adapted since the black patch had not been applied.) There was no change in the CFF of the occluded eye at any time (Fig. 1, bottom). Thus, the depression-enhancement phenomenon is specific to the nonoccluded eye (*4*).

Although numerous variables affect the CFF, it is difficult to understand how any of them can account for both our present and earlier (*3*) results for the nonoccluded eye. The unusual time course, together with the persistence of the phenomenon for many days, suggests the disturbance of some interocular mechanism in the higher levels of the visual system. We believe that prolonged monocular deprivation may be producing changes in certain areas of the primary sensory system, changes similar to the denervation supersensitivity that occurs in the higher neural centers after partial surgical deafferentation at lower levels of the central nervous system (*6*). For example, Spiegel and Szekely (*7*) reported that lesions in the posteroventral nucleus of the thalamus (relay nucleus for touch) are followed, after an initial period of depression of the somesthetic cortex, by a hyperexcitability of this region. [More than a century ago, Hall (*8*) observed that "the first effect of injury done to the nervous system is a diminution of its functions, whilst the second or ulterior effect is the augmentation of these functions."] Occlusion of one eye, therefore, may be producing a state of temporary partial deafferentation of the visual system, a condition that is reflected behaviorally in the production of our CFF phenomenon. However, in contrast to surgically induced deafferentation, this deafferentation is functional, that is, it is produced by depriving the normal, intact organism of some of its accustomed visual experience.

This hypothesis is consistent with Sharpless's (*9*) revision of the law of denervation (*6*), which has as its main thesis that supersensitivity results from prolonged disuse of neural pathways. Sharpless states, "Disuse may be the result of drugs, privation of sensory experience, or, most commonly, injury produced by severance of nervous pathways." Further, he says that supersensitivity is a compensatory process that occurs as a consequence of "a radical and sustained change in the level of input to an excitable structure." This explanation of disuse of neural pathways, with which we concur, has the merit of bringing together our results, the increased cutaneous sensitivity that occurs in human subjects after prolonged partial occlusion of the skin (*10*), and the various supersensitivity phenomena induced by surgery or by drugs. This explanation does not, however, adequately account for the presence of the CFF phenomenon in only one eye, nor does it indicate the specific neural locus of the interocular effect. Only future behavioral and electrophysiological research can provide satisfactory answers to these two problems.

Finally, our results are important in two general respects. First, they indicate that the monocular deprivation technique may provide a new method of attacking the complex problem of the physiological mechanisms underlying sensory isolation effects (*11*), an approach that can be used both in studies of humans and in electrophysiological studies in animals. Second, they suggest that many of the apparently contradictory results from isolation chamber studies (*11*), particularly those involving periods of 1 day or less and employing various sensory and perceptual-motor measures, may be accounted for by differences in the duration of experimental conditions. (The most commonly used periods have been 3, 9, 12, and 24 hours.) As we have demonstrated, performance on the same measure may be either impaired, improved, or not affected, the specific effect being dependent upon the duration of deprivation. It has been assumed by most previous investigators in the sensory deprivation area that this experimental variable is probably not too important and therefore can be ignored. This assumption is no longer valid.

JOHN P. ZUBEK, M. BROSS
Department of Psychology, University of Manitoba, Winnipeg, Canada

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19 November 1971

Gratings Mask Bars and Bars Mask Gratings: Visual Frequency Response to Aperiodic Stimuli

Abstract. *Gratings and bars produce unexpected mutual visual masking. A grating masks a bar much less than a bar masks a bar; and a bar masks a grating uniformly over the grating field. These effects suggest that neural populations selective for size and orientation may be involved in frequency analysis rather than in simple feature detection.*

After a subject observes a square-wave grating, the apparent contrast of an identical grating will be greatly reduced (*1, 2*). A similar effect occurs when a half cycle of a grating—a dark bar—is presented and then presented again at a shorter duration (*3*). The reduction in apparent contrast of a stimulus when it is presented after another stimulus is called a forward masking effect. The stimulus that loses apparent contrast is called the target; the other stimulus is called the mask.

These masking effects have been taken as evidence that the human visual system contains neural populations that are selective for size and orientation and that lose sensitivity after prolonged stimulation. The psychophysical evidence suggests this: The effects attenuate

