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SUMMATION OF VERY CLOSE SPATIAL FREQUENCIES: THE IMPORTANCE OF SPATIAL PROBABILITY SUMMATION

NORMA GRAHAM[1] and J. G. ROBSON[2]

[1]Department of Psychology, Columbia University, New York, NY 10027, U.S.A. [2]Cambridge University Physiological Laboratory, Cambridge CB2 3EG, England

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Abstract—In accounting for pattern thresholds it is necessary to consider probability summation (or equivalent nonlinear pooling) not only across detectors selective for different spatial frequencies but also across detectors in different spatial positions. Interestingly, calculation on this basis shows that the amount of summation between components of closely similar spatial frequency in a large grating is primarily determined by the variation in sensitivity of detectors at different spatial locations and is little affected by the spatial-frequency bandwidths of the detectors. To test this conclusion, we have measured the amount of summation between two components with spatial frequencies very close to 6 c/deg in two regions of the visual field: in the fovea (a region where sensitivity is very non-uniform) and in the periphery (where sensitivity is nearly uniform). As predicted, there was less summation between components of very closely similar frequencies in the nearly-uniform peripheral region than in the non-uniform foveal region. Measurements in the fovea of the summation of two components with spatial frequencies very near to either 1.5, 6 or 24 c/deg showed, as expected, that the amount of summation depends upon the ratio of the frequencies rather than their absolute difference, indicating that probability summation takes place over an area related to spatial frequency rather than over a fixed area.

Detection threshold Gratings Peripheral vision Spatial frequency Spatial vision Probability summation Spatial summation

INTRODUCTION

Current models of visual pattern detection assume that pattern thresholds are determined by detectors with linear spatial weighting functions which are selectively sensitive to patterns with particular spatial frequencies and spatial positions (e.g. Bergen *et al.*, 1979; Graham, 1985; Graham *et al.*, 1978; Mostafavi and Sakrison, 1976; Quick *et al.*, 1978; Watson, 1982, 1983). In such models detection of al but the simplest patterns depends upon probability summation (or some formally equivalent non-linear pooling) of the outputs of many detectors sensitive to different spatial frequencies (e.g. Sachs *et al.*, 1971; Graham *et al.*, 1978) and located at different spatial positions (e.g. Bergen *et al.*, 1979; King-Smith and Kulikowski, 1975; Legge, 1978; Mostafavi and Sakrison, 1976; Robson and Graham, 1981).

In using a probability-summation model to predict the detectability of an extended pattern it is necessary to take into account variations in sensitivity across the region of the visual field occupied by the pattern. When this is done for grating patterns having components of closely similar spatial frequencies, we can obtain predictions about the extent to which the components will appear to sum together to determine the overall detectability of the compound pattern. Interestingly, the predicted amount of summation between components with closely similar frequencies, and the way this changes with the separation between the frequencies, does not depend strongly upon the spatial-frequency bandwidths of the detectors. Rather, the predicted summation at close spatial frequencies is primarily determined by the way in which sensitivity varies with spatial position.

There has been one auditory study (Sondhi and Hall, 1977) which has used a similar approach to calculate—from the amount of summation between very close auditory frequencies—the time course of the presumed non-linear temporal integration which determines the detectability of a temporally extended sound (analogous to spatial probability summation). In this auditory context, however, there is no independent way of determining the time-course of integration (the analogue of visual sensitivity as a function of position in our experiments) and thus check the calculation.

This study

Results for compound gratings containing components at spatial frequencies close enough to test these predictions are not available in the literature. Previous studies have concentrated on the fovea and on larger spatial-frequency separations in the interest of measuring the spatial-frequency bandwidth of individual detectors. We have now examined the validity of a probability-summation model by measuring the detectability of compound gratings containing two components of closely similar spatial frequencies as a function of the difference between the frequencies. Moreover, in order to check the importance of variation in visual sensitivity over the region of visual field occupied by the stimulus, we have made measurements with both foveal and peripheral viewing, since with the peripheral viewing conditions adopted here the local sensitivity has previously been shown to be essentially constant over an extended pattern (Robson and Graham, 1981). This allows comparison with measurements made with a centrally-fixated pattern for which local sensitivity is very non-uniform.

