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ADAPTATION TO SQUARE-WAVE GRATINGS: INHIBITION BETWEEN SPATIAL FREQUENCY CHANNELS IN THE HUMAN VISUAL SYSTEM

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SUMMARY

1. The observation that the detection threshold for a square-wave grating depends only on that of its fundamental was confirmed by showing that adapting to the fundamental spatial frequency caused elevation of the square-wave threshold, to the same extent as the fundamental threshold was elevated by the same adapting pattern. Adapting to the third harmonic frequency had no effect on the square-wave threshold.

2. Adapting to a square-wave grating should elevate the thresholds for both the fundamental and third harmonic frequencies (Blakemore & Campbell, 1969), and the amount of elevation at each frequency should be predictable from the contrast of that frequency within the square-wave.

3. It was found, however, that both the fundamental and third harmonic, when present in the square-wave, were much less effective as suprathreshold adapting stimuli than would be predicted from their effects when viewed in isolation.

4. Adapting to a mixture of two sinusoidal gratings (with 3:1 frequency ratio) demonstrated that the fall in adapting power was not due to the higher harmonics of the square-wave nor to nonlinearities in the stimulus display. Similar effects were found when the phase relations of the adapting gratings were changed, showing that the interaction is not a special property of square-waves or of edges.

5. It is suggested that the spatial frequency channels subserving the fundamental and third harmonic frequencies inhibit each other when the patterns are some way suprathreshold. At or near threshold, there is no such reciprocal inhibition.

INTRODUCTION

Campbell & Robson (1968) showed that the detection threshold for a square-wave grating, whose spatial frequency was greater than about 1 c/deg, could be predicted from the threshold for its corresponding fundamental sine-wave grating. Further, the contrast at which the square-wave could just be distinguished from its fundamental was the contrast at which its third harmonic just exceeded its detection threshold. These experiments indicate that, over most of the visible range of spatial frequencies, the fundamental and third harmonic of a square-wave grating are detected independently by separate spatial frequency channels. Graham & Nachmias (1971) provide more general evidence for the independent analysis of these two components: they used a variety of contrast ratios and phase relations in a mixture of two sinusoidal gratings, one having a spatial frequency three times that of the other. They found that the detection threshold for such a mixture was the contrast at which one of the components reached its own threshold, there being no interaction between the two spatial frequencies of grating.

These observations can be explained by the existence of channels in the human visual system which are each sensitive to a narrow range of spatial frequency. Blakemore & Campbell (1969) attempted to determine the characteristics of these channels, by measuring the amount of threshold elevation obtained at different spatial frequencies after adapting to one high contrast sinusoidal grating. The elevation was found to be fairly specific to the region of the adapting spatial frequency: there was no elevation at spatial frequencies three times and one third the adapting frequency. These data are consistent with the proposition of Campbell & Robson (1968) that the fundamental and third harmonic of a square-wave grating are processed by quite separate channels.

Blakemore & Campbell (1969) found, not surprisingly, that adaptation to a high contrast square-wave grating produced marked threshold elevation in the frequency region of its third harmonic, as well as at its fundamental. It appeared superficially that, again, the fundamental and third harmonic were acting independently. However, Blakemore & Campbell (1969) did not determine whether the amounts of threshold elevation at the fundamental and third harmonic were predictable from the known contrast of these two components in the adapting pattern.

This paper sets out to examine this point. Is the amount of threshold elevation produced at the fundamental frequency, after adapting to a square-wave grating, identical to that produced by adapting to an equivalent amount (calculated by Fourier theory) of fundamental viewed in isolation? And, is the elevation at the third harmonic similarly predictable? In other words, do the fundamental and third harmonic act totally independently as suprathreshold adapting stimuli, or is there some suprathreshold interaction between the spatial frequency channels in the human visual system?

Blakemore & Campbell (1969) found that adapting to the third harmonic alone had no effect on the threshold of the fundamental, and so it would be expected that adapting to a square-wave grating would cause the predicted amount of threshold elevation at the fundamental. The third harmonic presents some difficulty because there is a fifth harmonic in the square-wave: this harmonic, when viewed alone, would be expected to slightly elevate the threshold of the third harmonic. Thus some interaction between the third and fifth harmonics might be expected.

Throughout this paper, the gratings used have had spatial frequencies above 2·5 c/deg as Campbell & Robson (1968) found that, for spatial frequencies below 1 c/deg, the square-wave threshold was no longer predictable from the threshold for its fundamental.

The data presented in this paper show clearly that there is some interaction between spatial frequency channels in the human visual system: the threshold elevation of the fundamental and third harmonic are both considerably *less* than predicted when one adapts to a square-wave grating. It is tentatively suggested that the results can be explained by inhibition between spatial frequency channels, analogous to that proposed by Blakemore, Carpenter & Georgeson (1970) in the orientation domain.

METHODS

All the patterns were generated on the face of a cathode ray tube (P31 phosphor). The screen was circular (diameter = 13 cm) and, viewed from 200 cm, subtended 3·7 deg of arc at the eye.

In all experiments, the patterns were vertically oriented. The adapting patterns were continuously present on the screen, whilst the contrast of the gratings used for detection threshold determinations was turned on and off at 1 c/sec. Contrast is defined as

$$\frac{L_{\max}-L_{\min}}{L_{\max}+L_{\min}},$$

where L is the luminance of a point on the screen.

