Vision Research **Vol.** 20. pp. 459 **to 466**
Pergamon Press Ltd 1980 **Printed in Great** Britain

ON INHIBITION BETWEEN SPATIAL FREQUENCY CHANNELS: ADAPTATION TO COMPLEX GRATINGS

S. KLEIN
Joint Science Department. Claremont Colleges, Claremont, CA 91711, and
Division of Biology. California Institute of Technology, Pasadena, CA 91125, U.S.A.

and

C. F. STROMEYER III
Division of Applied Sciences, Harvard University, Cambridge, MA 02138, U.S.A.

(Received 6 April 1978)

Abstract—Previous studies have shown that adapting to a complex grating may produce little rise in the contrast threshold of a test grating whose spatial frequency matches one of the higher harmonics of the adapting pattern. The present study shows that adaptation may be strong if the adapting component of a complex grating appears visible as a separate grating. The adapting component could be made to appear as a separate grating by sufficiently separating the spatial frequencies of the components, or by drifting the components relative to each other, or by substituting a jittering, noisy component for the stationary component. Under these conditions, the visible component produced strong adaptation. Inhibition between mechanisms tuned to different spatial frequencies does not readily account for our data. An alternate model with lateral inhibition between spatially adjacent mechanisms is in agreement with known results.

INTRODUCTION

Lateral inhibition limits the area of receptors that activate visual neurones (Ratliff, 1965). Low spatial-frequency light patterns that simulate both excitatory and inhibitory regions of a neurone's receptive field produce little net response. Lateral inhibition thus accentuates edges. It has been suggested (Blakemore *et al.,* 1970; Carpenter and Blakemore, 1973; Blakemore *et al.,* 1973) that mechanisms that are broadly tuned to line orientation and spatial frequency also inhibit each other to increase response selectivity. Tolhurst (1972) suggested that adaptation studies provide evidence for inhibition between spatial-frequency channels. The present paper examines this hypothesis.

Prolonged viewing of a grating increases the threshold for detecting patterns with similar orientation (Gilinsky, 1968) and spatial frequency (Pantle and Sekuler, 1968; Blakemore and Campbell, 1969). Blakemore and Campbell observed that a sinusoidal adapting grating maximally elevates the threshold of a grating at the same spatial frequency but has little effect on gratings one octave from the adapting frequency. They hypothesized that neural mechanisms respond to Fourier components in a complex visual scene. As a test of this hypothesis, they showed that a square-wave adapting grating raised the threshold for a test grating corresponding to the third harmonic of the adapting pattern.

Tolhurst (1972), however, observed that adapting to a square-wave grating produced somewhat less threshold rise at the third harmonic than adapting to the third harmonic of the square-wave viewed alone. Nachmias *et al.* (1973) found very little threshold rise at the third harmonic frequency upon adapting to either a square-wave grating or to the first and third harmonics of the square-wave. Tolhurst suggested the spatial-frequency channels inhibit each other when stimulated with a complex pattern, thus reducing the net adaptation.

The present study shows that a spatial frequency component of a complex grating may produce strong adaptation when the components of the adapting grating are sufficiently separated in spatial frequency or the components move rapidly relative to each other. When the component produces strong adaptation, it tends to appear *visible* as a *separate* component. This finding of strong threshold elevation in several channels simultaneously may require modification of models of inhibition between channels.

METHODS

Stimuli

Vertical gratings were generated on a CRT, following the method of Campbell and Green (1965). The stimulus field was white (P-4 phosphor) containing fine diagonal cross-hairs, with a black surround. The field was 4° in diameter, viewed from 122 cm by the left eye. The mean spatial luminance of the field was always 5 cd/m^2. Gratings with little harmonic distortion could be generated at contrast values as high as 60%.

