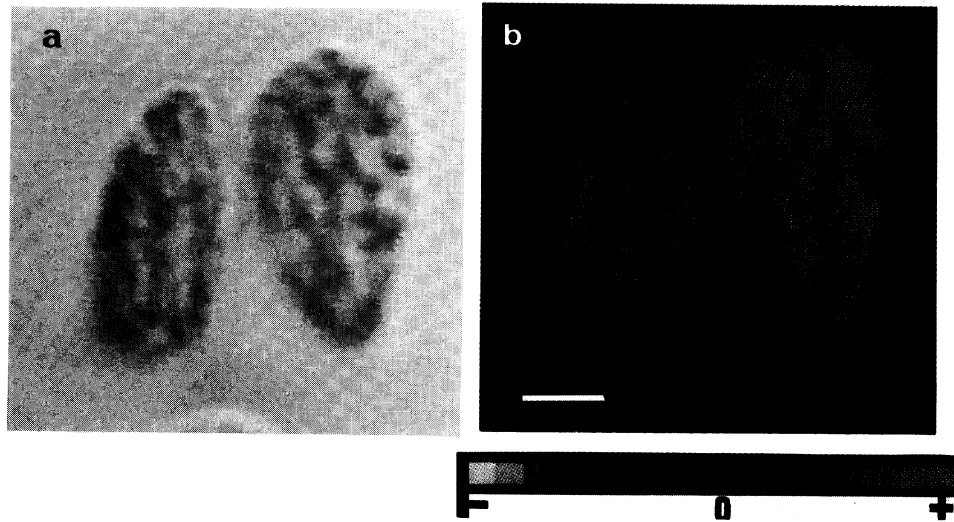


FIG. 2. (a) Nonpolarized image of two edge-aligned chloroplasts; (b) LD image $I_H - I_V / I_H + I_V$; horizontal polarization (H) is defined parallel to the bottom edge of this figure. The largest positive value of the dichroic ratio measured in this LD image was 0.11. Color scale for the dichroic values is shown. For this image the lightest shade of blue in the color bar corresponds to a dichroic ratio of 0.11. (Bar = 2 μm .)

Correction. The article "Texture interactions determine perceived contrast" by Charles Chubb, George Sperling, and Joshua A. Solomon, which appeared in number 23, December 1989, of *Proc. Natl. Acad. Sci. USA* (86, 9631–9635), was listed under the wrong classification in the Table of Contents. The article should have been listed under Psychology instead of Population Biology.

Correction. For the article "A case at last for age-phased reduction in equity" by Paul A. Samuelson, which appeared in number 22, November 1989, in *Proc. Natl. Acad. Sci. USA* (86, 9048–9051), the following printer's error should be noted. The incorrect listing in the Table of Contents was Biological Sciences. The correct category is Social Sciences.

Texture interactions determine perceived contrast

(spatial vision/perception/lateral inhibition)

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Contributed by George Sperling, August 24, 1989

ABSTRACT For a patch of random visual texture embedded in a surrounding background of similar texture, we demonstrate that the perceived contrast of the texture patch depends substantially on the contrast of the background. When the texture patch is surrounded by high-contrast texture, the bright points of the texture patch appear dimmer, and simultaneously, its dark points appear less dark than when it is surrounded by a uniform background. The induced reduction of apparent contrast is greatly diminished when (i) the texture patch and background are filtered into nonoverlapping spatial frequency bands or (ii) the texture patch and background are presented to different eyes. Our results are unanticipated by all current theories of lightness perception and point to a perceptual mechanism for contrast gain control occurring at an early cortical or precortical neural locus.