Before reporting the experiments verifying the predictions of the model, we consider the predictions themselves in more detail in both this introduction and in the Appendix.

PREDICTIONS

Peripheral vs foveal viewing

Contrast sensitivity for a patch of grating located on a horizontal line through the fixation point falls off steadily and rapidly as the patch is moved away from the fixation point. However, if the grating patch is located on a horizontal line some way above the fixation point, contrast sensitivity is essentially independent of the distance of the patch from the mid-line so long as the distance is not too great. For example, contrast sensitivity for a patch of grating with a spatial frequency of 6 c/deg located 7 deg above the fixation point is nearly constant out to 5 deg from the mid-line on either side (Robson and Graham, 1981). The same constancy is observed for both higher and lower spatial frequencies when measurements are made at locations whose eccentricity is scaled according to the spatial period of the grating used.

In the present experiments the compound gratings had a fairly large number (about 40) of relatively short vertical bars. When such a grating is centrally fixated the bars that are further from the fixation point are located in less-sensitive regions of the visual field and contribute less to the overall detectability of the pattern which is therefore primarily determined by the central part of the pattern alone. On the other hand, when the grating is positioned well above the fixation point so that it occupies an area of visual field where the sensitivity is essentially constant across the whole extent of the grating, the contribution of each bar or part of the grating to the visibility of the whole grating is the same.

Figure 1 shows the effective spatial response profiles for several simple sinusoids (1st, 2nd and 4th rows) and two compounds (3rd and 5th rows) where the contrast of each component in the compounds was half the contrast in the simple sinusoid. Each function shows the responses (vertical axis) of an array of detectors at different spatial positions (horizontal axis) but tuned to the same range of spatial frequencies. The array is either in the nearly-uniform peripheral region (left column) or in the non-uniform foveal region (right column) where sensitivity falls rapidly with distance from the center of the fovea. Response profiles are shown as smooth curves, although in a real nervous system a single presentation of a near-threshold pattern would give rise to a ragged, noisy response profile.*

In the nearly-uniform, peripheral region, the response profiles for simple components (left column; 1st, 2nd and 4th rows) have a nearly uniform envelope, whereas the response profiles for the compound stimuli (left column: 3rd and 5th rows) have decidedly non-uniform envelopes due to beating between the two components. It can be seen, however, that despite the beating the peak-to-trough amplitude in each of these response profiles is the same. Thus for deterministic detectors and, for example, a peak-to-trough detection criterion, an observer would be equally sensitive to all five stimuli.

On the other hand, if detection depends upon

*There may be many arrays of detectors tuned to different spatial frequencies, but for each array the effective spatial response profile would be very similar to that in Fig. 1 (on the assumption that the spatial frequencies are close enough together to be well within the spatial-frequency bandwidth of a single detector).

