APPLICATION OF FOURIER ANALYSIS TO THE VISIBILITY OF GRATINGS

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SUMMARY

1. The contrast thresholds of a variety of grating patterns have been measured over a wide range of spatial frequencies.

2. Contrast thresholds for the detection of gratings whose luminance profiles are sine, square, rectangular or saw-tooth waves can be simply related using Fourier theory.

3. Over a wide range of spatial frequencies the contrast threshold of a grating is determined only by the amplitude of the fundamental Fourier component of its wave form.

4. Gratings of complex wave form cannot be distinguished from sine-wave gratings until their contrast has been raised to a level at which the higher harmonic components reach their independent threshold.

5. These findings can be explained by the existence within the nervous system of linearly operating independent mechanisms selectively sensitive to limited ranges of spatial frequencies.

INTRODUCTION

Our ability to perceive the details of a visual scene is determined by the relative size and contrast of the detail present. This is clearly demonstrated when the scene is an extended grating pattern whose luminance perpendicular to the bars is modulated sinusoidally about a fixed mean level (sine-wave grating: Fig. 1). In this case the threshold contrast* necessary for perception of the bars is found to be a function of the spatial frequency of the grating. The reciprocal of the threshold contrast is the 'contrast sensitivity' and the variation of the sensitivity over a range of spatial frequencies is described by the 'contrast-sensitivity function'.

The first measurement of the contrast-sensitivity function of the human visual system was reported by Schade in 1956. Schade interpreted his

* In this work we follow Michelson (1927), who defined the contrast of a grating as the maximum luminance minus the minimum luminance divided by twice the mean luminance, as illustrated in Fig. 1.

findings in terms of the modulation transfer function of a diffraction limited optical system together with the effects of spatial interactions within the nervous mechanism of the retina. More recently, the actual modulation transfer function of the dioptric mechanism of the eye has been measured directly and the contrast-sensitivity function of the visual nervous system has been independently determined (Arnulf & Dupuy, 1960; Campbell & Green, 1965; Campbell & Gubisch, 1966).
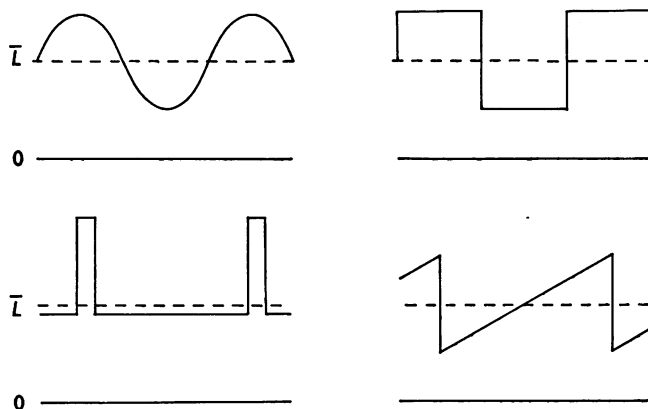

Fig. 1. Luminance distribution across sine-, square-, saw-tooth- and rectangular-wave gratings of contrast 0·5. The space-average luminance is indicated by a dashed line. The contrast, m, is defined by $m = (L_{max} - L_{min})/(2\bar{L})$, where $\bar{L}$ is the space-average luminance. The spatial frequency of the grating is the reciprocal of the angular subtense at the observer's eye of one complete cycle. The rectangular wave-grating is characterized by its duty cycle, r, which is the ratio of the angular width of the lighter bar to the width of one complete cycle.

Using the measured modulation transfer function of the dioptrics it is possible to calculate the retinal light distribution for any object (e.g. Gubisch, 1967). However, it is not known whether the contrast threshold of any target other than a sine-wave grating can be calculated from a knowledge of the contrast-sensitivity function of the visual system. In calculating the light distribution in the retinal image, linear theory can certainly be used since the principle of superposition necessarily applies to the formation of optical images (e.g. Hopkins, 1962). However, in calculating a contrast threshold it is not certain that simple linear theory can be used since the principle of superposition does not necessarily apply to the nervous interactions of the visual system. The purpose of this investigation was to find out to what extent the contrast-sensitivity function could be used for the prediction of contrast thresholds.

A convenient technique for calculating the light distribution in the image of a non-sinusoidal grating is to consider separately the imaging of each of the Fourier components of the grating wave form. In this study,

the contrast thresholds of gratings with various wave forms (Fig. 1) have been measured and the results have been considered in terms of the sensitivity of the visual system to the individual harmonic components of these wave forms.