The subjects set their thresholds by adjusting the contrast of the grating with a logarithmic attenuator having 0·025 log unit steps. The mean luminance was unaffected by this procedure and was maintained constant at about 100 cd/m^2.

The majority of the data was obtained on one subject (the author) but the findings were confirmed on another subject. The gratings were viewed binocularly, and no artificial pupils or refraction were used; both subjects were emmetropic.

The linearity of the screen was assessed using a linear phototransistor (TIL67, Texas Instruments Ltd). Up to a contrast of 0·1 there was very little harmonic distortion of a sinusoidal grating. At a contrast of 0·3, there was about 2 % of second harmonic and 1 % of third harmonic; while, at a contrast of 0·65, there was 8 % of second harmonic and 2 % of third harmonic.

RESULTS

According to Fourier theory, a square-wave grating, which is a function of x, can be considered to be the sum of the infinite series:

$$\frac{4m}{\pi}\left\{\sin\frac{2\pi x}{X}+\frac{1}{3}\sin 3\frac{2\pi x}{X}+\frac{1}{5}\sin 5\frac{2\pi x}{X}+\ldots\right\},$$

where m is the contrast of the square-wave and X is its period. Thus, the contrast of the fundamental within the square-wave is $4m/\pi$ ($\sim$ 1·27m) and the contrast of the third harmonic is $4m/3\pi$ ($\sim$ 0·42m). If the contrast of the third harmonic is m', then the contrast of square-wave containing that amplitude of third harmonic is $3\pi m'/4$ ($\sim$ 2·36m').

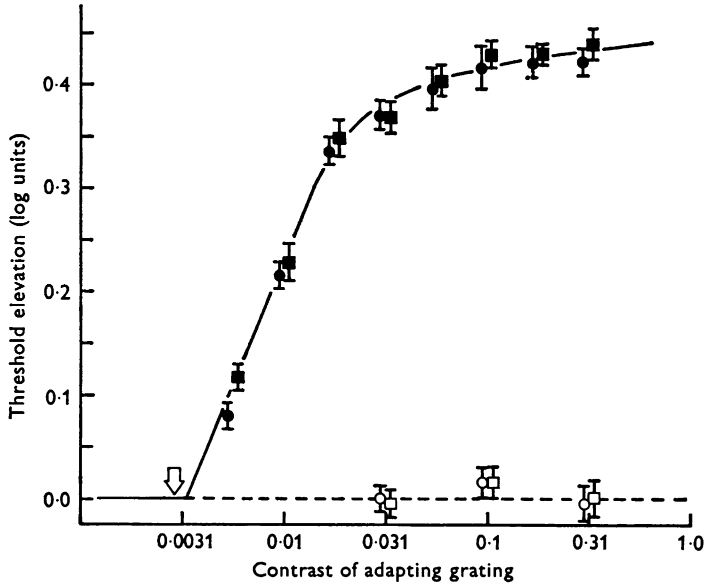

Fig. 1. Elevation of threshold, in log units, for a 4·5 c/deg sine-wave grating (●) and a 4·5 c/deg square-wave grating (■) after adapting to a 4·5 c/deg sine-wave grating. The arrow indicates the initial detection threshold for the adapting grating. Also illustrated are the effects on the threshold for a 4·5 c/deg sine-wave grating (○) and a 4·5 c/deg square-wave grating (□) of adapting to a sine-wave of 13·5 c/deg. The square symbols have been shifted slightly to the right and the circles slightly to the left. Subject: D. J. T.

Elevation of square-wave thresholds

If the threshold of a square-wave grating is determined solely by the threshold of its fundamental sinusoid, as proposed by Campbell & Robson (1968), then adapting to a sine-wave grating of the fundamental spatial frequency should elevate the square-wave threshold. Moreover, the amount of elevation produced by adapting to a given contrast of fundamental should be identical to the elevation of threshold of the fundamental itself, produced by the same adapting grating. Fig. 1 shows the results of an experiment designed to test this prediction.

Contrast threshold elevation, in log units, for a 4·5 c/deg sine-wave grating is plotted against the contrast of the adapting 4·5 c/deg sine-wave (filled circles). Also plotted is the elevation of threshold of a 4·5 c/deg square-wave grating (filled squares) after adapting to the same sine-wave gratings. The arrow pointing to the abscissa indicates the control threshold for the 4·5 c/deg sine-wave grating. Initially the subject made five threshold settings each for the square-wave and sine-wave gratings. He then viewed the adapting grating for 3 min, moving his eyes across the screen to prevent the generation of after-images. Alternate threshold settings were then made for the sine- and square-wave gratings, allowing 20–30 sec further adaptation between each setting. Five threshold settings were made at each adapting contrast. Thus, each data point in Fig. 1 is the differences between two means of five settings; 1 S.E. of the elevation is indicated.

At each adaptation level, the actual sensitivity to the square-wave was always about $4/\pi$ ($\sim$ 1·27) times greater than that to the sine-wave, as predicted from Fourier theory, but the elevation of threshold for both the sine- and square-wave were very nearly the same, as predicted above. This appears to confirm the observation that the square-wave threshold is dependent only on that of its fundamental.

A further indication that this is true is given by the results of adapting to a sine wave of 13·5 c/deg, the third harmonic of the square wave. The open circles in Fig. 1 represent the threshold elevation of the 4·5 c/deg sine-wave and the open squares represent that of the 4·5 c/deg square-wave after adapting to various contrasts of the 13·5 c/deg sine-wave. In neither case is the amount of threshold elevation statistically significant. This is not surprising, in view of the known narrowness of spatial frequency channels.