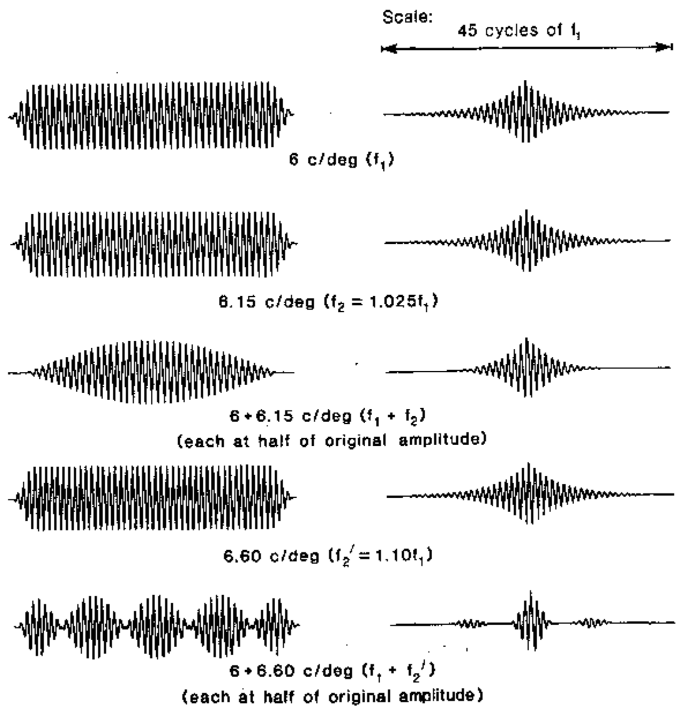

Fig. 1. The effective spatial response profiles for five stimuli (rows) centered on the fixation point (right column) or 42 periods above the fixation point (left column). Each profile gives the effective magnitude of response (vertical axis) of each of an array of detectors that are centered at different spatial positions (horizontal axis) but are all tuned to the same range of spatial frequencies. To compute the effective spatial response profile, the stimulus luminance profile was multiplied by the fourth power of the function giving sensitivity at each spatial position; this weighting was used because an exponent of four in the Quick Pooling Formula provides a good model of spatial probability summation. In the periphery, sensitivity was assumed to be exactly uniform. In the fovea, sensitivity was assumed to decline 0.025 log units per period.

spatial probability summation, the observer's sensitivity will depend on the average responses at all spatial positions, with greatest weighting for the largest average responses. In the nearly-uniform peripheral region, the spatial response profiles for the compound stimuli contain many fewer positions yielding maximal or near-maximal average responses than do those for the simple stimuli.* Thus, the observer may be a good deal less sensitive to the compounds than to the single components. In other words, much less than complete summation is predicted between 6 and 6.15 c/deg (3rd row) and between 6 and 6.6 c/deg (5th row) for peripherally viewed patterns (see also Graham, 1980). Quantitative explanations are presented in Bergen *et al.* (1979), Hall and Sondhi (1977), and Quick *et al.* (1978).

In the non-uniform, foveal region, however, the non-uniformity hides the effect of the beating if the compound contains such close spatial frequencies that only the high-amplitude part of the beat period is effective. Thus the response profiles shown in the first three rows of the right column of Fig. 1 (6 c/deg alone, 6.15 c/deg alone and their compound) all have very similar envelopes. It is therefore to be expected that with foveal viewing all three of these patterns will be approximately equally detectable and there will be effectively complete summation between 6 and 6.15 c/deg. By the time the spatial frequencies are as far apart as 6 and 6.6 c/deg, however, the envelope of the spatial response profile for the compound (Fig. 1, bottom row,

*Although, in principle, spatial probability summation (or equivalent nonlinear spatial pooling) might not occur over all the stimulated region of the visual field, the evidence suggests otherwise (Robson and Graham, 1981).

right column) is clearly narrower than that for the single components (Fig. 1, 1st and 4th rows, right column) and less than complete summation is predicted for the compound even in the non-uniform foveal region.

Prediction for different spatial frequencies with foveal viewing

When distance is measured in degrees of visual angle, the decline in sensitivity with distance from the foveal center (for a grating patch of constant size) is much more rapid for high spatial frequencies than for low (e.g. Hilz and Cavonius, 1974; Koenderink *et al.*, 1978a, b; Rovamo *et al.*, 1978). But, for some conditions at least, when distance is measured in number of periods, the decline is similar for all spatial frequencies (about 0.025 log units per period; Robson and Graham, 1981). It follows that the amount of summation between two components of closely similar spatial frequencies should depend much more on the ratio of the two frequencies than on their difference.

Since sensitivity as a function of the number of periods away from the foveal center declines in approximately the same way for all spatial frequencies and since distance on the horizontal axis of Fig. 1 is given in number of periods, the response profiles in the right-hand column of Fig. 1 labelled 6.0 and 6.15 c/deg could just as well be labelled 1.5 and 1.5375 c/deg or 24.0 and 24.6 c/deg or indeed any other pair in the ratio 6.15/6.0 = 1.025. Similarly, those labelled 6 and 6.6 c/deg could just as well be labelled 1.5 and 1.65 or 24.0 and 26.4 or any other pair in the ratio 6.6/6.0 = 1.1. Thus we predict the same amount of summation for compounds containing components in the same spatial-frequency ratio.