Simultaneous Brightness Contrast. The perceived lightness of a uniformly luminant disc viewed on a large uniform surrounding background depends not directly on the luminance of the disc, but rather on the ratio of disc luminance to background luminance (1–3). Even a spatially restricted background affects perceived lightness as illustrated by the illusion shown in Fig. 1 *a* and *b*. The discs in Fig. 1 *a* and *b* are equiluminant; nonetheless, the disc in *a* appears lighter than the disc in *b*. This phenomenon of *simultaneous contrast* is interpreted in terms of a ratio rule by noting that in *a* the ratio of the disc's luminance to background luminance is greater than 1; in *b*, the ratio is less than 1.

Lateral Inhibition. A natural way to explain simultaneous contrast is in terms of *lateral inhibition*. Many models based on lateral inhibition have proposed that, at some level of visual processing, neurons strongly stimulated by the high-intensity background of the disc in Fig. 1 *b* suppress the less strongly stimulated neurons responding to the interior of the disc. In Fig. 1 *a*, the corresponding neurons within the disc receive no such inhibition from the weakly stimulated neurons surrounding them. Consequently, the neurons located within the disc of Fig. 1 *a* respond more vigorously than their counterparts in *b*.

Under the crudest lateral inhibition model, the lightness of a given point in the visual field would be suppressed in proportion to the intensity of each nearby point (1). But such a scheme would result, for example, in lower lightness values for points near the edge of the disc in Fig. 1 *b* than for points in its interior. The fact that both discs in Fig. 1 *a* and *b* appear to be of uniform lightness across their full expanse suggests a more complex form of lateral inhibition (4). Regardless of their details, all models that invoke the principle of lateral inhibition rest on the assumption that the primary factor determining the perceived lightness of either disc in Fig. 1 *a* or *b* is the ratio, at the disc edge, of disc luminance to background luminance.

Induced Reduction of Apparent Contrast. We report here an apparent lightness phenomenon that is beyond the scope of all such models. The basic effect can be observed in a display analogous to Fig. 1 *a* and *b*, except that—instead of varying luminance between a disc and its background—we vary the *contrast* of a random visual texture. In Fig. 1 *c*, the zero-luminance (black) background of Fig. 1 *a* becomes a zero-contrast (mean-luminant) gray field; the high-luminance white field of Fig. 1 *b* becomes a high-contrast texture field in Fig. 1 *d*; and the two gray discs become discs of intermediate texture contrast (0.5).

It is an empirical fact that all observers perceive the texture disc of Fig. 1 *c* as being somewhat higher in contrast than the texture disc in Fig. 1 *d*, despite the fact that the two discs are identical. (We describe a stronger form of the illusion below.) The bright pixels in the texture disc of Fig. 1 *c* appear brighter than their counterparts in *d*, and simultaneously the dark pixels in the disc of *c* appear darker than their counterparts in *d*.

For each of the discs in Fig. 1 *c* and *d*, the average difference in luminance at the border between the disc and its background is 0 (except for random fluctuations). In fact, every single pixel in Fig. 1 *c* and *d* has an expected luminance equal to the mean luminance. Therefore, except for random fluctuations, any two areas of Fig. 1 *c* and *d* have the same average luminance, and any consistent difference in appearance between the discs of Fig. 1 *c* and *d* cannot be accounted for by standard (luminance-based) lightness models.

EXPERIMENTS 1 AND 2: CONTRAST AND LIGHTNESS INDUCTION

Method. To compare Fig. 1 *c* and *d*, most observers shift their eyes back and forth between the two texture discs. To produce a stronger version of the texture-contrast illusion that does not involve eye movements, we use just Fig. 1 *d* and modulate the contrast of the background texture sinusoidally in time between extreme contrasts of 0 and 1. In addition, we produce a new, independent realization of the random pattern instantiated by Fig. 1 *d* 60 times per second. This produces 60-Hz texture flicker over the whole field, but it eliminates any figural cues and renders negligible any effects of eye movements on the spatiotemporal frequency content of the retinal stimulus. The slow contrast modulation of the background causes subjects to perceive the contrast of the texture disc to be modulating in antiphase. When background contrast is high, texture-disc contrast appears to be low, and vice versa.