METHODS

The method used to generate grating targets with different modulation wave forms was based on that of Schade (1956). A raster of 2000 lines was produced on the screen of a cathode-ray tube at a frame frequency of about 100/sec. The beam intensity was modulated by a signal from a wave-form generator. With suitable synchronization of the time-base and wave-form generators, stationary gratings of any desired spatial frequency could be displayed on the screen of the cathode-ray tube. The contrast of the grating pattern could be varied by adjusting the modulation voltage. It was found that the contrast was proportional to the amplitude of the modulating voltage, at least for contrasts of less than 0·6. The mean screen luminance (500 cd/m²) was independent of the contrast or spatial frequency of the grating being displayed. For making measurements of contrast threshold the modulating voltage was switched on and off at 0·5 c/s so that the pattern was periodically introduced and removed without any change in the mean luminance.

In front of the white screen of the cathode-ray tube was placed a sheet of white cardboard 30 cm in diameter having a central aperture either 10 × 10 cm or 2 × 2 cm. The cardboard surround was illuminated to match the cathode-ray tube screen.

Unless otherwise stated, viewing was monocular, the eye was homatropinized and an artificial pupil of 2·5 mm diameter was used. The refraction was always corrected for the viewing distances to within 0·25 D. Contrast thresholds were determined by the subject adjusting the contrast of a grating of a given spatial frequency until the pattern was barely detectable. Either five or ten observations were made for each threshold determination. This gave a standard error of the mean of less than 10 %. The authors acted as subjects. In every experiment both subjects gave consistent and very similar results.

RESULTS

When gratings were displayed which had frequencies of more than 10 c/cm on the screen it was noted that there was a significant decrease in their contrast due to limitations of the cathode-ray tube. This limitation made it necessary for the subject to view the screen from two distances in order to cover a sufficiently wide range of spatial frequencies without the number of visible bars of the grating being too few. Observation shows that contrast thresholds are significantly raised if less than four cycles of the grating are visible. In Fig. 2 the contrast-sensitivity functions (F.W.C.) for the two viewing distances of 57 and 285 cm are shown. The results shown as triangles (△) were obtained at the further distance where the 10 × 10 cm aperture subtended 2° × 2°. The maximum sensitivity occurred at a spatial frequency of 4 c/deg and the sensitivity decreased at both higher and lower frequencies. Some of the decrease of sensitivity at the lower frequencies might have been due to the small number of bars being displayed. Therefore the observations were repeated at the nearer

viewing distance where the large aperture subtended $10° \times 10°$. These results are shown as squares (□). The sensitivities at spatial frequencies less than 3 c/deg were substantially greater than at the further viewing distance. This change was almost certainly due to the increased size of field but it might possibly have been connected with the actual viewing distance although the eye was accurately refracted for both distances.
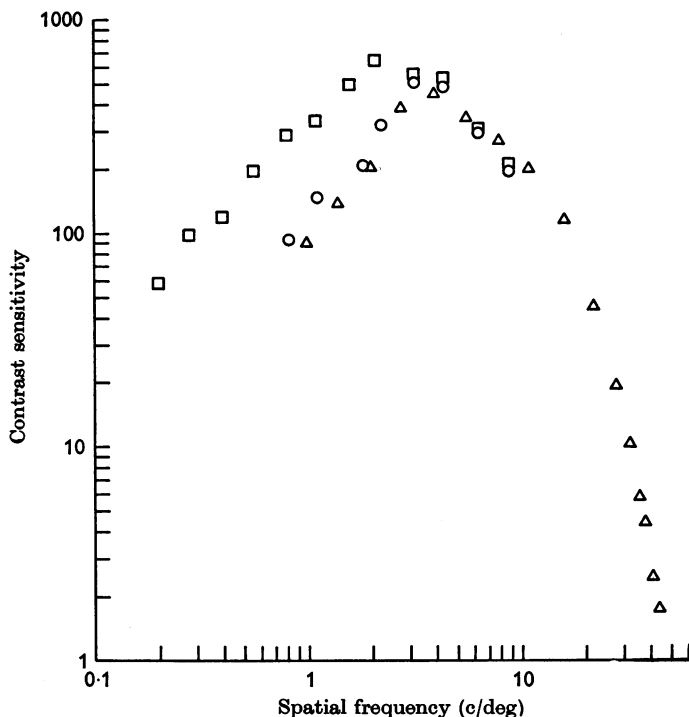

Fig. 2. Contrast sensitivity for sine-wave gratings. Subject F.W.C., luminance 500 cd/m². Viewing distance 285 cm and aperture $2° \times 2°$, △; viewing distance 57 cm, aperture $10° \times 10°$, □; viewing distance 57 cm, aperture $2° \times 2°$, ○.