METHODS AND PROCEDURE

Stimulus patterns

Each stimulus was a wide grating with short vertical bars containing either one or two spatial frequencies. The gratings were centered on the fixation point or on a point 7 deg above the fixation point.

The spatial frequencies were 1.5, 6.0 or 24.0 c/deg, each paired with several different higher frequencies. All three base frequencies were used in the fovea while only 6.0 c/deg was used in the periphery. The high-amplitude part of a beat period was always at the center of the grating.

The edges of the vertical gratings were not sharp (see Fig. 2). The contrast varied vertically as a Gaussian function with a space constant equal to 1.5 periods of the lower frequency. In the horizontal direction, the luminance profile was a sum of two sinusoids weighted by an envelope that was flat for the central 37.5 cycles and then fell off on each edge as a Gaussian function with a space constant of 2.5 periods.

The patterns were also turned on and off smoothly (see Fig. 2) as a Gaussian function of time, with a time constant of 100 msec.

The patterns were presented as a raster display on a cathode ray tube with a P31 phosphor. This display had a mean luminance of 340 cd/m^2 and appeared a desaturated green. It was seen through a rectangular hole (20 cm vertically and 29 cm horizontally) in a large screen (61 × 61 cm) illuminated to approximate the cathode ray tube in luminance and hue. The electronic and computing equipment has been briefly described by Graham *et al.* (1978).

In order to have a large number of cycles of the pattern on the display while not having the period of the grating so small as to tax the resolution capability of the equipment, we varied spatial frequency by varying the viewing distance of the observer (57, 228 or 912 cm). The lower spatial-frequency component of the pair

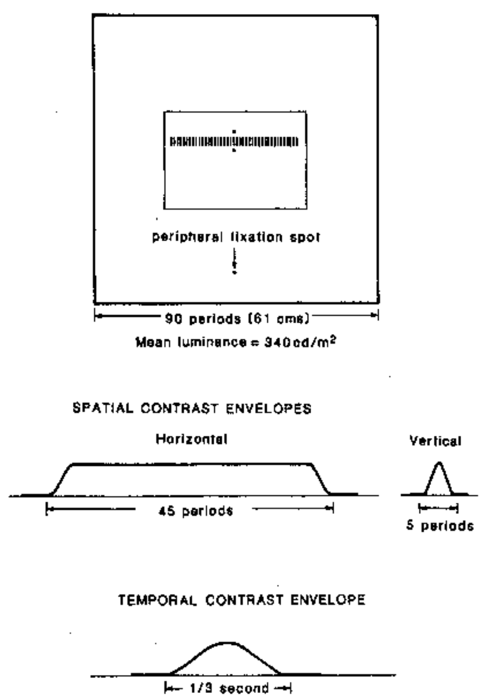

Fig. 2. Diagrams of the stimulus configurations.

being studied (1.5, 6.0 or 24 c/deg) always had a frequency of 1.5 c/cm on the screen.

Fixation spots were used. For the peripheral location the observer fixated on a dark spot, 28 cm below the center of the patterns. For the foveal location the observer fixated half-way between two spots 6 cm apart, one below and one above the midpoint of the patterns. The observers viewed the patterns binocularly with natural pupils.

PROCEDURES

To determine the threshold contrast we used the QUEST yes–no staircase procedure of Watson and Pelli (1983). In any one run involving a particular pair of closely similar spatial frequencies, five patterns were available for presentation all in the same location. These five patterns were: a simple grating of the lower spatial frequency, a simple grating of the higher spatial frequency and three compound gratings each containing both spatial frequencies but in different proportions (i.e. different contrast ratios). While determining the threshold for a compound grating, the contrast of both components was changed together keeping the ratio of the contrasts of the two components constant.

Each run contained 360 systematically randomized trials (60 for each of the five patterns and 60 blanks) and produced one estimate of threshold contrast for each of the five patterns, threshold contrast being defined as that contrast producing 50% detection after correction for guessing. The false-alarm rates in different runs varied (apparently randomly) from 0 to 0.15 with a median of 0.06.