All patterns were vertically-oriented. The test pattern was a single stationary sinusoidal grating. Various adapting patterns were used. (1) Two phase-locked sinusoidal gratings of different spatial frequencies. Square-wave gratings were also used. (2) Two sinusoidal gratings which were presented alternately. (3) A stationary sinusoidal grating plus a right-drifting sinusoid (the observer fixated a cross-hair when viewing drifting gratings). (4) A stationary sinusoidal grating plus dynamic, vertical noise stripes. To produce the noise stripes, white noise was passed through cascaded Kron-Hite 330 NR band-pass filters, which combined had skirts of 48 dB/octave from the 6 dB attenuation points. Two bands of noise were used. For the results in Table 1, the center of the band was at 1.9 c/deg and the 6 dB points were 1.5 and 2.5 c/deg. (This noise was chosen so most of the power would be below 2.5 c/deg.) For the results in Table 2, the center was 5 c/deg; the 6 dB points were 4 and 6.5 c/deg. The noise gratings looked like a high-contrast, approximately regular grating with rapidly jittering bars. The CRT sweep rate was 20msec/sweep. Average noise contrast is specified by σ_L/L_0, where L_0 is mean spatial luminance and σ_L is the standard deviation of the Gaussian luminance distribution of the noise (Stromeyer and Julesz, 1972). The term σ_L is proportional to the V_{rms} of the noise (measured with a true V_{rms} meter).

Psychophysical methods

A signal detection method was used for the first experiments. The adapting pattern was alternately presented for 10 sec periods, each followed by a 3 sec period during which the observer pressed a button to present a single exposure of a 7.5 c/deg sinusoidal test grating for 750 msec. For some runs, a single test contrast was used; in other runs, three contrast values were used. Blanks were randomly intermixed with the test pattern. On each trial, the observer rated the visibility of the pattern on a whole-number scale of 1-5 and was then told which test pattern had been presented. ROC curves were fitted to the ratings by a maximum likelihood estimate to determine the detectability, d', of each test pattern (Stromeyer and Klein, 1975). The maximum likelihood program also produces error bars for each value of d'. Each run was preceded by several minutes of viewing the stimulus sequence.

In order to assess the effectiveness of the different adaptation patterns, the data are plotted as log d' vs log test contrast. The power law transducer function which has been found between d' and contrast, c, (Stromeyer and Klein, 1974) would cause the data to lie along straight lines in a plot with log axes. Straight lines are fit to the data points. Each line is for a different adapting pattern. The lines are constrained to be parallel. The axes are scaled such that a 45° line corresponds to $n = 2$ in the relationship $d' = c^n$. A steeper slope corresponds to a larger n. The fit with parallel lines allows the difference in thresholds between conditions to be easily determined. In the least squares program, each data point is weighted by the inverse of the variance. These lines provide quite a good fit to the data. The logarithmic vertical axis cause a magnification in variance for low d', so the least squares fit is mostly determined by the larger values of d'.* Some data points appear to fall far from the fitted lines. However, these are points where d' is low and the logarithmic axis exaggerates distances. See for example Fig. 4, which shows how the error bars increase at low values of d'.

Other experiments were done with the method of adjustment (these were done first). The threshold rise produced by the adapting pattern is expressed in units of the pre-adaptation threshold; a value of 1.0 means that the adapted threshold is 100 per cent higher than the threshold prior to adaptation. The observer set the threshold contrast with a potentiometer. The observer first made 5-10 pre-adaptation threshold setting of the test pattern. Next, the adapting grating was presented for 15 sec periods which alternated with 5 sec blank periods during which the test pattern appeared, being successively on for 500 msec and off for 500 msec. The threshold rise reached a stable plateau after 5-8 min adaptation, and then the observer made 10 usable threshold settings. Each data point is based on several sessions.

RESULTS

Stationary, first and third harmonic adapting gratings

The experiment examines whether adaptation to a square-wave grating *or* to the first and third harmonics of a square-wave produces any threshold rise at the spatial frequency of the third harmonic of the square-wave. Adapting patterns reversed contrast every 0.5 sec..