To establish that field size was the crucial factor, further measurements were made at the near distance with the 2×2 cm aperture which subtended $2° \times 2°$. The results are shown as circles (○) in Fig. 2 and correspond to the results (△) obtained at the further distance with the same aperture subtense. We therefore feel justified in combining results obtained at these two viewing distances where this is necessary to obtain a wide coverage of spatial frequency. At spatial frequencies of 0·4 c/deg and less, the contrast sensitivity will probably have been slightly raised because of the small number of cycles visible in the 10° aperture.

Visibility of sine- and square-wave gratings

Fourier theory shows that a square wave can be considered as the sum of a number of sine-wave components whose frequencies are odd multiples of the fundamental frequency. Thus a square wave which is a function of x having unit amplitude (peak-to-peak amplitude $= 2$) and period X can be considered as the sum of the infinite series

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

Thus the amplitude of the fundamental (first harmonic) component of a square-wave grating of contrast m is $4m/\pi$, while the amplitudes of the third, fifth and higher harmonics are respectively $4m/3\pi$, $4m/5\pi$ and so on. The even harmonics all have zero amplitude.

The contrast-sensitivity function of the visual system falls off rapidly at spatial frequencies above 3 c/deg and it might therefore be expected that the visibility of a square-wave grating of high frequency would be determined largely by the amplitude of its fundamental component. That is, the contrast sensitivity for a square-wave grating would be expected to be about $4/\pi$ times greater than the contrast sensitivity for a sine-wave grating of the same spatial frequency.

To test this hypothesis we determined the ratio of the sensitivities for sine- and square-wave gratings, by measuring alternately the thresholds for the two types of grating at various spatial frequencies. This procedure gave more precise values of the ratio than would have been obtained by first measuring the thresholds at all frequencies for one wave form and later for the other wave form.

The results shown in Fig. 3 were obtained at a mean luminance of 500 cd/m² with subject J.G.R. It is clear that at all spatial frequencies the contrast-sensitivity for square-wave gratings (□) was greater than that for sine-wave gratings (○). The ratio of these sensitivities (square/sine sensitivity ratio) at each spatial frequency is plotted below (●) The straight line drawn through the ratios is at the predicted value of $4/\pi = 1\cdot273$. The measured ratio did not deviate systematically from this value until the spatial frequency was reduced to less than about 0·8 c/deg when the ratio became rapidly much greater.

It is interesting to note that when the spatial frequency of a square-wave grating whose contrast is just at threshold is greater than 0·8 c/deg, the grating is not perceived as different from a sine-wave grating. However, square-wave gratings with spatial frequencies of less than 0·8 c/deg are perceived to differ from sine-wave gratings of the same frequency as soon as the contrast is great enough for them to be seen.

The experiment was repeated on subject F.W.C. at two luminance levels

(Fig. 4). At the higher luminance (500 cd/m²), the square/sine sensitivity ratio was found to be $1 \cdot 280 \pm 0 \cdot 025$ s.e. when all the measurements in the frequency range 1–35 c/deg were lumped together. This value does not differ significantly from $4/\pi = 1 \cdot 273$. For frequencies below 0·8 c/deg the square/sine ratio was clearly greater than $4/\pi$.
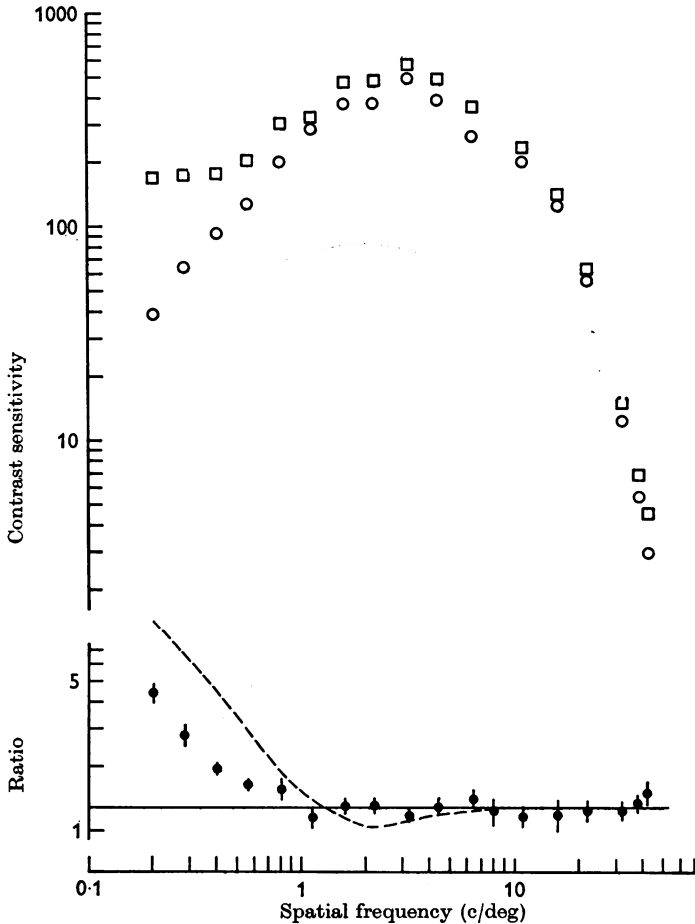