The three ratios of contrasts in the compound grating were chosen, on the basis of preliminary measurements, to straddle closely the ratio at which each component's contrast was proportional to its own threshold.

The observer started each trial by pushing a button whereupon, after a short delay, the stimulus was presented accompanied by a tone. At the end of each trial the observer pushed one of two buttons to indicate whether or not a pattern had been seen. Three completely separate runs were made for each frequency-pair studied. The order of the runs was haphazard, although those involving 6 c/deg usually preceded those involving 1.5 or 24 c/deg.

The relative sensitivity measure for a compound grating

As an indicator of the amount of summation we used the relative sensitivity measure of Quick *et al.* (1978). To estimate relative sensitivity from experimental measurements of threshold contrast, we first plotted the set of thresholds for the three compounds and two simple gratings on a diagram of the kind shown in the upper part of Fig. 3.

In this diagram the horizontal co-ordinate of a threshold point represents the relative contrast of the lower-frequency component—that is the contrast in this component divided by the contrast threshold for the component by itself—while the vertical co-ordinate represents the relative contrast in the higher-frequency component. We then fitted a smooth curve through the five threshold points and found where this curve crossed the positive diagonal. If the co-ordinates of this intersection are x,y then relative sensitivity is defined as $1/x$ (or, equally, $1/y$). Relative sensitivity is equal to 2.0 if there is complete summation (lower left, Fig. 3) and 1.0 if there is no summation (lower right, Fig. 3).

Relative sensitivity was estimated separately for each run. This makes it possible to get some idea of the variability of the whole procedure from Fig. 4 where relative-sensitivity estimates from the three independent runs are plotted. Further details of the fitting procedure are given in Appendix Note 1. That our conclusions are not critically dependent upon the particular fitting procedure used is indicated by our finding that much simpler procedures (such as using the one data point that was closest to the diagonal) gave almost exactly the same results.

Observers

The observers in this experiment were the two authors, both of whom have normal visual acuity when corrected.

RESULTS AND DISCUSSION

Region of the visual field

Figure 4 shows the results for compound gratings viewed either foveally (solid symbols) or peripherally (open symbols) for observers J.R. (left panel) and N.G. (right panel). The lower spatial frequency was always 6 c/deg. Relative sensitivity (see Methods) is plotted on the vertical axis. The difference between the spatial frequencies of the two components is

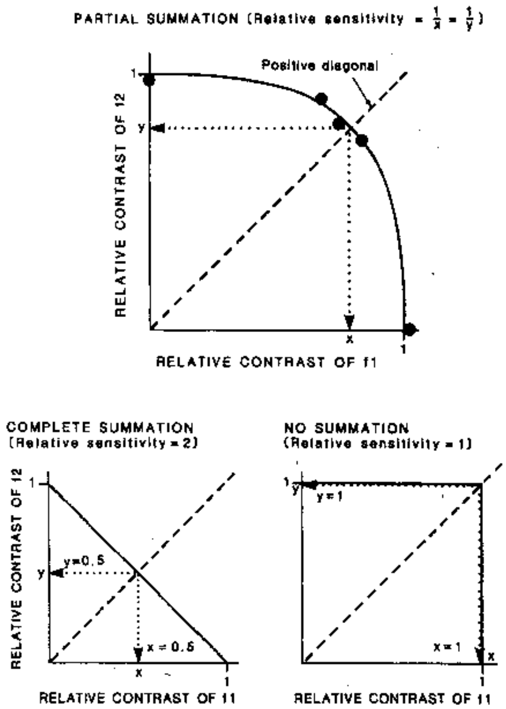

Fig. 3. The relative sensitivity measure for cases of partial summation (top), complete summation (bottom left) and no summation (bottom right).

plotted on the horizontal axis. The individual data points are estimates from individual runs; the lines connect the medians.

As predicted, summation between close spatial frequencies is greater in the fovea than in the periphery.