We used two nulling experiments to measure the induced modulation of the apparent lightness of both the dark and bright pixels of the texture disc. In the first nulling experiment, subjects viewed the texture disc while the contrast of the surrounding background was being sinusoidally modulated (at 0.47 Hz) between 0 and 1. Simultaneously, the contrast of the center disc was modulated in phase with the background. The mean luminance of the texture disc was

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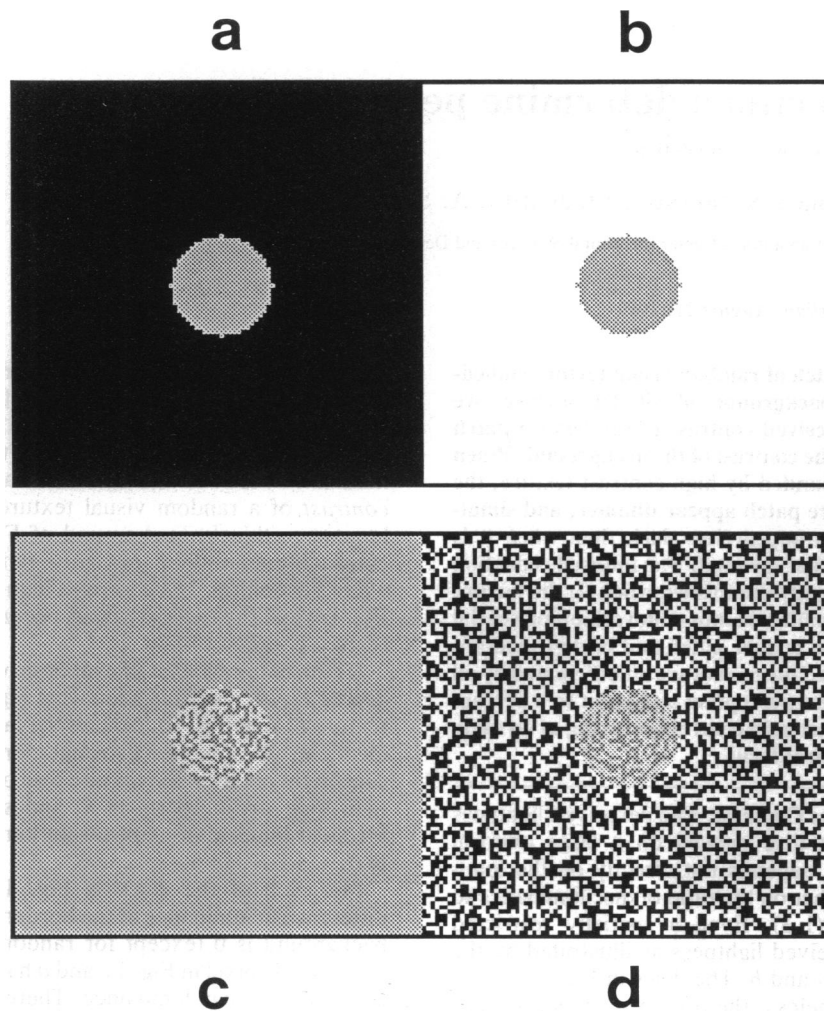


FIG. 1. Two factors influencing the lightness values assigned points in the visual field. (*a* and *b*) Classical lightness contrast. The lightness of a disc viewed on a background depends not only on the luminance of the disc but also on the ratio of disc luminance to background luminance (boundary contrast). The ratio of the luminance of disc to background is greater than 1 for *a* and less than 1 for *b*. Although discs in *a* and *b* have the same luminance, that in *a* appears lighter than that in *b*. (*c* and *d*) Induced contrast reduction. Like the mean-luminant discs in *a* and *b*, the texture discs in *c* and *d* are identical; each is of contrast ≈ 0.5 . Because of the lower-contrast background, the disc in *c* appears to be of higher contrast than that in *d*.

kept constant in time. Subjects adjusted the modulation amplitude of the disc's contrast until disc contrast appeared constant in time.