Fig. 3. Contrast sensitivity for sine-wave gratings (O) is compared with that for square-wave gratings (□) for subject J.G.R. at a luminance of 500 cd/m². The ratio of the contrast sensitivities at each spatial frequency is plotted at the bottom of the figure (the bars show ± s.e. of mean). A continuous line is drawn through the ratios at $4/\pi = 1 \cdot 273$. The dashed line indicates the predicted ratio assuming a simple peak detector mechanism.

The lower pair of curves in Fig. 4 was obtained at a luminance of 0·05 cd/m². At this lower luminance the contrast-sensitivity curves were shifted to lower frequencies and lower sensitivities and the square/sine sensitivity ratio only deviated from $4/\pi$ at frequencies below 0·4 c/deg.

DePalma & Lowry (1962) measured the contrast threshold for sine- and square-wave gratings at a variety of viewing distances. At a distance of 35 in. (89 cm) they found no significant difference in the contrast thresholds for sine- and square-wave gratings. However, at viewing distances of 10 and 14 in. (25 and 36 cm) they found that the contrast threshold for square-wave gratings was greater than for sine-wave gratings at high spatial frequencies but less at low spatial frequencies. The inconsistencies in their results for these three distances may have been due to incomplete accommodation at the nearer distances (Fincham, 1955) for they state: 'No artificial pupils were used and other optics were purposely omitted so that the observer looked directly at the test object.' We found that our results were quite consistent when a cycloplegic and artificial pupil were used and the observers were carefully refracted for the viewing distance. Measuring the threshold for sine- and square-wave gratings alternately at each spatial frequency probably also assisted in obtaining consistent results.
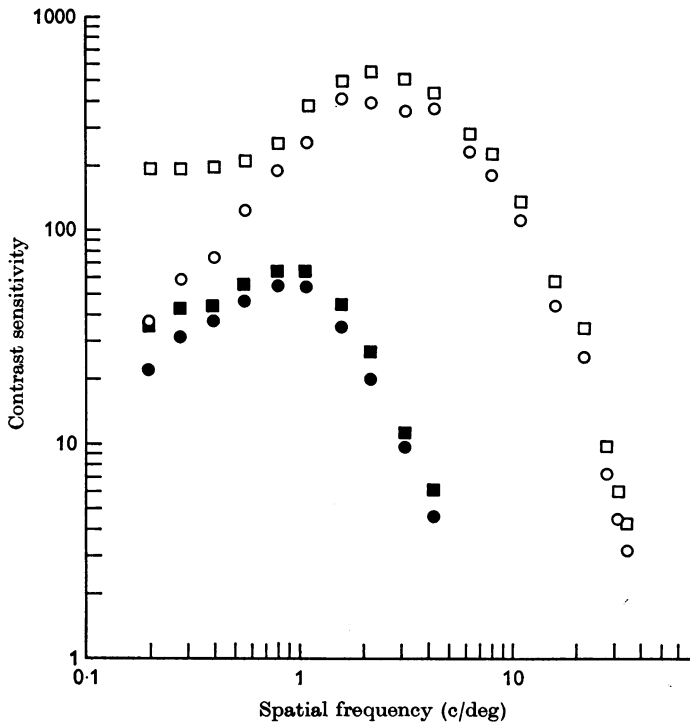

Fig. 4. Contrast sensitivity for sine-wave gratings (○, ●) is compared with that for square-wave gratings (□, ■) for subject F.W.C. Upper pair of curves for luminance of 500 cd/m². Lower pair of curves for luminance of 0·05 cd/m².

Visibility of other gratings

Rectangular-wave gratings. The variation in luminance across a rectangular-wave grating (Fig. 1) is described by the contrast, m, and the duty cycle, r. The amplitudes of the first, second, third and successive harmonics are respectively $(4m\sin\pi r)/\pi$, $(4m\sin 2\pi r)/2\pi$, $(4m\sin 3\pi r)/3\pi$ and so on. The amplitudes of all the higher harmonic components are less than that

of the fundamental although when the duty cycle is either very small or very nearly unity the amplitudes of the first few harmonics are very nearly as great as the amplitude of the fundamental.