Spatial frequency

Figure 5 shows relative sensitivity for compounds with base frequencies of 1.5 c/deg (open circles), 6 c/deg (solid circles) or 24 c/deg (triangles) all presented in the fovea. Only the medians of the three estimates are shown (variability was similar to that shown in Fig. 4).

The results are plotted in two ways. In the top panels relative sensitivity is plotted as a function of the *difference* between the spatial frequencies of the two components, while in the bottom panels the relative sensitivity is shown plotted against the *ratio* of the two spatial frequencies. The dotted curve is discussed in the section on quantitative predictions.

As predicted, when relative sensitivity is plotted against the *ratio* of the spatial frequencies (Fig. 5, bottom) the functions are quite similar for all spatial frequencies. When relative sensitivity is plotted against the *difference* between the two spatial frequencies (Fig. 5, top), the functions are rather different from one another and are ordered from lowest spatial frequency (lowest curve) to highest (highest curve).

The experimental variability makes it difficult to judge whether or not the functions in the bottom of Fig. 5 are really identical. The amount of summation at close spatial frequencies is primarily determined by the sensitivity variations in the first few periods away from the fixation point. These variations cannot

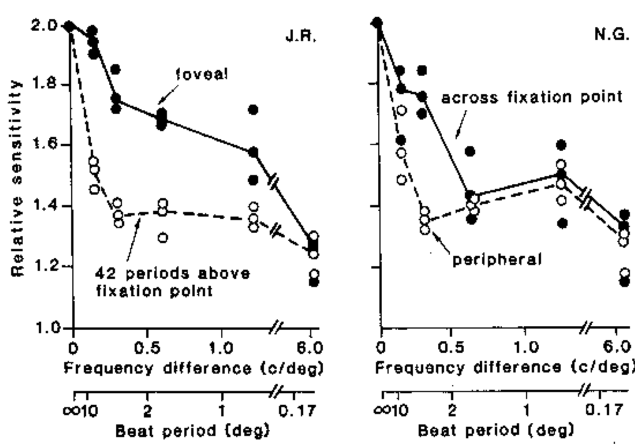

Fig. 4. Relative sensitivity to compound gratings (vertical axis) as a function of absolute spatial-frequency difference between the components (horizontal axis) for gratings centered on the fixation point (solid symbols) or centered 7 degrees above the fixation point (open symbols) for two observers (left and right panels). The lower spatial frequency was always 6 c/deg. The individual data points are estimates from individual runs; the lines connect the medians.