Adaptation to square-wave gratings

Third harmonic threshold

If the fundamental and third harmonic of a square-wave grating are treated independently above threshold, then the amount of threshold elevation of the third harmonic, produced by adapting to a square-wave, should be predictable from the contrast of the third harmonic in the adapting pattern. A certain contrast of third harmonic will be present in a square-wave of $3\pi/4$ times that contrast. Thus, one would expect to obtain the same amount of threshold elevation for a 15 c/deg sine-wave by adapting either to a 15 c/deg sine-wave of contrast 0·1 or by adapting to a 5 c/deg square-wave grating with a contrast of 0·236. Fig. 2 illustrates the results of an experiment to test this point.

The ordinate of Fig. 2 shows the elevation of contrast threshold for the 15 c/deg sine-wave grating in log units, after adapting to various gratings. The lower abscissa scale shows the contrast of 15 c/deg sinusoidal adapting gratings and also the contrast of the 15 c/deg component of the 5 c/deg square-wave adapting grating. The upper abscissa scale shows the actual

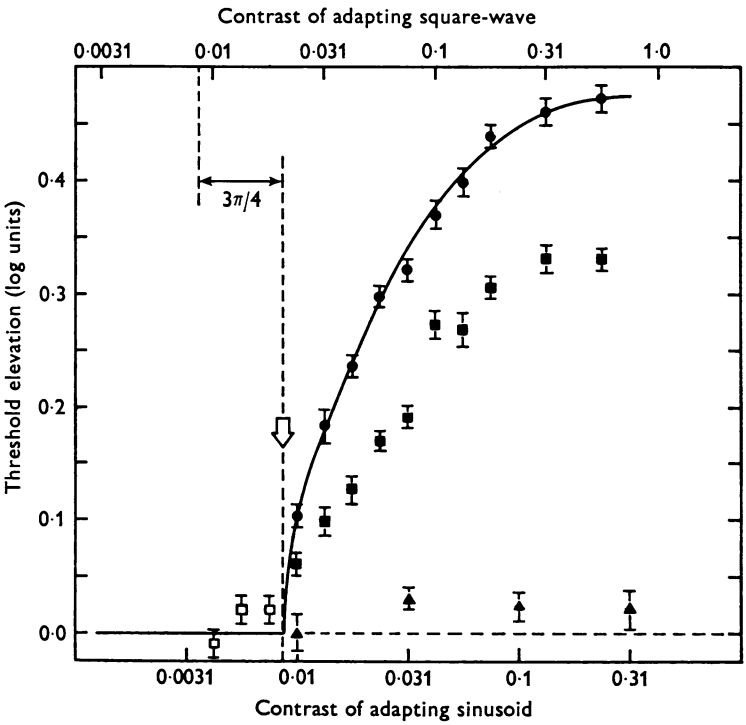

Fig. 2. The third harmonic of a 5 c/deg square-wave grating. Threshold elevation, in log units, for a 15 c/deg sine-wave grating is plotted against the contrast of various adapting gratings. The lower abscissa scale represents the contrast of the adapting 15 c/deg sine-wave (●), 5 c/deg sine-wave (▲) and the 15 c/deg component of the 5 c/deg square-wave. The upper abscissa scale represents the contrast of the adapting 5 c/deg square-wave (□, ■) and is thus shifted $3\pi/4$ times relative to the lower scale. The arrow points towards the control threshold for the 15 c/deg sine-wave and is also aligned, on the upper scale, with the contrast at which a 5 c/deg square-wave can just be distinguished from its fundamental. The open squares show the contrasts at which the adapting square-wave was indistinguishable from its fundamental, the solid squares the contrasts at which the square-wave grating actually appeared square. Subject: D. J. T.

contrast of the 5 c/deg adapting square-wave grating, and is thus shifted $3\pi/4$ times relative to the lower scale. The arrow pointing towards the lower abscissa scale indicates the control threshold of the test 15 c/deg sine-wave grating; it is aligned, on the upper scale, with the contrast at which a 5 c/deg square-wave could just be discriminated from its fundamental, a value determined in the same manner as that used by Campbell & Robson (1968).

The filled circles represent the elevation of threshold of the 15 c/deg sine-wave after adapting to various contrasts of 15 c/deg sine, and the squares represent the elevation of threshold after adapting to 5 c/deg square-wave gratings. The filled squares represent the range of adapting contrast over which the square-wave actually appeared square, while the open squares show the contrasts when the square-wave was indistinguishable from its fundamental. Each point is the mean of sixteen readings; the elevation of threshold produced by adapting to the 15 c/deg sine- and the 5 c/deg square-wave were made as comparable as possible by alternating periods of adaptation. Four readings were made after adapting to the 15 c/deg sine-wave of a particular contrast. Then, after a 30 min rest, during which the threshold returned towards normal, four readings were made after adapting to the theoretically equivalent contrast of square-wave. After a further 30 min, this sequence was repeated. Thus, eight readings were obtained for each pair of data points. In the experiment illustrated in Fig. 2, the above procedure was repeated, giving a total of sixteen readings for each data point. In this way, it was hoped that such factors as cumulative adaptation and any changes in the apparatus or subject could be ruled out as causes of any differences in threshold elevation that might be found when comparing the effects of adapting to a square-wave or its third harmonic. In Fig. 2, ± 1 S.E. of the mean elevation is indicated; each S.E. was computed from the standard errors of the initial control threshold and the threshold after adapting.