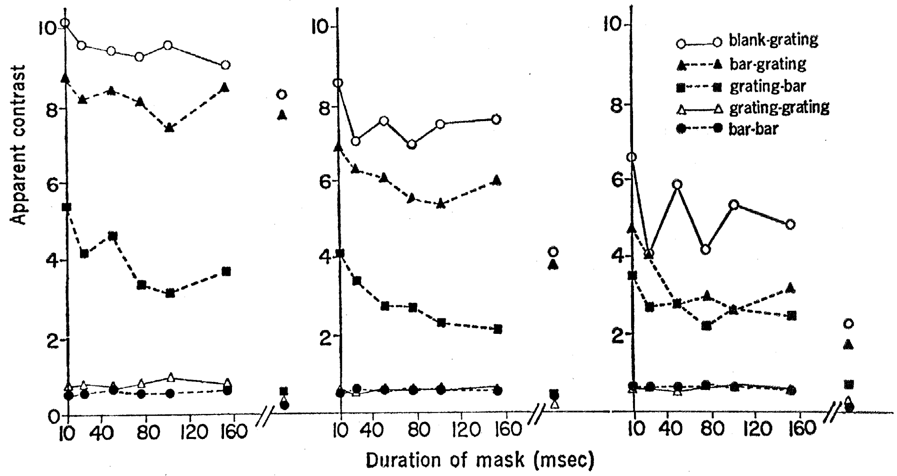

Fig. 1. Apparent contrast of target after subjects viewed masks. Spatial frequencies were 3 (left), 10 (center), and 15 cycle/deg (right). Mask-target conditions are indicated on the figure. Each point is a geometric mean across subjects and ISI's. The results for 10 seconds are given by symbols unconnected to other data points.

in proportion to the amount the target differs from the mask in width, length, and orientation. Moreover, after prolonged viewing of a mask grating, averaged evoked potentials diminish in amplitude at the same time that a target grating decreases in apparent contrast (*2*).

In our study bars as masks were paired with gratings as targets (hereafter called bar-grating condition), and gratings as masks were paired with bars as targets (grating-bar condition); also gratings were paired with gratings, and bars with bars (grating-grating and bar-bar conditions). Masking was found in all four cases. The bar reduced the apparent contrast of the grating uniformly over the grating field. The effects of a bar on a subsequent grating and a grating on a subsequent bar were greater than the uniform field masking effect (that is, the effect of a blank field as mask) but were less than the effect when both mask and target were identical.

Such data are startling. They suggest that the response of neural populations selective for size cannot be equated simply with the coding of the size of a stimulus. If size coding alone were responsible, a bar should have little subsequent effect on a grating (except perhaps at the center of the grating, where the bar had been) and a grating should mask as effectively as one bar superimposed on another.

The masking stimuli, transilluminated Kodalith slides presented tachistoscopically in a viewing field measuring 6.7° of visual angle horizontally by 4° vertically, consisted either of a blank field, a vertical square-wave grating, or a dark bar of width equal to one half cycle of the grating (that is, to a dark bar in the grating). The mean luminance of all mask fields was 17 mlam; the seven mask durations were 10, 25, 50, 75, 100, and 150 msec and 10 seconds. The targets consisted of the same stimuli, presented for 16 msec at 3.4 mlam after a variable interstimulus interval (ISI) of 5, 10, 20, or 30 msec (measured from mask offset to target onset). Three subjects were told to fixate on the center of the field but did not have a fixation point; under this condition, the contrast was 1. Except for the 10-second mask, the overall duration of the mask-target sequence was short enough so that even when subjects had no fixation point, one can consider that the flashes projected on an essentially fixed retinal area. However, two additional subjects fixated on a tiny black fixation dot in the center of a field continuously illuminated at 2.2 mlam. This reduced the contrast of the mask to 0.78 and that of the target to 0.23.

Each of the five subjects made ten magnitude estimations (*4*) for each combination of variables (mask, target, mask duration, and ISI) at each of three spatial frequencies (3, 10, and 15 cycle/deg). Subjects estimated the apparent contrast of each target as a proportion of the contrast of the same target unmasked. In conditions where the target was a grating, subjects were instructed to note whether the grating faded uniformly or whether only parts of the grating were fading. There were very few instances in which the grating did not fade uniformly.

One mask-target combination was presented per session. At each session, the seven mask durations were used in random order and the four ISI's were presented in random order for each duration. The order of sessions was made random for each subject.

The results are shown in Fig. 1, in which the mean apparent contrast for each of the target-mask conditions is graphed as a function of the duration of the mask. (Data for different subjects and ISI's are averaged. Averaging for these variables does not obscure features of the data since each subject showed essentially the same rank ordering of means and apparent contrast increased only slightly as a function of increasing ISI.) The greater the apparent contrast, the less the masking.

The top function shows the uniform field masking effect. Next, in rank order of mean amount of masking, are the bar-grating and grating-bar conditions. The two bottom functions are the grating-grating and bar-bar conditions, and there is not much difference between them.

The main features of these data are apparent from a simple tally. Sign tests across duration for each subject and frequency separately showed more masking in the bar-grating than in the blank-grating condition for all subjects at 3 cycle/deg ($P < .01$) and for four out of five subjects at 10 and 15 cycle/deg ($P < .01$). When data are combined across subjects, then, there was both more bar-grating than blank-grating masking and more grating-grating than grating-bar masking ($P \ll .001$).