The purpose of the second experiment was to determine whether or not there was a modulation of texture-disc overall lightness induced by modulating the contrast of the texture background. Accordingly, the contrast and the mean luminance of the texture disc were simultaneously modulated in phase with the background. The modulation amplitude of texture-disc contrast was fixed at the level (determined for each subject in the first experiment) at which the induced contrast modulation was nulled. Then, subjects adjusted the amplitude of texture-disc mean luminance modulation until the overall lightness of the disc appeared constant in time.

All displays were viewed binocularly from a chin rest at a distance of 1 m. At this distance, the texture disc was 1.35° in diameter centered in the 3.6° square background texture field.

Results. We tested texture discs with mean contrasts ranging from 0.2 to 0.5, and for all (*i*) the induced contrast modulation of the texture disc was substantial, while (*ii*) the induced overall lightness modulation was negligible. Thus, modulating the contrast of the texture background induces joint modulations of the apparent lightnesses of dark and bright pixels in the texture disc—joint modulations that are

canceled by equal and opposite modulations of the luminances of dark and bright pixels in the disc.

The magnitude of this illusion is illustrated graphically in Fig. 2 for a mean texture-disc contrast of 0.4. The sinusoidal broken line gives the contrast of the background as a function of time. For a texture disc whose mean contrast (over time) is fixed at 0.4, subjects found it necessary (in the first nulling experiment) to modulate texture-disc contrast in accordance with the solid line of Fig. 2 in order to make texture-disc contrast appear constant in time. Thus, the texture disc appears to remain at a constant contrast (as shown by the flat broken line of Fig. 2) when its contrast is actually modulating in conformity with the solid line of Fig. 2. The amplitude of this nulling modulation (averaged for two subjects) is 45% of the texture disc's mean contrast. Similar data were obtained in other conditions.

EXPERIMENT 3: INTEROCULAR INDUCTION

Method. Is the induced modulation of texture-disc apparent contrast the result of an early or a late visual process? One way of investigating this question is to see whether or not the induction can occur across different eyes. Interocular induction implies that the neurons responsible for the induction must be at the level of the cortex or a higher visual center.

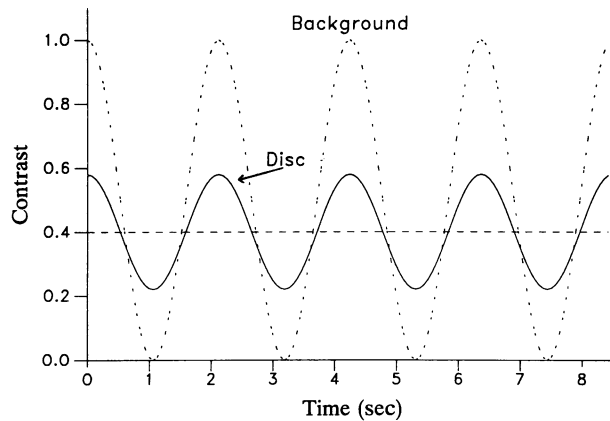


FIG. 2. Induced modulation of the apparent contrast of a texture disc. When a texture disc is viewed against a texture background whose contrast is sinusoidally modulated, the apparent contrast of the texture disc varies in antiphase to the background. In exp. 1, the background contrast varied between 0 and 1 at 0.47 Hz as shown by the sinusoidal broken line. For a texture disc whose mean contrast (over time) was fixed at 0.4, subjects found it necessary to modulate texture-disc contrast in accordance with the solid line to null the induced contrast modulation (i.e., to make contrast of the disc appear to follow the flat broken line). The amplitude of the nulling modulation was 45% of the texture disc's mean contrast.