The subject could be presented with either a rectangular-wave or a sine-wave grating of the same spatial frequency (11 c/deg) and the same space-average luminance (500 cd/m²). The subject made settings of the threshold
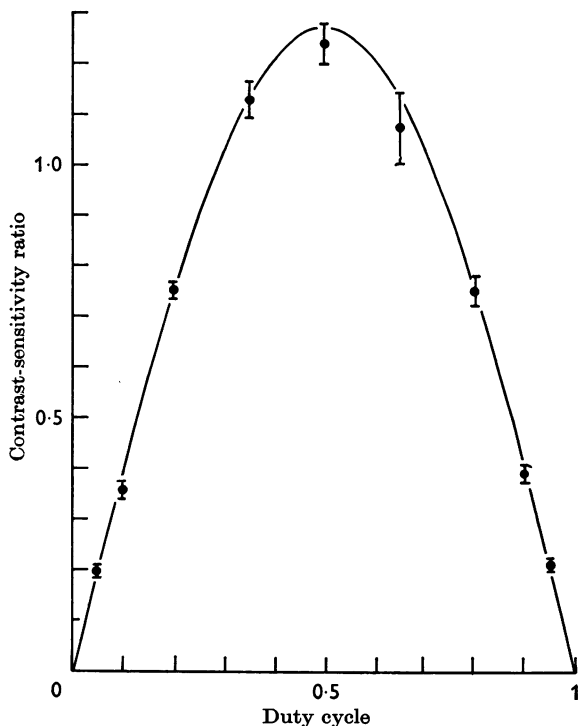

Fig. 5. The ratio of the threshold contrast for a sine-wave grating to the threshold contrast for a rectangular-wave grating as a function of the duty cycle (width of bright bar/width of whole cycle). The bars indicate ±1 S.E. of mean. Subject J. G. R., mean screen luminance 500 cd/m², spatial frequency 11 c/deg. The curve through the measurements is that expected theoretically.

contrast for the two kinds of grating alternately. Ten pairs of readings were made and used to calculate the ratio of the contrast sensitivities for the sine-wave and rectangular-wave grating. This procedure was repeated for rectangular-wave gratings with different duty cycles ranging from 0·05 (light bars on a darker background) to 0·95 (darker bars of the same width on a lighter background). In this experiment the subject viewed the display binocularly from a distance of 285 cm and no cycloplegic was used.

Figure 5 shows the results obtained with subject J. G. R. The measured

values for the contrast-sensitivity ratio for rectangular-wave and sine-wave gratings (rectangular/sine sensitivity ratio) have been plotted against the duty cycle of the rectangular-wave. The contrast-sensitivity ratio reaches a maximum when the duty cycle is one half (square-wave grating) and falls symmetrically as the duty cycle is reduced towards zero or increased towards unity.

The curve shows $(4\sin \pi r)/\pi$ which is the contrast-sensitivity ratio that would be obtained if only the fundamental component of the rectangular-wave grating contributed to its visibility. The measured values do not deviate significantly from this curve.

We have already shown that the rectangular/sine sensitivity ratio for rectangular waves with a duty cycle of one half (i.e. square waves) is constant for all spatial frequencies above about 0·8 c/deg, indicating that at these frequencies only the fundamental of the square-wave is important in determining the threshold. However, a square wave has no second or other even harmonics and the amplitudes of the odd harmonics fall off rapidly with increasing spatial frequency. On the other hand a rectangular-wave grating whose duty cycle approaches zero or unity has both even and odd harmonics, the first few of which have amplitudes nearly as great as that of the fundamental. We might therefore expect that the higher harmonics of such rectangular waves would affect the threshold contrast to a greater extent when the spatial frequency was lowered than is the case for the square wave.

We have measured the rectangular/sine sensitivity ratio for a rectangular wave grating with a duty cycle of 0·1 at various spatial frequencies under the same conditions as the previous experiment. Figure 6 shows the result for J.G.R. The contrast-sensitivity ratio was found to deviate from the value of $(4/\pi)\sin (\pi/10)$ only at spatial frequencies below about 6 c/deg.

Saw-tooth gratings. A saw-tooth wave is illustrated in Fig. 1. The amplitudes of the first, second, third and successive harmonics of a saw-tooth of contrast m are $2m/\pi$, $2m/2\pi$, $2m/3\pi$ and so on.

The threshold contrast for a saw-tooth grating with a spatial frequency of 11 c/deg was measured and compared with the threshold contrast for a sine-wave grating of the same frequency, the measurements being made alternately as before. The saw-tooth/sine sensitivity ratio was found to be $1·65 \pm 0·11$ s.e. This value does not differ significantly from the ratio of the amplitudes of the fundamentals of the two waveforms ($\pi/2 = 1·57$).