Figure I shows d' values for observer CFS for the third harmonic test grating (7.5 c/deg). The horizontal and vertical axes arc plotted in units of log contrast and log d'. Straight lines arc fitted to data for adaptation to a square-wave grating (squares 2.5 c/deg. 50% contrast), to the first harmonic of the square-wave (circles 63% contrast), to the first plus third

* Two reasons may be given for why the least squares fit is mostly determined by the larger values of d'. (1) The transducer function is an accelerated function of contrast and the threshold is more accurately determined where the transducer slope (on a linear scale) is greater. (2) The slope of a line which is known to go through the origin tends to he most accurately determined by data which are farthest from the origin. However, in an experiment in which blanks arc randomly intermixed with a single test pattern, it is difficult to accurately measure large </' since there is insufficient overlap between the responses to the two stimuli. For this reason, in most of our experiments, we intermix blanks with test patterns of *three* different contrast levels. The contrast levels are chosen so that there is good overlap between the responses to the four test patterns. By this means, it is possible to obtain $d' > 2$ with good accuracy leading to accurate threshold determinations.

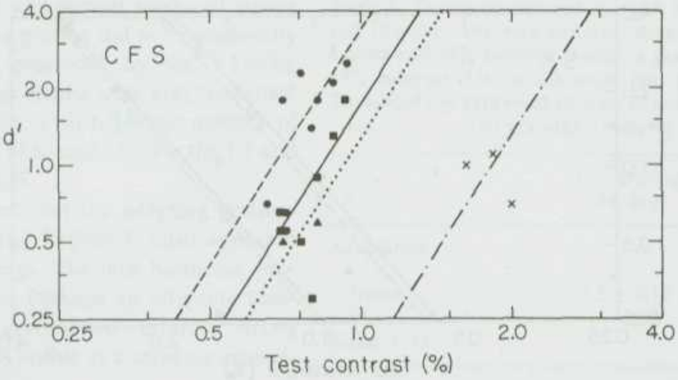

Fig. 1. Detectability d' of test grating of 7.5 c/deg whose contrast is indicated on abscissa. Adaptation patterns are either a 2.5 c/deg square-wave grating of 50% contrast or some particular harmonics of that square-wave grating: ■ square-wave grating (continuous line); ● first harmonic of square-wave (dashed line); ▲ first plus third harmonic of square-wave (dotted line); × third harmonic (dot-dashed line). Lines are fitted to the data by least squares, with the constraint that lines are parallel. Each point based on one run of 50 trials. Observer CFS.

harmonics of the square-wave (triangles), and to the third harmonic of the square-wave (crosses 21% contrast). In the least squares fit to the data, the lines are constrained to be parallel as discussed in Methods.

The solid and dot-dashed curves (adaptation to the square-wave and to the third harmonic gratings) are displaced, respectively, about 20 and 170% to the right along the contrast axis relative to the dashed curve (adaptation to the first harmonic). Adapting to the square-wave grating reduces the detectability of the third harmonic test pattern only slightly more than does adapting to the first harmonic alone.

Figure 2 shows *d'* for observer SK. for similar conditions. These results were obtained two years after the results in Fig. 1. The adapting patterns did not reverse in contrast. The results show that (1) the curves for adaptation to a square-wave grating (squares) or to first and third harmonics (triangles) are displaced about 40% along the contrast axis relative to the blank (open circles) or first harmonic (solid circles) adapting patterns; (2) the curved for adaptation to the third harmonic viewed alone (crosses) are displaced about 100%. The presence of the fundamental strongly reduces the magnitude of adaptation at the third harmonic.

Facilitation by the first harmonic?

Barfield (1976) and Tolhurst and Barfield (1978) observed that adaptation to the first harmonic could facilitate detection of the third harmonic. Thus, one reason why the square-wave grating may produce a reduced threshold rise at the third harmonic is that adaptation to the first harmonic might facilitate detection of the third harmonic, thus cancelling the effect of the third-harmonic adapting component. That is, the facilitation of detection produced by adapting to the first harmonic of the square-wave grating may counteract the threshold rise produced by adapting to the third harmonic of the square-wave grating.