Strictly monocular induction implies that the locus of the induction is an early cortical or precortical cell population. Accordingly, we performed a third experiment in which the inducing background was delivered to one eye and the test disc to the other eye. Again we used the method of adjustment. There were four kinds of trials: (i) both disc and background were presented to the right eye; (ii) both were presented to the left eye; (iii) the left eye saw only the disc and the right eye saw only the background; and (iv) the right eye saw the disc and the left eye saw the background. Whenever a region of one eye's retina was presented with texture, the corresponding region of the opposite retina was presented with uniform mean luminance.

To minimize binocular rivalry, we used the following presentation sequence: The texture disc (which was 1.1° in diameter) was flashed periodically. Each flash lasted 133 ms, and flashes were separated by 500-ms periods of uniform mean luminance. Two types of disc flashes were alternated: background-on flashes and background-off flashes. On background-on flashes the texture disc was surrounded by a (2.9°) square texture background of contrast 1. On background-off flashes, the texture disc was surrounded by a background of contrast 0 (i.e., a uniform mean-luminant field). For some δ , under the subject's control, the contrast of the texture disc was $0.4 + \delta$ on each background-on flash and $0.4 - \delta$ on each background-off flash. On each trial, the subject adjusted δ (which was randomly initialized) until the contrast of the texture disc on background-on flashes appeared equal to its contrast on background-off flashes.

Results. Virtually identical data were obtained for two subjects; the data for one subject are shown in Fig. 3. On the trials in which both texture disc and texture background were presented to the same eye (either both to the right eye or both to the left), subjects had to make the contrast of the texture disc 40% higher on the background-on presentations than on the background-off presentations to equalize the apparent contrast of the texture disc across alternating background-on and background-off presentations. However, when texture disc and texture background were presented to opposite eyes, no such compensating adjustment was required. We infer that the contrast of the texture background influences the apparent contrast of the texture disc only when disc and

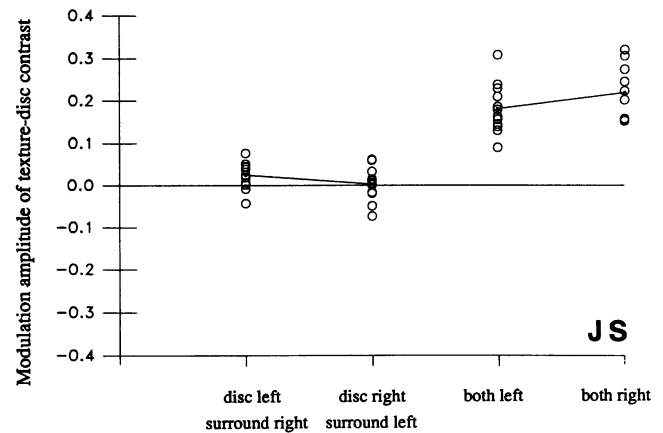


FIG. 3. Does the induced contrast modulation occur when texture disc and background are presented to opposite eyes? The subject modulates the contrast of a texture disc between two values around a mean of 0.4 so that it appears constant when the disc is viewed alternately against a high-contrast texture background and a mean-luminant background. Ordinate indicates the difference (resulting from subject adjustments) in texture-disc contrast between high-contrast-background presentations and mean-luminant-background presentations. Abscissa indicates the eye to which the disc and background are presented. Data (10 trials per condition) are shown for one subject (JS). Lines are drawn between the means. Only same-eye presentations induced a reduction of apparent contrast; this indicates an early cortical or precortical site for contrast gain control.

background are presented to the same eye. This finding restricts the physiological location of the mechanism underlying this induction to an early cortical or precortical neuron population (5, 6).