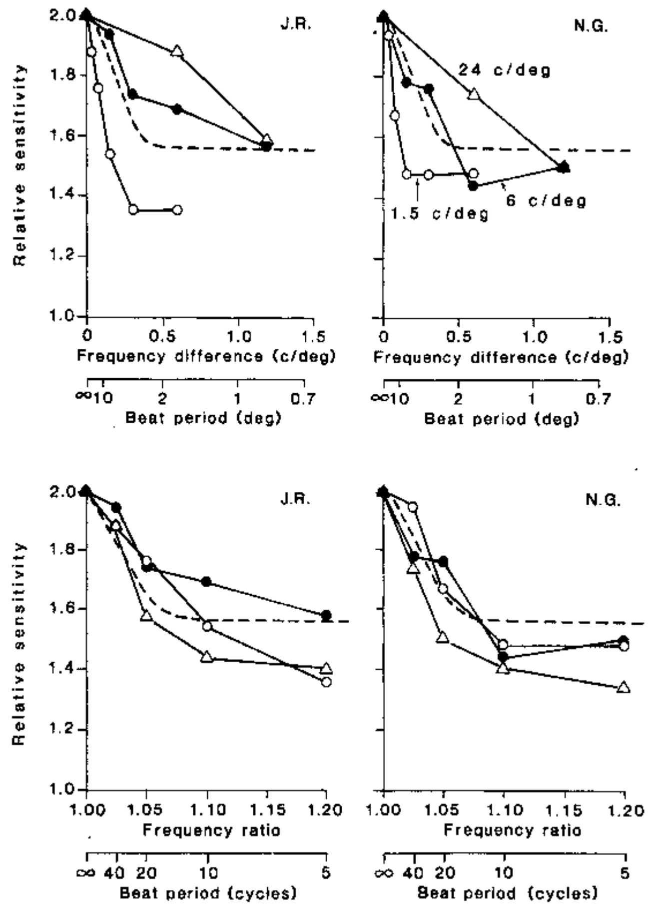

Fig. 5. Relative sensitivity to compound gratings (vertical axis) centered on the fixation point plotted against the difference between the two spatial frequencies in the compound (top panels) or against the ratio of the two spatial frequencies in the compound (bottom panels) for two observers (left and right panels). The beat period in degrees of visual angle (top panel) or in periods of the lower spatial-frequency component (bottom panels) is indicated on a second line of labels below each horizontal axis. The lower spatial-frequency was either 1.5 c/deg (open circles), 6 c/deg (solid circles) or 24 c/deg (triangles). Only the medians of the relative-sensitivity estimates from the three runs are shown. (Note that, due to the differences between the horizontal axes, two of the points for 24 c/deg in the bottom panels are absent from the top panels. Similarly, one of the 1.5 c/deg points from the top panels is missing from the bottom panels. The 6 c/deg results are the same as those shown in Fig. 4.) The dotted theoretical curves are the predictions (Quick *et al.*, 1978) from a model assuming spatial probability summation (or equivalent nonlinear spatial pooling) across an area having an effective extent of 2 deg of visual angle (top panels) or 12 periods of the lower frequency (bottom panels). See further description in text.

be measured exactly with patches containing four cycles as used by Graham and Robson (1981), nor by patches containing fewer cycles since these contain too broad a range of spatial frequencies. However across a broader range of visual field, sensitivity certainly does not fall off by exactly the same amount per period for all spatial frequencies nor does it fall off completely uniformly (Robson and Graham, 1981). For example, sensitivity falls off slightly more slowly (per period) for 24 c/deg than for 6 or 1.5 c/deg. Thus when plotted against relative spatial-frequency difference (bottom), slightly less summation is predicted at 24 c/deg than at the lower spatial frequencies.

Quantitative predictions

Foveal viewing. The dotted curves shown in Fig. 5 are predictions based on calculations by Quick *et al.* (1978). For these predictions the linear detectors are assumed to have large spatial-frequency bandwidths. Thus, the sharp drop in the dotted theoretical curves is due entirely to spatial probability summation and the beating between the components and is not a consequence of having detectors with narrow spatial-frequency bandwidths. If narrower spatial-frequency bandwidths in line with current estimates are assumed, the theoretical curves show the same sharp drop at small frequency differences but then continue to drop more slowly before reaching an asymptote close to 1.0. (For such narrower-bandwidth predictions see Quick *et al.*, 1978, Fig. 3).

In calculating the theoretical curves, spatial probability summation has been modelled with the well known formula of Quick (1974), using an exponent of 4. For the bottom panels of Fig. 5, sensitivity has been assumed to decrease 0.028 log units per period away from the foveal center—consistent with the measurements of Robson and Graham (1981). Thus, the extent of the spatial-pooling is 12 periods of the lower frequency (see Appendix Note 2). For the top panels, the extent of spatial pooling has been assumed to be 2 deg of visual angle. (Note that the extent of spatial-pooling in top and bottom panels is equivalent only when the lower frequency is 6 c/deg.) Other details of the calculations can be found in Quick *et al.* (1978).

As predicted, the theoretical curve in the bottom panels of Fig. 5 agrees well with the results for frequency ratios close to unity, where relative sensitivity is declining quickly. For greater spatial-frequency ratios, the theoretical curve tends to be above the experimental measurements, as one would expect since spatial-frequency bandwidth limitations were not taken into account.

In describing their own results, Quick *et al.* (1978) assumed that spatial pooling occurred over a fixed extent of 2 deg of visual angle—as in the top panels of Fig. 5—for all spatial frequencies ranging from 5 to 21 c/deg. Their use of this description suggests a conclusion contrary to ours. However, Quick *et al.* made very few measurements at close spatial frequencies and there is no real conflict between our observations and theirs.