These results cast doubt on the notion that visual pattern processing begins with simple feature detectors that code size and orientation. This notion of visual processing assumes that when a single unit fires at its optimum rate (that is, fires to a stimulus of a particular width and orientation that correspond most closely to dimensions of its own receptive field), the unit is signaling the presence in the visual field of a particular set of features—orientation, width, and length. We call this a feature analysis model (*5*).

But consider feature analysis in light of the results obtained here. Assume that the first stimulus has a masking influence on the second stimulus because the same neural populations in the visual system are stimulated by both target and mask and cannot respond with as large an amplitude to the second stimulus (the target) after presentation of the first (*6*). If the visual system were coding for size, then for the bar-grating condition one would expect masking of only the center bar of the grating or, at most, one or two bars on either side of the center bar. One certainly would not expect that the grating would uniformly decrease in contrast. Similarly, one would expect as much masking for the grating-bar condition as for the bar-bar condition.

While these results cast doubt on a feature analysis model, they suggest that the visual system may be processing stimuli at least partially in terms of their spatial frequency components (or Fourier spectra) (*7*). This notion of visual processing we call a frequency analysis model, and one way of interpreting the role played by neural populations selective for features is to assume that a single unit firing at its optimum rate is conveying information about the range and distribution of frequencies contained in the spatial frequency transform of a single (aperiodic) stimulus. The presence in the visual field of other elements of the same width and orientation (such as a grating) would then change the response of that single unit, since the frequency spectrum would have changed (*8*). Thus, coding in this case would not be for a particular size or feature without regard for the number of times it is present elsewhere, but would be for the frequency components of the visual field (*9*).

While other explanations undoubtedly exist, our results do suggest frequency analysis. The Fourier transforms of a dark bar on a 6.7° field and of a corresponding grating differ; however, they share certain frequency components. If it is assumed, as discussed above, that the first stimulus has a masking influence on the second because the same neural populations in the visual system cannot respond with as large an amplitude the second time, then if neural populations were responding to the frequency content of the stimuli, one would expect masking both for the grating-bar and the bar-grating conditions. These effects would in neither case be as pronounced as when the spectra of the mask and target matched; but for each frequency tested some masking should be expected. It is difficult to predict how the magnitude of these effects would vary with frequency, since data are not yet available on many factors which might influence this relation, such as tuning curves of analyzers, the difference between visual response to light and dark bars, and so forth. But it is important that the effect occurred for each frequency tested, since this indicates that the effect is probably not an artifact due to high or low frequency or phase (*10*).

Masking in the bar-grating condition differs most from that in the blank-grating condition at short durations and is most similar at the 10-second duration. A similar relation exists between the grating-bar and grating-grating conditions. It is premature to speculate about the stage in visual system processing at which a frequency analysis may occur. However, different types of operations occur at different times in the visual system (*11*). Frequency analysis might be one such operation.

If this is so, our experiment has implications for all studies with small field sizes of gratings alone, or of stimuli that include gratings, since continuous spectral components will be present in these cases. In particular, Weisstein (*12*) reported that when a subject viewed a grating that was partially obstructed by a cube, a subsequent grating was masked in that area of the visual field where the cube had been. The results reported here suggest that such an effect might be due to frequency components introduced by truncation of the grating, although other data (*13*) indicate that spectral analysis alone is not sufficient to account for the effect of the interrupted grating.

The visual system is capable of spectral analysis for periodic stimuli. For instance, with periodic patterns containing more than one spatial frequency, detection of each frequency component appears to be independent (*14*). However, from these results one cannot necessarily predict that the visual system will analyze frequency, as opposed to code features, for aperiodic stimuli as well. Since in most studies sinusoidal gratings or sums of sinusoids were used (and thus there were only a handful of frequencies in the transform domain), it could be assumed that neural populations were acting essentially as separate spatial filters. Under this assumption, each neural population would respond selectively to elements of a particular size in a compound periodic pattern. It would be hard to distinguish whether the populations were responding to the actual size of each element in the visual field or to the transform of that stimulus, which would be a single spectral component of the same period. Thus, with periodic stimuli, the distinction between feature coding and frequency analysis is blurred.

On the other hand, with aperiodic stimuli the same neural populations cannot simultaneously perform a feature analysis and a frequency analysis. Whereas the transform of a sinusoidal grating has a single frequency component, the transform of a single aperiodic stimulus, such as a narrow dark bar, has an infinite number of frequency components. In a feature coding system, presentation of a dark bar would mean that a particular size would be registered and presentation of a grating would mean that a particular size would be registered a number of times; in a frequency coding system, presentation of a dark bar would mean that a broad range of periods would be registered, whereas presentation of a grating would mean that only a limited number of periods would be registered. We used aperiodic stimuli, and our results suggest that the frequency components, rather than simply the size of the stimuli, may be registered in some way.

NAOMI WEISSTEIN

Department of Psychology,
Loyola University,
Chicago, Illinois 60626

JOHN BISAHA

Department of Psychology,
Mundelein College, Chicago 60626

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3 December 1971; revised 13 March 1972