EXPERIMENT 4: INDUCTION BETWEEN SPATIAL FREQUENCY BANDS

Method. In a fourth experiment, we examined whether or not texture filtered into one spatial frequency band could influence the perceived contrast of texture in a different spatial frequency band; that is, whether contrast induction is narrowly or broadly tuned for spatial frequency. We spatially filtered the texture of the disc through an ideal, octave-wide, nonoriented filter. The background was filtered by one of three adjacent octave-wide filters. The middle background filter was identical to the texture-disc filter (the frequencies passed by this filter were between 5.8 and 11.6 cycles per degree at a viewing distance of 1 m). Examples of each of the three textures are shown in Fig. 4.

Results. The results for two subjects are shown in Fig. 5. For both subjects, the largest contrast modulation is induced when the background texture is the same as the disc texture. When the background texture is in an adjacent octave-wide band, either one octave above or one octave below the disc texture, the induction is much weaker for both subjects. These results show that the reduction in apparent contrast of a disc induced by a textured background is spatial-frequency-specific. Preliminary investigations into orientation specificity indicate that when an oriented background texture is not in the same orientation as the disc texture, its influence on the perceived contrast of the disc texture is diminished.

DISCUSSION

The results of the fourth experiment suggest that, at some level of visual processing, neurons tuned to roughly a single octave (or less) in spatial frequency interact across space

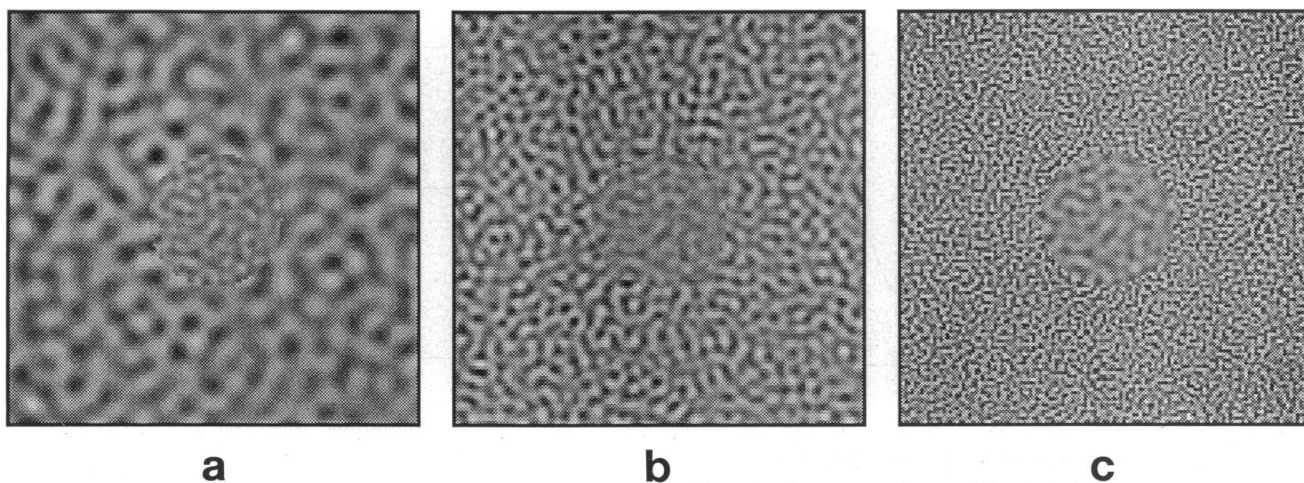


FIG. 4. Can texture of one spatial frequency affect the apparent contrast of texture of a different spatial frequency? Freeze frames of stimuli in which background and disc were filtered through ideal, octave-wide, spatial-frequency filters. (a) Background spatial frequencies are one octave below disc frequencies; (b) background and disc frequencies are the same; (c) background frequencies are one octave above disc frequencies.

with similarly tuned neurons. Taken together, our results support a model in which the output gain of such a band-selective neuron is normalized relative to the average response amplitude of nearby neurons with the same frequency tuning. Neurons differing in frequency tuning by more than an octave have much less influence on each other.