To determine whether there was any statistically significant difference in the threshold elevation produced by adapting to the 15 c/deg sine-wave and its theoretically equivalent square-wave, the S.E. of the post-adaptation threshold readings alone were used, as the elevation values were based on the same controls. These S.E. are thus less than those displayed in Fig. 2.

If the third harmonic and fundamental of the square-wave were, in fact, treated independently by the visual system, the threshold elevation of the third harmonic spatial frequency after adapting to a particular contrast of square-wave should be identical to that produced by adapting to a sine-wave grating of the third harmonic frequency and $4/3\pi$ times that contrast. In other words, the data points for the threshold elevation after adapting to the square-wave (squares) should lie along the same curve in Fig. 2 as the points obtained after adapting to the third harmonic alone (filled circles). Fig. 2 shows clearly that the same curve does *not* fit both sets of points and that the elevation produced by adapting to a square wave is considerably less than predicted over the whole range of adapting contrasts at which the square-wave appeared square (i.e. when the third harmonic within the square-wave was visible). The difference between each supposedly equivalent pair of means is extremely significant statistically. In the range of contrasts where the adapting square-wave was

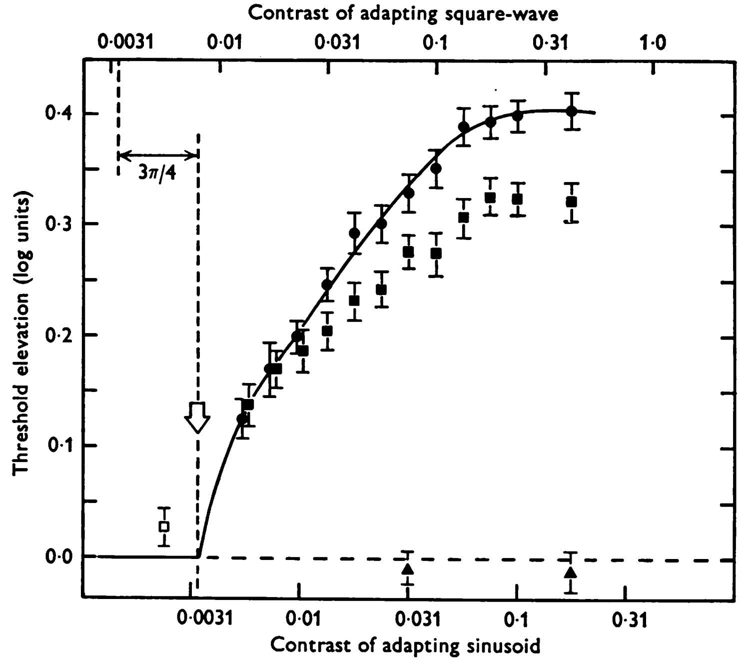

Fig. 3. Third harmonic of a 3 c/deg square-wave grating. Conventions as for Fig. 2. The elevation of threshold for a 9 c/deg sine-wave grating is plotted against the contrast of various adapting patterns: 9 c/deg sine-wave (●), 3 c/deg sine-wave (▲) and 3 c/deg square-wave (□, ■). The arrow points towards the control threshold for the 9 c/deg sine-wave. Subject: D. J. T.

indistinguishable from its fundamental (open squares), there is, as expected, no statistically significant elevation of threshold of the third harmonic spatial frequency.

The filled triangles in Fig. 2 represent the elevation of threshold at 15 c/deg after adapting to a sine-wave of 5 c/deg (the lower abscissa scale is relevant to this grating). Again, it can be seen that the fundamental, when presented alone, has no effect on the third harmonic threshold. However, when presented with the third harmonic, it decreases the adapting power of the third harmonic.

Similar results have been obtained at several spatial frequencies and on one other subject. Fig. 3 shows the results of an experiment in which the square-wave had a spatial frequency of 3 c/deg and the test sine-wave grating had a spatial frequency of 9 c/deg. Threshold elevation was tested after adapting to a 9 c/deg sine-wave (filled circles), a 3 c/deg square-wave (squares) and a 3 c/deg sine-wave (filled triangles). The results are basically similar to those in Fig. 2 with one difference: up to an adapting contrast of about 0·01, there is no significant difference between the amounts of elevation produced by adapting to the square-wave and its theoretically equivalent third harmonic viewed alone. Above an adapting contrast 0·01, however, the third harmonic produces significantly less elevation than predicted when it is present with the fundamental; again, the fundamental alone had no effect on third harmonic threshold.

Fundamental threshold

The third harmonic has been shown to be less effective as an adapting stimulus when it is present in the square-wave. Is the fundamental also less effective when present with the higher harmonics? Fig. 4 shows the results of an experiment designed to examine this point.

The ordinate shows the elevation of contrast threshold (in log units) for a 3 c/deg sine-wave grating after adapting to various patterns. The circles represent the elevation after adapting to a 3 c/deg sine-wave grating and the squares after adapting to a 3 c/deg square-wave grating. The lower abscissa scale shows the contrast of the adapting sine-wave gratings and also the contrast of the fundamental within the square-wave. The upper scale shows the actual contrast of the adapting square-wave; the two scales are thus shifted $4/\pi$ times relative to each other. The filled arrow indicates on the lower abscissa scale the control threshold for the 3 c/deg sine-wave, and is aligned on the upper scale with the control threshold for the square-wave. The open arrow indicates the contrast of the square-wave at which the third harmonic is just visible.