The perception of suprathreshold gratings

So far we have considered *detection* of the presence of a grating when we switch from a uniform field of a given luminance to a field of the same mean luminance having a grating pattern of low contrast upon it. We now

consider the *perception* of gratings whose contrast is above the minimum level required for their presence to be detected. In particular we consider the contrast level at which saw-tooth and square-wave gratings can be distinguished from sine-wave gratings having the same spatial frequency and the same fundamental amplitude.
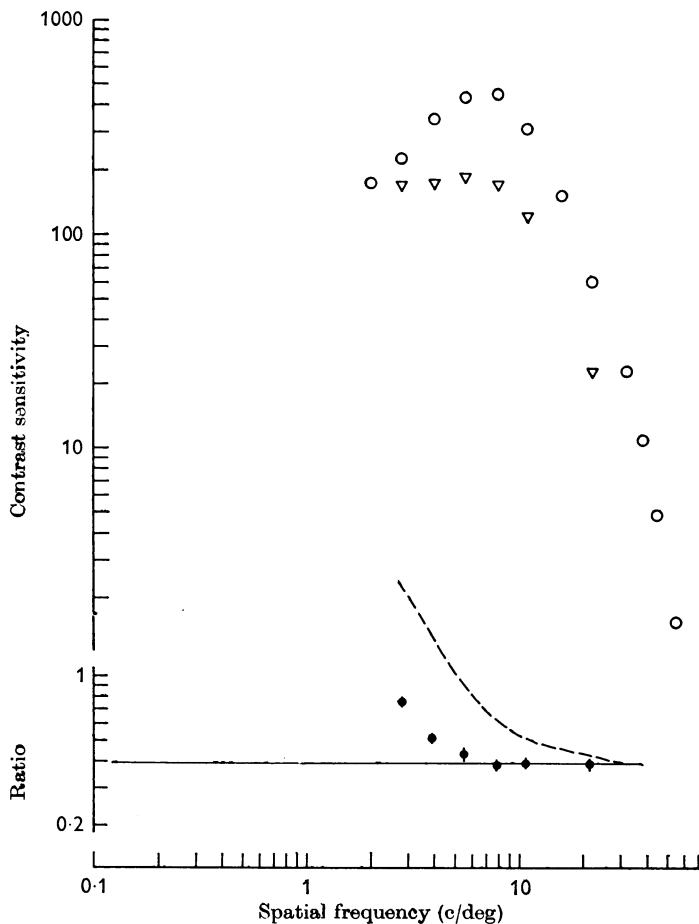

Fig. 6. The sensitivity for sine-wave gratings (O) and rectangular-wave gratings with a duty cycle of 0·1 (▽) as a function of the spatial frequency. The ratio of the sensitivities is plotted below (the bars show ±1 s.E. of mean). A continuous line is drawn through the ratios at $(4/\pi)\sin(\pi/10) = 0·393$. Subject J.G.R., luminance 500 cd/m². The dashed line indicates the predicted ratio assuming a simple peak detector mechanism.

Square-wave grating. A relay was introduced into the circuit which modulated the beam intensity of the cathode-ray tube so that the pattern on the screen could be switched alternately at 0·5 c/s from a sine-wave to a

square-wave grating. There was no change in the mean luminance of the screen nor any lateral shift of the pattern when the wave form was changed.

The experimenter set the sine/square contrast ratio to $4/\pi$ and the subject was provided with a control which enabled him to adjust the contrast of both gratings together while maintaining the ratio of their contrasts constant. At each pre-set spatial frequency the subject raised the
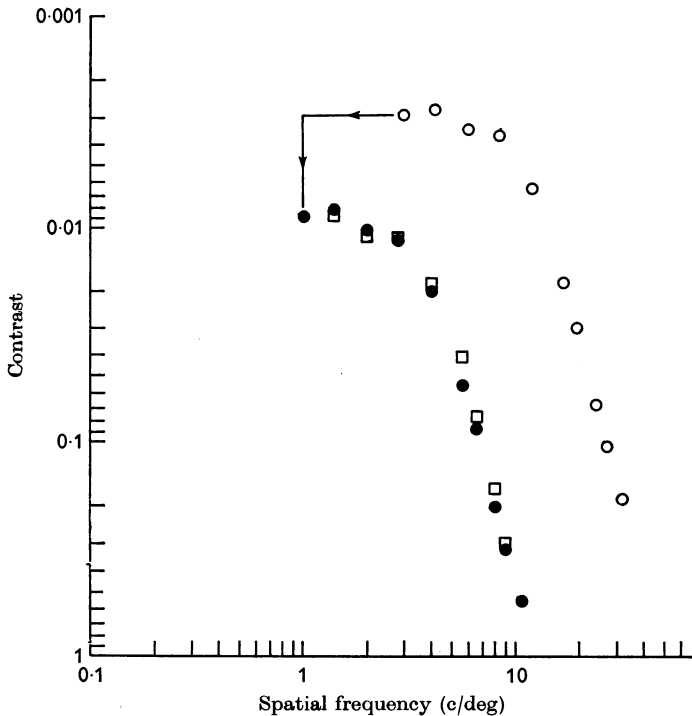