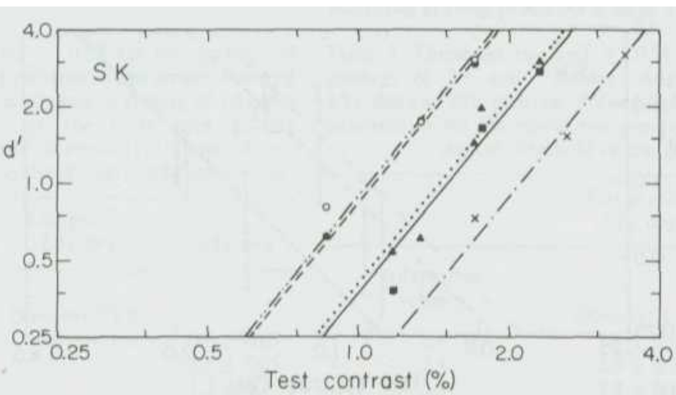

Fig. 2. Detectability *d'* of test grating of 7.5 c/deg whose contrast is indicated on abscissa. Adaptation patterns: ■ square-wave grating of 2.5 c/deg and 50% contrast (continuous line); ▲ first plus third harmonic of square-wave (dotted line); ○ blank field (double dot-dashed line); ● first harmonic (dashed line); × third harmonic (dot-dashed line). Each line is based on an average of several runs; several contrasts were used in each run of 80 trials. Observer SK.

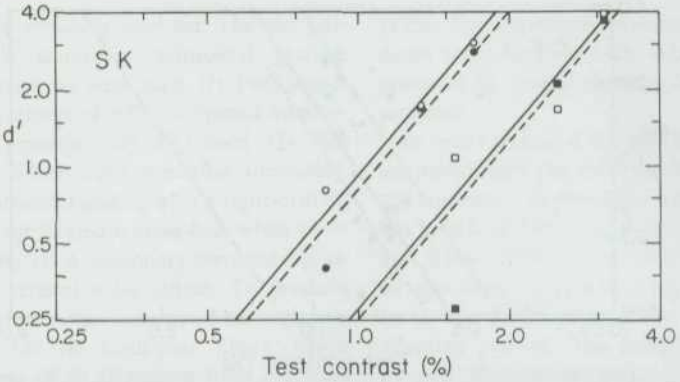

Fig. 3. Detectability d' of test grating of 7.5 c/deg whose contrast is indicated on abscissa. Adapting patterns: ○ blank field (continuous line); ● 2.5 c/deg sinusoid of 63% contrast—reverses contrast at 1 Hz (dashed line); □ blank field alternating at 1 Hz with 7.5 c/deg sinusoid of 21% contrast (continuous line); ■ 2.5 c/deg sinusoid of 63% contrast alternating at 1 Hz with 7.5 c/deg sinusoid of 21% contrast (dashed line). Each curve based on two or more runs of 80 trials. Observer SK.

To test this notion, the third-harmonic adapting grating (7.5c/deg, 21% contrast) alternated at 1 Hz with either a blank field or with the first harmonic (2.5 c/deg, 63% contrast).

Figure 3 shows that both adaptation conditions similarly affect the third-harmonic test grating. The adapting effectiveness of the third harmonic is thus not reduced by any facilitating effect that might have been produced by the first-harmonic adapting grating.

Similar results were obtained in earlier experiments. The adapting patterns were 3 and 9 c/deg at 60 and 20% contrast, respectively, which alternated at 0.5 Hz. The d' values for 9 c/deg test gratings of 1.5 and 2.5% contrast, for observer CFS, were 0.5 and 3.1 upon adapting to the alternating 3 and 9 c/deg gratings and 0.6 and 3.8 upon adapting to the alternating blank field and 9 c/deg grating.

Thus, when the first- and third-harmonic adapting patterns are presented *sequentially,* the adapting effectiveness of the third harmonic is not reduced by the first harmonic. Thus, any facilitative effect produced by the first harmonic is apparently not the reason why the third harmonic of a square-wave grating produces little adaptation.