Each point is the mean of eight readings; as with the previous experiment, four readings were made after adapting to the sine-wave and, after a rest of 30 min, four readings were made after adapting to the theoretically equivalent square-wave. After a further 30 min the process was repeated. In the Figure, ± 1 S.E. of the mean elevation is indicated.

It can readily be seen that, over some of the range of adapting contrast, the elevation of fundamental threshold is not the same after adapting to the sine-wave and its theoretically equivalent square-wave. As with the third harmonic, the fundamental appears to be less effective as an adapting stimulus when it is present in a square-wave. In contrast to the third harmonic data, the fundamental only becomes less effective at higher contrasts. Thus, in Fig. 4, there is no significant difference between the effects of the fundamental and the square-wave below an adapting contrast of 0·03.

Fig. 5 shows a similar experiment, using 5 c/deg sine- and square-waves. Again, there is no real difference between the effects of adapting to the fundamental and the theoretically equivalent square-wave below a contrast

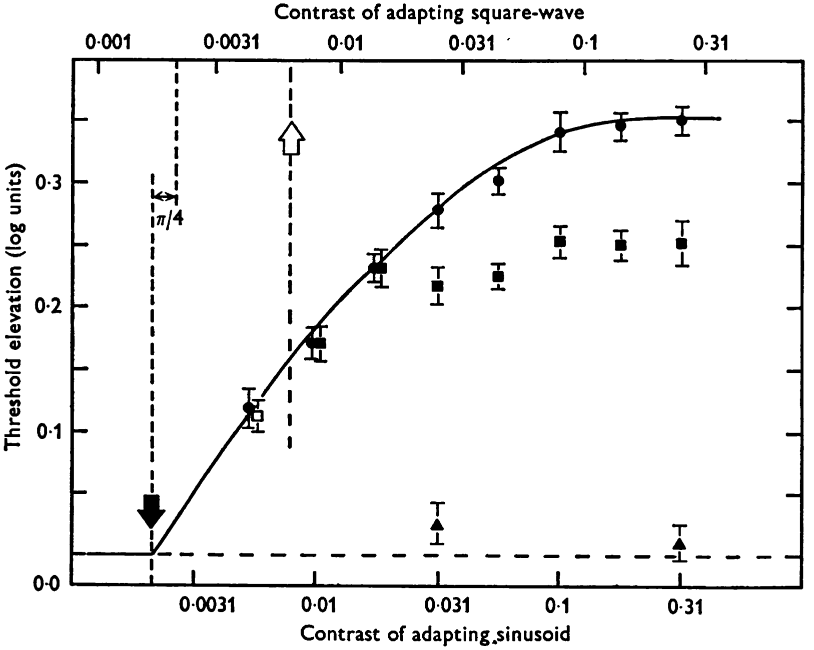

Fig. 4. Fundamental of a 3 c/deg square-wave grating. Threshold elevation, in log units, for a 3 c/deg sine-wave grating is plotted against the contrast of various adapting patterns: 3 c/deg sine-wave (●), 3 c/deg square-wave (□, ■) and 9 c/deg sine-wave (▲). The open squares represent the adapting contrasts at which the square-wave was indistinguishable from its fundamental, the filled squares when it actually appeared square. The lower abscissa scale shows the contrast of adapting sine-waves and the 3 c/deg sinusoidal component of the square-wave, while the upper scale shows the actual contrast of the square-wave grating. The upper scale is thus shifted $4/\pi$ times relative to the lower scale. The filled arrow indicates the control threshold for the 3 c/deg sine-wave and is aligned on the upper scale with the control threshold for the 3 c/deg square-wave. The open arrow indicates the contrast at which the 3 c/deg square-wave can just be distinguished from its fundamental. Over the lower range of adapting contrasts the square symbols have been shifted slightly to the right, the circles to the left. Subject: D. J. T.

of 0·1. One might expect no difference in effect while the third harmonic was still invisible (open squares), but, in fact, there is no difference until the third harmonic is considerably above threshold. In all experiments on the fundamental, this was found to be true. A further difference between the data for the fundamental and the third harmonic is the magnitude of the effect. The third harmonic is about 0·12 log unit less adapted by the square-wave than expected, along the plateaux of the elevation curves; while the fundamental is only about 0·06–0·10 log unit less adapted. This