Fig. 7. The contrast level of the sine-wave grating which can just be distinguished from a square-wave grating with the same fundamental amplitude (□). The contrast threshold for a sine-wave grating measured in isolation (○) is shown as well. The filled circles (●) correspond to the sine-wave threshold measurements (○) translated by a factor of 3 in both frequency and contrast as indicated for the lowest frequency point by the arrowed lines. Subject F.W.C., luminance 500 cd/m².

contrast of both gratings together until he could distinguish one grating from the other; that is, until he could see a transition as the circuit switched from one wave form to the other. As both subjects were familiar with the appearance of sine and square-wave gratings they could in practice name the type of modulation presented as soon as the transition was apparent.

The results are shown in Fig. 7. The squares represent the contrast at

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which sine-wave gratings could be distinguished from square-wave gratings. How can these results be explained? Consider the hypothesis that when a square grating is distinguishably different from a sine-wave grating the third harmonic present in the square wave has reached its own threshold. This hypothesis can be readily checked in the following manner. The open circles are measurements of the threshold contrast for sine-wave gratings. Now the third harmonic is 3 times higher in frequency and 3 times less in amplitude than the fundamental, so that if the latter curve is displayed by a factor of three along the frequency scale and by a factor of three along the contrast scale it should fall upon the squares (the contrast above which sine-wave gratings can be distinguished from square-wave gratings). The filled circles represent the appropriately translated sine-wave data. The fit is remarkably good.

We conclude that a square-wave grating is perceived to be different from a sine-wave grating when the third harmonic of the square-wave reaches its own threshold: conversely, it may also be concluded that when the third harmonic is itself below threshold it does not contribute to the apparent contrast of the square-wave grating, or to its perception as a square-wave.

It will be noted from Fig. 7 that at high frequencies the contrast has to be raised well above threshold before sine-wave gratings can be distinguished from square-wave gratings. For example, at 8 c/deg the contrast must be about 40 times the threshold level before the discrimination is possible. On the other hand, at the lowest frequency used, 1·4 c/deg, the gratings can be discriminated almost as soon as they reach the threshold for detection. At frequencies lower than this, measurements could not be made because even at threshold the square wave could be seen to differ from the sine-wave grating.

Saw-tooth grating. The previous experiment was repeated but this time comparing a sine-wave grating with a saw-tooth grating at a spatial frequency of 11 c/deg. The ratio of the contrasts was fixed at $2/\pi$, which is the inverse ratio of the amplitudes of the fundamentals of these wave forms. Measurements of the contrast at which these gratings could be distinguished were alternated with measurements of the contrast threshold for a sine-wave grating of frequency 22 c/deg.

It was found that the sine-wave and saw-tooth gratings could be distinguished when the contrast was 12 times greater than the threshold for detection. The contrast required for discrimination was $0·99 \pm 0·03$ s.e. ($n = 10$) times the contrast at which the second harmonic reached its own independent threshold.

DISCUSSION

Because of the deficiencies inherent in any optical system the contrast of the retinal image of a grating will be less than that of the target grating. Even if we assume that the dioptric mechanism of the eye is ideal, image formation is still limited by diffraction at the pupil. With a pupil diameter of 2·5 mm, Fourier components of the object pattern with spatial frequencies greater than 78 c/deg (λ = 560 nm) are not represented at all in the image. Hence a square-wave grating with a fundamental spatial frequency greater than 26 c/deg will give rise to a retinal image in which the higher harmonics (78 c/deg and above) are completely absent. In other words the image of such a square-wave grating will be a sine-wave grating with the same spatial frequency. Thus it is inevitable that the relative contrast-sensitivities for square- and sine-wave gratings whose frequencies are greater than 26 c/deg should be exactly proportional to the relative amplitudes of their fundamental components. The same arguments apply, of course, not only to square-wave gratings but to extended gratings with any periodic modulation wave form. It must be noted, however, that if the wave form has a second harmonic the retinal image will only be sinusoidal if the fundamental frequency exceeds one half the diffraction limit.

When the fundamental frequency of a square-wave grating target is less than 26 c/deg then a proportion of its third harmonic is present in the retinal image. The possibility then exists that the contrast threshold for the square-wave grating may no longer be determined solely by the amplitude of the fundamental. However, we cannot expect the square/sine sensitivity ratio to deviate detectably from $4/\pi$ unless the over-all sensitivity of the visual system to the higher harmonic components of the square-wave grating is sufficiently great relative to the sensitivity at the fundamental frequency.