Several investigators have reported lateral inhibitory interactions between adjacent complex stimuli—for example, between textures of different spatial frequency (7), between lines differing in orientation (8, 9), and between different local velocities (10). The interactions have been small because these paradigms required the two stimuli to differ in their critical dimension: spatial frequency, orientation, or velocity. In a precursor of the present paradigm, Sagi and Hochstein (11) used a grating whose contrast was spatially modulated analogously to luminance in the Craik-O'Brien-

Cornsweet illusion (12) to provide evidence for lateral texture-contrast inhibition. However, their display did not permit measurement of the effect.* Interneuron texture interactions have also been proposed on the basis of data obtained in searching for a target among distractor items (13). Precise though such a theory may be, the data themselves admit other explanations and provide only indirect indications of texture interactions. Thus, the present experiments illustrate a kind of robust, spatial, feature-specific interaction that is (i) similar to gain control as observed in physiological experiments (14) and (ii) anticipated in the explanation of complex search tasks (13), but that has not, to our knowledge, been unambiguously observed before with simple textured stimuli in a psychophysical setting.

SUMMARY AND CONCLUSION

We have demonstrated the dependence of the perceived lightness of a point in space on lateral texture interactions in the visual display. The perceived contrast of a patch of texture is dramatically influenced by the contrast of surrounding texture. In particular, for spatial texture in a certain frequency band, the perceived contrast varies inversely with the contrast of surrounding texture in the same band. We showed that this lateral inhibitory effect is strictly monocular and that it is narrowly tuned for spatial frequency. The possible implications for perceptual theories are profound. On the one hand, it appears that the lightness of a point in space is a far more complex function of its environment than had hitherto been suspected—it will take a great deal of work to elaborate the precise spatiotemporal properties of the textural interactions sketched out here. On the other hand, if there are such specific lateral connections between spatial-frequency-tuned neurons and their similarly tuned neighbors, might there not be equally specific connections to normalize the responses of other classes of neurons? Is self-normalization a universal perceptual principle?

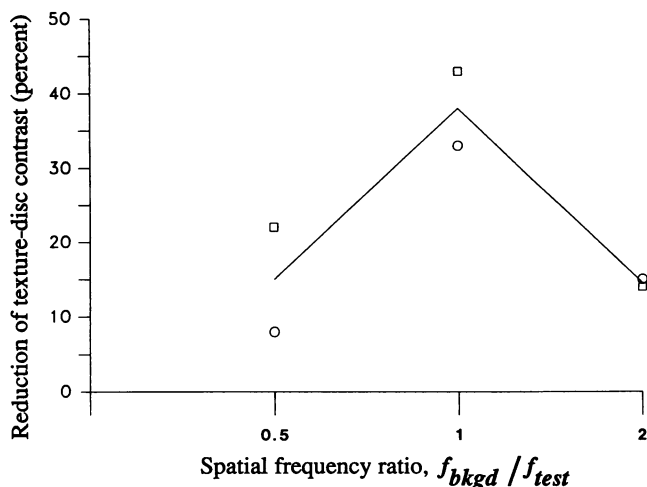


FIG. 5. Induction of texture-disc apparent contrast is narrowly tuned for spatial frequency. A nulling procedure was used with the stimuli of Fig. 4. Ordinate indicates the difference in contrast between a texture-surrounded test disc (of contrast 0.4) and a texture disc matched in apparent contrast to the test disc, viewed against a uniform grey background. Abscissa indicates the spatial frequency of the background. Symbols indicate data for each of two subjects; each point is the average of the last 10 reversals of a staircase. Measurement error is approximately equal to symbol size. These data suggest that induced contrast reduction has approximately a one-octave spatial-frequency bandwidth.

*Sagi and Hochstein also reported that a light bar of a grating adjacent to a zero-contrast area appeared lighter than other bars. It is possible to account for this effect in terms of simple luminance interactions; it does not strictly require texture interactions.

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