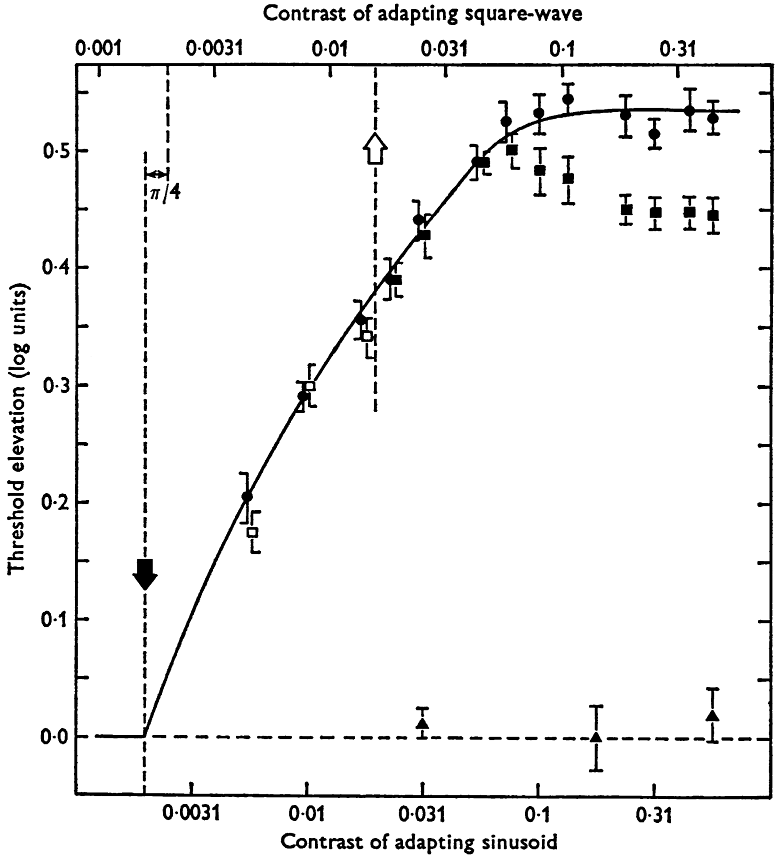

Fig. 5. Fundamental of 5 c/deg square-wave grating. Conventions as for Fig. 4. Threshold elevation for a 5 c/deg sine-wave is plotted against the adapting contrast of 5 c/deg sine-wave (●), 5 c/deg square-wave (□, ■) and 15 c/deg sine-wave (▲). The solid arrow indicates the control threshold for the 5 c/deg sine-wave, while the open arrow indicates the contrast at which the 5 c/deg square-wave is just distinguishable from its fundamental. Over the lower range of adapting contrasts the circles have been shifted slightly to the left, the squares to the right. Subject: D. J. T.

may be a real difference, which could readily be explained by the fact that, in the square wave, there is less third harmonic present than fundamental; thus the third harmonic might be expected to have less of an effect. It is possible, also, that a similar explanation could account for the apparently higher contrast needed before the fundamental in the square wave begins to be a less effective adapting stimulus than predicted.

The triangles in Fig. 4 and Fig. 5 show the elevation of fundamental threshold after adapting to the third harmonic frequency of sine-wave alone. There is little elevation of threshold after adapting to the third harmonic, so that the third harmonic has an effect on the fundamental only when it is present with the fundamental as an adapting stimulus.

The role of higher harmonics

When viewed alone, neither the third harmonic nor the higher harmonics of the square-wave will cause threshold elevation of the fundamental spatial frequency (Blakemore & Campbell, 1969). Thus the differences between the adapting effects of the square-wave and its fundamental are unlikely to be due to the contamination of the fundamental spatial frequency channel by the higher harmonics. The third harmonic channel will not be affected by the fundamental but viewing the fifth harmonic alone would be expected to cause some elevation of third harmonic threshold (Blakemore & Campbell, 1969). Thus some of the decrease of adapting power of the third harmonic within the square-wave might be due to contamination by the higher harmonics. To remove this complication from the interpretation of the results, the higher harmonics were removed from the adapting pattern.

The adapting pattern consisted of a mixture of two sinusoidal gratings: one of 6 c/deg and the other of 18 c/deg. The gratings were not presented simultaneously, but each was present on alternate sweeps of the raster, whose repetition rate was 250 c/sec. At this rate, the gratings appeared to be fused. This method of display was used because the screen was found to be slightly non-linear; with alternate presentation, addition of one grating to the pattern could not alter the contrast of the other.

The test grating had a spatial frequency of 18 c/deg and was also sinusoidal. Initially, the subject adapted to a pattern consisting only of the 18 c/deg sine-wave whose contrast was 0·1; the amount of threshold elevation obtained was 0·41 log unit. After a rest of 30 min, the subject adapted to the same grating but, in addition, a 6 c/deg sine-wave with a contrast of 0·33 was present in the same phase as is found in a square-wave. The presence of this grating reduced the adapting power of the original 18 c/deg grating: the amount of threshold elevation fell to 0·31 log unit. Each elevation was the mean of five readings and the standard errors were about 0·03 log unit. The reduction in adapting power is thus statistically significant, and it can be concluded that a large part, at least, of the reduction in adapting power of the third harmonic within the square-wave is not due to the presence of the higher harmonics but is due simply to the presence of the fundamental.

A similar experiment was conducted to prove that the fifth and higher harmonics had little or no effect on the adapting power of the fundamental. The test grating had a spatial frequency of 6 c/deg. After adapting to a 6 c/deg sine-wave with a contrast of 0·015, a threshold elevation of 0·27 log units was obtained. After adapting to the same grating but with the addition of a sine-wave of 18 c/deg and contrast of 0·1, the threshold elevation was reduced to 0·18 log units. It appears that the third harmonic alone is responsible for the large decrease in the adapting power of the fundamental within the square-wave.

It is possible that the effect of the fundamental on the third harmonic and vice-versa is some special property of the phase in which they are found in square-waves. Neurones, whose line-weighting functions have odd symmetry, would be ideally suited for the detection and analysis of edges (Tolhurst, 1972). A square-wave can be considered as a series of edges, and the interaction between the fundamental and third harmonic may result from their effects on edge detector neurones. Alternatively, the interaction may result only from the simultaneous presence of the two gratings, so that the phase would be unimportant.