Stationary, first and fifth harmonic adapting gratings

The results suggest that the first harmonic only reduces the adapting power of a third harmonic grating when both patterns are presented *simultaneously.* In this case, the third harmonic does not appear separately visible when the first harmonic is of high-contrast (see Fig. 2b, Stromeyer *et al.,* 1973). With a greater separation between the spatial frequency of the adapting components, each component may be seen as a separate grating (Stromeyer *et al.,* 1973) and perhaps produce strong adaptation.

To test this idea, observers adapted to a first (1.5 c/deg) and fifth (7.5 c/deg) harmonic grating simultaneously presented in peaks-add phase. Figure 4 shows d' values for a test grating of 7.5 c/deg upon adapting to four possible adapting patterns composed of a first harmonic with contrast of either zero or 55% and a fifth harmonic with contrast of either 0 or 11%. There were 80 trials per run. Both cases in

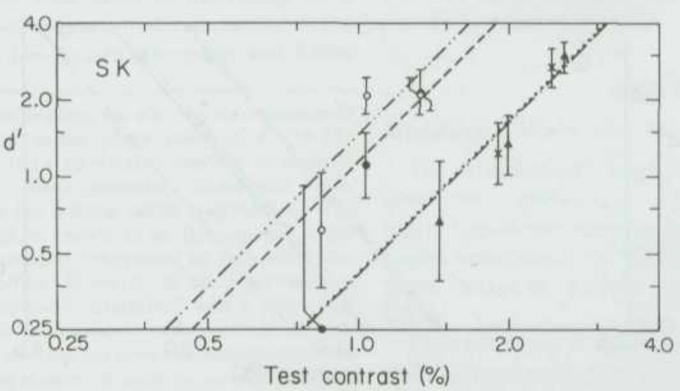

Fig. 4. Detectability d' and ± 1.0 SE for test grating of 7.5 c/deg whose contrast is indicated on abscissa. Adapting components are combinations of the first (1.5 c/deg; 55% contrast) and fifth harmonics (7.5 c/deg; 11% contrast) of a square-wave grating: ○ blank field (double dot-dashed line); ● first harmonic (dashed line); × fifth harmonic (dot-dashed line); ▲ first plus fifth harmonic (dotted line). Each curve is based on a single run of 80 trials. Observer SK.

which the fifth harmonic was present produced strong adaptation. The 1.5 c/deg grating did not significantly reduce the adaptation produced by the 7.5 c/deg adaptation pattern. These results were also confirmed on observers CFS and SK with triple the number of trials and with contrasts of 63 and 21% for the 1.5 and 7.5 c/deg adapting gratings.

The observers reported that the adapting gratings separated by a 1:5 spatial frequency ratio appeared visible as separate gratings. The fifth harmonic produced strong adaptation. Perhaps an adapting component of a complex grating will produce strong adaptation whenever it is visible as a separate sinusoidal component.

The remaining experiments explore conditions that cause a *third*-harmonic adapting grating to appear separately visible when presented with a high-contrast first-harmonic adapting component. The experiments suggest that when the third harmonic is separately visible, it may produce strong adaptation. The method of adjustment was used.

Noise adapting gratings

The third-harmonic can be made visible as a separate grating when the first harmonic is rapidly jittering, so that the third-harmonic is seen through the jittering noise stripes (Stromeyer and Julesz, 1972).

Table 1 shows that a noise grating (1.9 c/deg, 30% contrast) produces a large threshold rise at 2.5 c/deg but no threshold rise at the frequency of 7.5 c/deg. This noise grating was chosen so that most of the noise power would be below the first-harmonic-frequency of 2.5 c/deg (Methods). A stationary, 7.5 c/deg adapting grating (13% contrast), when viewed alone or in the presence of the noise grating, produces a large threshold rise at 7.5 c/deg. The 7.5 c/deg adapting grating often appeared as a separate grating in the rapidly varying noise, and it produced considerable adaptation.

Table 2 shows similar results using higher spatial frequencies of 5 and 15 c/deg. In this case, the noise adapting grating was centered at 5 c/deg (see Methods).