In considering just how great an effect the higher harmonic components of a square-wave grating could be expected to have upon its threshold it is necessary to make some assumptions about the determinants of the threshold contrast of gratings. Let us consider the results of assuming that the threshold is determined by the peak value of the function obtained by passing the modulation wave form of the grating through a filter whose attenuation characteristic has the form of the contrast-sensitivity function. Making this assumption we can calculate the square/sine sensitivity ratio that would be expected at different spatial frequencies. The calculated ratio is shown as a dashed line in Fig. 3. Although the measured square/sine ratio rises above $4/\pi = 1\cdot273$ at frequencies below about 1 c/deg as would be expected it does not rise as fast as the theory predicts. Moreover there is little sign of the predicted reduction of the square/sine ratio below

$4/\pi$ at frequencies around 2 c/deg. The higher harmonic components of the square-wave seem to have less effect upon the threshold than the peak-detector theory requires.

When we consider the contrast-sensitivity measurements made for a rectangular wave grating with a duty cycle of 0·1 (Fig. 6) we see that the rectangular/sine sensitivity ratio does not rise above $(4/\pi)\sin(\pi/10)$ until the spatial frequency is reduced below about 6 c/deg. In this case the simple peak-detector theory would predict a rise at considerably higher spatial frequencies (as shown by the dashed line in Fig. 6). Again the higher harmonic components seem to be having less effect than would be expected from a consideration of the relative contrast-sensitivities at the fundamental and higher harmonic frequencies. Thus it seems that we cannot satis-factorily model the over-all visual system by a simple peak detector follow-ing a spatial filter.

As a modification of this theory we may assume that the mechanism which is detecting the fundamental of the grating is in fact much less sensitive at the higher harmonic frequencies than is suggested by the relative thresholds for sine-wave gratings at these frequencies. Thus we may suppose that the visual system behaves not as a *single* detector mechanism preceded by a *single* broad-band spatial filter but as a number of independent detector mechanisms each preceded by a relatively narrow-band filter 'tuned' to a different frequency.

Each filter and detector would constitute a separate 'channel' and each channel would have its own contrast-sensitivity function. On this basis the envelope of the contrast-sensitivity functions of all the channels would be the contrast-sensitivity function of the overall visual system.

Such a model could account for our findings that the contrast thresholds for square-wave and rectangular-wave gratings seem to depend much less upon the amplitude of their higher harmonics than might be expected. Moreover, a model of this kind could also account for our finding that the contrast level at which saw-tooth and square-wave gratings can be distin-guished from sine-wave gratings is that at which the higher harmonics reach their own threshold since the mechanisms detecting the fundamental and the harmonics are assumed to operate more or less independently.

The independence of channels, 'tuned' to different frequencies cannot, of course, really be complete since there is a limit to how narrow the band-width of the channels can be. Such a limit is set by the maximum extent of the grating pattern or retina over which spatial integration can occur. The experimental results that we have obtained do not enable us to deter-mine at all precisely either the bandwidth of the channels whose presence we have suggested or the range that their optimum spatial frequencies might span. The evidence that we have does, however, suggest that a

frequencies 3 times higher and lower than their optimum frequency individual channels are much less sensitive than they are at the optimum frequency itself. It also seems that there are individual channels for most of the spatial frequency range that we have investigated.

The existence within the visual system of separate channels (having band-pass characteristics with different optimum spatial frequencies) has been shown neurophysiologically. By studying the responses of cat retinal ganglion cells to sine-wave gratings Enroth-Cugell & Robson (1966) have shown that a band-pass type of contrast-sensitivity characteristic is already established at the retinal ganglion cell level. The contrast-sensitivity functions of individual ganglion cells are narrower than the over-all human contrast-sensitivity function and the contrast-sensitivity functions of ganglion cells with receptive fields of different diameters have different optimum spatial frequencies. Since in any one part of the retina the ganglion cells have receptive fields with a fairly wide range of sizes (Wiesel, 1960), it is possible that here is a physiological basis for the frequency-selective channels suggested by the psychophysical results. Further processing of visual signals at higher levels in the nervous system could, of course, give rise to band-pass characteristics even narrower than those found at a retinal level. However, the maximum selectivity that could be achieved would still be limited by the area over which integrative processes could operate.

Thus a picture emerges of functionally separate mechanisms in the visual nervous system each responding maximally at some particular spatial frequency and hardly at all at spatial frequencies differing by a factor of two. The frequency selectivity of these mechanisms must be determined by integrative processes in the nervous system and they appear to a first approximation at least, to operate linearly. Remembering that all the experiments reported here relate to conditions in which the mean retinal illumination (in both space and time) remains constant, the existence of linear operation is not very surprising. Enroth-Cugell & Robson (1966) have demonstrated linear spatial processing at the retinal ganglion cell level in the cat under similar conditions and it may well exist at higher levels in the nervous system as well.

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