An attempt was made to distinguish between these two hypotheses by repeating the above experiments with a mixture of two sine-waves, but presented 180 deg out of phase (i.e. they were present in the same phase as is found in a triangular wave). Adapting to a mixture of an 18 c/deg sine-wave (contrast 0·1) and a 6 c/deg sine-wave (contrast 0·33) caused 0·295 log units of elevation of the threshold for the 18 c/deg test grating. This value is very similar to that obtained by adapting to these gratings in the square-wave phase (0·33 log units). The threshold for the 6 c/deg sine-wave was elevated 0·18 log units after adapting to a 6 c/deg sine-wave (contrast 0·015) added to the 18 c/deg sine-wave (contrast 0·1) in the triangular wave phase. This value is identical to that obtained previously when the gratings were in the square-wave phase.

It can be concluded that the reduction in the adapting power of the fundamental and the third harmonic is independent of the phase relation of the two components; the effects are not a special property of square-wave gratings or of edge-detector neurones, but are due simply to the simultaneous presence of more than one spatial frequency of sinusoidal grating.

DISCUSSION

Campbell & Robson (1968) and Graham & Nachmias (1971) have demonstrated that, at threshold, two gratings are detected entirely independently when their spatial frequency ration is 3:1. They suggested that there are channels in the human visual system which are each sensitive to only a narrow range of spatial frequencies. Blakemore & Campbell (1969) found that adapting to a high contrast sine-wave grating caused elevation of threshold over a limited range of frequencies, centred on that of the adapting pattern. It is tempting to suppose that the threshold elevation function represents the sensitivity function of a spatial frequency channel. But this is unlikely as Sachs, Nachmias & Robson (1971) have found these channels to be considerably narrower than the elevation functions.

As regards the present study, the most important findings of Blakemore & Campbell (1969) are the following. Adapting to one spatial frequency of sine-wave grating caused *no* elevation of threshold for frequencies three times and one third the adapting frequency, but adapting to a square-wave grating caused marked elevation at the fundamental frequency and also at the third harmonic frequency. It appeared that the fundamental and third harmonic of the square-wave were acting independently as adapting stimuli.

As these two components of the square-wave act independently at threshold, one might expect them to act independently suprathreshold as adapting stimuli. After adapting to a square-wave of contrast m, one should obtain as much elevation of fundamental threshold as is obtained by adapting to the fundamental alone, but with a contrast of $4m/\pi$ (calculated from Fourier theory). Similarly, identical amounts of elevation of the third harmonic threshold should be obtained either by adapting to the square wave with contrast m or the third harmonic alone with contrast $4m/3\pi$. If the fundamental alone determines the square-wave threshold (Campbell & Robson, 1968), then adapting to the fundamental sine-wave should elevate the square-wave threshold, and the amount of elevation should be identical to that of the fundamental threshold after adapting to the same grating. This paper has examined these predictions.

Square-wave thresholds

As predicted, the square-wave threshold was elevated by adapting to the fundamental frequency of sine-wave. The amounts of square-wave and sine-wave threshold elevation after adapting to a particular contrast of fundamental were almost identical. Adapting to the third harmonic in isolation caused no elevation of threshold of the square-wave, thus confirming that the square-wave threshold depends only on that of its fundamental.

This tidy conclusion is deceptive, however. Consider the possible situation where the sensitivity to the fundamental was extremely lessened. Then, the visual system would be more sensitive to the third harmonic in the square-wave than to the fundamental. From the hypothesis that the fundamental and third harmonic are detected independently, we would expect that the square-wave would now be detected when the third harmonic reached its own threshold. The square-wave threshold would no longer depend on the fundamental, and the square-wave would appear indistinguishable from the third harmonic at threshold.

In the experiments reported here, the fundamental threshold could not be elevated enough by adaptation for this situation to arise. The maximum elevation obtained was about 0·4 log unit, whilst 0·5–0·9 log unit of elevation would be required before the square-wave could be detected as third harmonic (there is three times, i.e. 0·447 log unit, more fundamental than third harmonic in the square-wave, and the visual system is about 0·1 to 0·5 log unit more sensitive to the fundamental in the first place).

Julesz & Stromeyer (1970) have shown that the fundamental threshold can be sufficiently raised for the square-wave to appear indistinguishable from its third harmonic at threshold. They viewed a square-wave grating in the presence of one-dimensional white noise, in which there was a sharp-sided trough in the region of the third harmonic frequency. The fundamental threshold was considerably elevated by the masking noise, while the third harmonic was less affected due to the lack of noise in its locality. Under these conditions, only the third harmonic of the square-wave was perceived.

Adapting to square-wave gratings

It is clear from the results of adapting to square-wave gratings that the predictions are not borne out: when present in a square-wave, both the fundamental and third harmonic are less effective as adapting stimuli than when they are present singly. These results would be explicable if it could be shown that there was inhibition between spatial frequency channels. There is an alternative explanation which must be dismissed before the hypothesis of inhibition is discussed. It is possible that the non-linearities of the screen might have caused the fall in adapting power of the gratings when they are present in the square-wave.