Table 1. Threshold rise and ± 1.0SE for test gratings of 2.5 and 7.5 c/deg. Adapting patterns: noise stripes centered at 1.9 c/deg and 30% contrast (noise); a grating of 7.5 c/deg and 13% contrast (7.5); or the noise plus grating (noise + 7.5). Threshold rise expressed in units of unadapted threshold of test gratings—zero indicates no rise

	Test grating 2.5 c/deg	7.5 c/deg
Adaptation		
	Observer CFS	
Noise	1.0 ± 0.1	0.0 ± 0.05
7.5		1.2 ± 0.05
Noise + 7.5		1.2 ± O.I
	Observer SK	
Noise	1.3 ± 0.1	0.0 ± 0.05
7.5		1.3 ± 0.05
Noise + 7.5		1.2 ± 0.05

Table 2. Threshold rise and ± LOSE for test gratings of 5 and 15 c/deg. Adapting patterns: noise stripes centered at 5 c/deg and 38% contrast (noise); a grating of 15 c/deg and 13% contrast (15); or the noise plus grating (noise + 15). Threshold rise expressed in units of unadapted threshold of test gratings. Observer CFS

	Test grating 5 c/deg	15 c/deg
Adaptation		
Noise	1.2 + 0.10	-O.I + 0.05
15		1.2 ± 0.11
Noise + 15		I.I ± 0.11

Drifting adapting gratings

In the previous experiment, the noise grating may not have strongly interfered with the adapting effectiveness of the stationary, high-frequency adapting grating for the noise grating *itself* may have been less effective as an adapting pattern than a regular sinusoidal grating. The experiment provided no information on what 'equivalent contrast' sinusoidal grating produces adaptation equivalent to the noise grating.

The present experiment is similar to the previous experiment but a drifting sinusoidal adapting grating is substituted for the noise grating. Table 3 shows that a drifting first-harmonic adapting pattern of 2.5 c/deg and 38% contrast strongly elevates a first-harmonic test pattern but has no effect on a third harmonic test pattern. The adapting grating does *not* consistently produce weaker adaptation as its velocity is increased.

Next, we examined whether these drifting gratings would reduce the adapting power of a stationary third-harmonic grating of 13% contrast—1/3 the contrast of the drifting gratings. The adapted threshold for the third-harmonic test grating is shown in Fig. 5 as a function of the drift rate of the first-harmonic adapting grating. The stationary third-harmonic adapting grating produces a large threshold rise when

Table 3. Threshold rise and ± 1.0 SE for stationary test gratings of 2.5 and 7.5 c/deg. Adaptation grating of 2.5 c/deg and 38% contrast, drifting rightward with velocity indicated in Hz. Threshold rise expressed in units of unadapted threshold of test gratings

	Test grating 2.5 c/deg	7.5 c/deg
Adaptation velocity		
	Observer CFS	
0.0 Hz	1.5 + O.I	0.0 + 0.05
2.4	2.0 + 0.2	0.1 ± 0.05
3.4	2.0 ± 0.1	0.2 ± 0.05
	Observer SK	
0.0 Hz	1.7 ± 0.2	0.0 + 0.5
2.4	1.6 + 0.2	0.0 ± 0.1
3.4	1.3 + 0.1	O.I + O.I

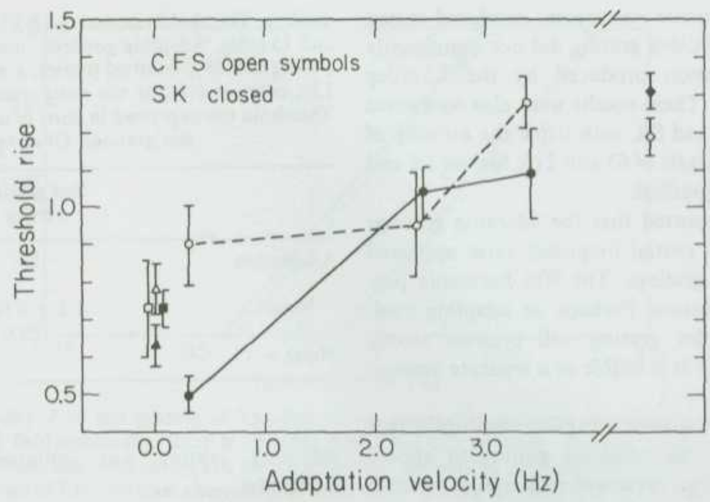

Fig. 5. Threshold rise and ±1.0 SE for test grating of 7.5 c/deg. Threshold rise is in units of unadapted test contrast. Adaptation patterns: diamonds, 7.5 c/deg sinusoid, 13% contrast; squares, stationary 2.5 and 7.5 c/deg sinusoids in peaks-subtract phase, 38 and 13% contrast, respectively, and triangles, same gratings in peaks-add phase; circles, 2.5 c/deg sinusoid, 38% contrast, drifting rightward with velocity indicated on abscissa *plus* stationary 7.5 c/deg sinusoid, 13% contrast. The velocity in Hz indicates how many cycles of the grating pass the center fixation point in 1 sec.

the first harmonic drifts at the most rapid rate, as may be seen by comparing the threshold rise to the large effect produced by the third-harmonic adapting grating viewed alone (diamonds). The third-harmonic adapting grating produces a smaller threshold rise when paired with the *stationary* first harmonic in either peaks-add phase (triangles) or peaks-subtract phase (squares). At the faster drift rates, the adapting components appeared as separate gratings some of the time (the components rivalled, being sequentially fused or unfused) and adaptation was strong. At the slow drift rate of 0.3 Hz, the adapting components appeared continually fused, and adaptation was weak. We observed, using similar drift rates, that when the first harmonic drifted across a second harmonic, the complex grating appeared to change shape, but the two harmonics did not appear to separate.

DISCUSSION

The results suggest that a sinusoidal component of a complex grating produces very little adaptation when that component is not separately visible and produces considerable adaptation when the component is separately visible. The adapting component could be made visible by separating sufficiently the spatial frequencies of the adapting components, by presenting alternately the two components, by drifting one component across the other, or by substituting a noise component for a stationary component. By "separate visibility" we mean the component tends to appear, at least part of the time, as a regular pattern of stripes. Although the present results suggest that the "separate visibility" of a component may lead to strong adaptation at the spatial frequency of the component, there may be other patterns, quite different than those examined in this study, in which a spatial-frequency component appears entirely separately visible but produces no adaptation.

Pairs of stationary adapting sinusoids with different spatial frequency ratios

The adapting effectiveness of a 7.5 c/deg sinusoid was strongly reduced by adding a 2.5 c/deg sinusoid (Figs 1 and 2) to the adapting pattern (1:3 spatial frequency ratio), whereas adding a 1,5 c/deg component (Fig. 4) had little if any effect (1:5 spatial frequency ratio).

Georgeson (1975) observed that the adapting effectiveness of a 8 c/deg sinusoid (21% contrast) was little affected by addition of a 1.8 c/deg sinusoid (67% contrast). He also showed that the adapting effectiveness of a 15 c/deg sinusoid (10.5% contrast) was much less affected by a 3 c/deg sinusoid than by sinusoids of 5 to 7.5 c/deg (31.5% contrast). Cushman (1976) used adapting sinusoids of nearly equal contrast (each contrast was 12 times the unadapted threshold) with spatial frequency ratios of 1 :2 and 1:5. The lower frequency component reduced the adapting effectiveness of the higher frequency component by a small amount less than 0.1 log unit, and there was no strong effect of the frequency ratio.

The present results and those of Georgeson (1975) suggest that the adapting effectiveness of a component is not strongly reduced by a component about five times lower in saptial frequency but is strongly reduced by a component about three times lower in frequency. We next consider why a first harmonic might reduce the adapting effectiveness of a third harmonic.

Inhibition between frequency channels?