Screen non-linearities. At contrasts below about 0·1, there was little harmonic distortion of a sinusoidal signal by the screen. As the contrast was increased from 0·1, the amount of second harmonic generated by the non-linear screen rose to 8 % at a contrast of 0·65; at this contrast there was also 2% of third harmonic. These spuriously generated harmonics may have been the cause of the decrease in adapting power of the square-wave components, but there are several reasons for rejecting this as even a partial cause of the effect.

The contrasts of adapting squares waves that produced a fall in adapting power, see especially Figs. 2 and 5, were often well below 0·1. This is in a region of contrast over which there was a negligible amount of harmonic distortion. If the spuriously generated third harmonic from the fundamental had subtracted from the intentionally present third harmonic frequency, then it is difficult to understand how so little reduction in contrast could produce so large a fall in adapting power.

The experiments with the mixture of two gratings (with a 3:1 frequency ratio) suggest that non-linearities in the screen were unimportant. The gratings were mixed in such a way as to prevent one grating from changing the contrast of the other; each grating might still have generated its own higher harmonics. Consider the reduction of the adapting power of the third harmonic. If this was due to third harmonic generated from the fundamental grating, then a shift in phase of the fundamental by 180 deg should cause the addition of the intended and spurious third harmonic, resulting in an increase in the adapting power of the third harmonic. This was clearly not found, and it can be concluded that the spurious third harmonic was not responsible.

Consider now the decrease of the fundamental's adapting power in the experiments with a mixture of two spatial frequencies. In no way could non-linearities in the screen explain these results: the 18 c/deg grating may have generated higher harmonics but could not generate a 6 c/deg or a 12 c/deg component which might interfere with the adapting prowess of the 6 c/deg fundamental grating.

Thus, it must be concluded that non-linearities in the screen, although present, cannot explain the fall in adapting power of the fundamental and third harmonic when they are present together. There must be some kind of suprathreshold interaction between spatial frequency channels.

Inhibition between spatial frequency channels. If one adapts to a high contrast sine-wave grating, there is no elevation of threshold at frequencies three times and one third the adapting spatial frequency. Thus, it is unlikely that the third harmonic would activate the same adaptation channel when both frequencies are present together in the adapting pattern. Any such interaction (simultaneous activation of the same channel) would be expected to depend on the phase relations of the two components; it was found, however, that the decrease in adapting power of each component was unaffected by a shift in the phase of the fundamental by 180 deg. The results show that there is a powerful interaction between the first two components of a square-wave and, as spatial frequency channels are so narrow, this interaction cannot be the simultaneous activation of the same channel.

One explanation for the lessening of the adapting power of a grating by the presence of another grating is that the two spatial frequency channels involved inhibit each other. Thus, the third harmonic channel would decrease the level of activation of the fundamental channel which would lead to a decrease in the amount of adaptation of that channel. Now, Campbell & Robson (1968) showed that the contrast at which a square-wave could be distinguished from its fundamental was the contrast at which the third harmonic reached its own contrast threshold. There was no inhibition between the fundamental and the third harmonic of the square-wave, although the fundamental was above threshold. This is perhaps consistent with the present findings that the decrease in adapting power did not occur until the square-wave was well above the third harmonic threshold (except Fig. 2). The reciprocal inhibition between the spatial frequency channels appears to have a higher contrast threshold than the actual detection threshold for the inhibiting grating.

Inhibition between spatial frequency channels would be analogous to that between orientation channels proposed by Blakemore, Carpenter & Georgeson (1970) to explain the observation that, when two lines are placed at an acute angle to each other, the angle between them appears to be greater than it really is. They supposed that reciprocal inhibition between orientation channels causes a shift in the channel which is most excited. A corollary of this hypothesis is that the level of activity of the most excited channel will be considerably less than in the situation where only one line is present. This might be interpreted by the visual system as a decrease in apparent contrast of the line.

Thus reciprocal inhibition in the spatial frequency domain should result in a divergent shift in the apparent spatial frequencies of the two gratings and also a fall in apparent contrast of both. The results in this paper could be explained by such a fall in apparent contrast, although this has not been demonstrated directly.

If there is reciprocal inhibition between spatial frequency channels, then two testable predictions can be made. First, the simultaneous apparent spatial frequency shift should exist: in the presence of a lower frequency grating, a particular grating should appear to have a higher spatial frequency than it really has; whilst, in the presence of a higher frequency grating, its own spatial frequency should appear to be decreased. Secondly, the phenomenon of disinhibition should be demonstrable as in the orientation domain (Blakemore *et al.* 1970). The adapting power of a 6 c/deg grating, for instance, will be reduced by the simultaneous presence of a grating of 18 c/deg. If, now, a third grating of even higher spatial frequency is added, then disinhibition should result: the adapting power of the 6 c/deg grating should return towards normal. The third grating would inhibit the 18 c/deg grating so that its effect on the 6 c/deg grating would be lessened.

If these two phenomena could be demonstrated, the hypothesis of inhibition between channels would be considerably strengthened. Whether the effects reported in this paper represent this inhibition will require more proof as another candidate for such inhibition already exists. The adaptation channels of Blakemore & Campbell (1969) are considerably broader than the true spatial frequency channels demonstrated by Sachs *et al.* (1971). If adaptation is an after-effect of prolonged inhibition (Blakemore, Carpenter & Georgeson, 1971), then the channels of Blakemore & Campbell might represent the spread of inhibition between channels. The interaction demonstrated in this study may represent a second type of inhibition, which does not cause adaptation as an after-effect and which has a greater spread in the spatial frequency domain.

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