Tolhurst (1972) suggested that multiple sinusoidal gratings may produce weak adaptation because the channels responding to the components may inhibit each other, thus reducing adaptation. For example, in adapting to a square-wave grating, the first harmonic may stimulate optimally channels tuned to the first harmonic, and the third harmonic may stimulate optimally channels tuned to the third harmonic. The two sets of channels may mutually inhibit each other, thus reducing the total adaptation.

The present results suggest that this inhibition is reduced when the first harmonic adapting grating jitters or moves at relatively slow drift rates (e.g. 3.4 Hz), rather than being stationary. It might be supposed that the inhibition only occurs between channels of the same type shape-channels (sustained detectors) or movement-channels (transient detectors). This explanation, however, does not readily account for our results, for several experiments indicate that shape-channels are strongly adapted both by moving and by stationary patterns. Tolhurst (1973) showed that the visibility of a stationary grating of 1.5 c/deg, which was presumably detected by shape-channels, was strongly reduced by an adapting grating moving at 5 Hz. Also, Kulikowski and Tolhurst (1973) showed that gratings of 0.8 and l() c/deg strongly affected the shape channels when the gratings flickered in counterphase in the range from 0 to 7 Hz. Thus, the observation that a stationary third-harmonic grating is a potent adapting pattern in the presence of a moving or noisy first-harmonic pattern is not readily explained by postulating that stationary and moving patterns adapt different types of channels, for the moving patterns presumably stimulate strongly the shape-channels as well as the movement-channels. Further problems with the inhibition model are discussed in Tolhurst and Barfield (1978).

Shielding of mechanisms through phase-inhibition?

Rather than inhibition between mechanisms tuned to different spatial frequencies, consider the consequences of inhibition between spatially contiguous mechanisms tuned to similar spatial frequencies but having different phase-selectivities (Stromeyer and Klein, 1974). For example, a well-stimulated "edge" (antisymmetric) mechanism may inhibit adjacent "light or dark line" (symmetric) mechanisms. Phase-inhibition would emphasize the dominant feature at each spatial location and thus aid pattern recognition.

Phase-inhibition might account for the present adaptation data. Consider the adapting pattern of first and third harmonics in square-wave phase. The edge mechanisms that respond to *both* the first and third harmonics would be more strongly stimulated than the symmetric, line mechanisms that respond to the same harmonics (Stromeyer and Klein, 1974). These edge mechanisms may inhibit the line mechanisms, thus preventing strong adaptation of the latter mechanisms. The relatively unadapted line mechanisms could then be used to detect the third harmonic test pattern, and thus there would be little threshold rise. Adaptation to a pattern of stationary third harmonic and *slowly* drifting first harmonic also produces little threshold rise (Fig. 5). Although this pattern may strongly stimulate both edge and line mechanisms, the mutual inhibition between the mechanisms may result in little net adaptation. When the first harmonic adapting grating jitters or moves *rapidly* past the third harmonic, the third harmonic pattern is often seen clearly as a separate grating. Mechanisms with different phase-selectivities are equally stimulated. Phase-inhibition would not strongly suppress the activity of mechanisms, on the assumption thai the inhibition is strongly reduced when the relative phase of the patterns is changing rapidly. Therefore patterns with rapidly changing relative phases could produce significant **adaptation** at each of the component spatial frequencies.

The model may also account for the weakness of interactions obtained with adapting patterns of first and fifth harmonics. The bandwidth of the mechanisms may not be broad enough for any mechanism to be strongly stimulated by both the first and fifth harmonics (Stromeyer *et al.*, 1973; Stromeyer and Klein, 1974). Thus there would not be stimulation strongly dependent on the relative phase of the two harmonics, and phase-inhibition would be weak.

Adaptation studies have revealed phase-selective, broad-band mechanisms such as edge- and line-selective mechanisms (Stromeyer *et al.*, 1973; DC Valois, 1977; Sansbury *et al.*, 1978), but interactions between such mechanisms have not been systematically explored.

Acknowledgements We thank Professors Karl Pribram and Leo Ganz of Stanford University. Professor Derek Fender of California Institute of Technology and Professor Richard Kronauer of Harvard University for their generous support. This work was supported by Grant EY 01774 from the National Institutes of Health.

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