Peripheral viewing. Since sensitivity in the peripheral region is almost uniform over an area larger than the gratings used here (about 40 periods), spatial pooling should occur over the whole extent of the gratings. Therefore, as soon as the two spatial frequencies in a compound are far enough apart for the beat period to equal approx. 40 periods of the lower frequency, the decline in relative sensitivity of the compound due to spatial probability summation should be complete. The frequency difference necessary to get a beat period of 40 cycles when the lower frequency is 6 c/deg is 0.15 c/deg. This was the smallest difference for which measurements were made in this study. Median relative sensitivity at this point had already fallen to 1.52 and 1.58 for the two observers (Fig. 4: leftmost open circles). These values are indeed consistent with the asymptotic value expected from spatial probability summation. (There is a suggestion in the experimental results of a further decline at larger spatial-frequency differences before an asymptote is reached—particularly in the case of N.G. As the relative sensitivities are below the asymptotic value expected from spatial probability summation, however, this further decline is probabily due to detector–bandwidth limitations and measurement error.) Thus, the peripheral summation results also seem quantitatively consistent with predictions from the current models.

CONCLUSION

We have demonstrated that, under one set of experimental conditions, the summation of very close spatial frequencies can be predicted by current models of pattern vision assuming spatial probability summation and taking into account the way in which sensitivity varies with position in the visual field. We see no reason to suppose that these models would not apply equally well in other conditions.

According to these models, the summation of very close spatial frequencies does not give information about the spatial-frequency bandwidth of individual detectors but rather about the variation in sensitivity at different spatial positions in the visual field.

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APPENDIX

Technical Notes

Note 1. Curve fitting procedure for estimating relative sensitivity

A curve equal to the upper right quadrant of a circle defined by a Minkowski metric, that is, a curve of the form

$$\left[\frac{x}{a}\right]^k + \left[\frac{y}{b}\right]^k = 1$$

was fitted to the thresholds for five patterns (two components by themselves, three compounds) as plotted on a summation square. The pair of values x and y give the *actual* contrast in the two components for one of the five patterns (unlike the usage of x and y in the main text or Fig. 3). The parameters a and b are the intersections of the curve with the horizontal and vertical axes and give the contrast thresholds for the two components when alone. The exponent k is a measure of how much summation there is. Note that on the positive diagonal

$$\frac{x}{a} + \frac{y}{b} = (0.5)^{1/k}.$$

Thus the relative sensitivity measure used here is the reciprocal of x/a (or y/b) on the positive diagonal expressed in terms of k, i.e.

$$\text{Relative sensitivity} = (0.5)^{-1/k}$$

When $k = 1$ there is complete summation and when $k = \infty$ there is no summation. Note that in this curve-fitting application, this family of curves has no theoretical meaning. It is simply a convenient family for interpolating results that are necessarily quite symmetric around the positive diagonal (since the three compounds were all quite close together in the summation square by design).

The curve was fitted to the five thresholds from a single run by specifying the three parameters (k, a and b) that minimized the distance in the corresponding metric from that curve, that is, by minimizing the following expression (which will be called "the sum of distances" but notice that distance does not mean Euclidian or least squares distance):

$$\sum_{i=1}^{i=5}\left|\left[\frac{x_i}{a}\right]^k + \left[\frac{y_i}{b}\right]^k - 1\right|.$$

The following step-wise procedure was used. Initially a and b were set equal to the measured thresholds for the components by themselves. Values of k were looped through first in a large step size (1.0) and then in a small step size (0.1 or 0.05) until the minimum of the above expression was located with sufficient accuracy. (Note that, for low ks, the value of k needs to be located to a greater precision than for higher ks in order to get the same precision in the relative sensitivity measure.) Then the estimates of a and b were set to be the original estimates plus or minus 0.1 or 0.2 and the best value of k was searched for again. The value of k which, for any of the tested estimates of a and b, gave the lowest sum of distances was used in computing the relative sensitivity measure. As it turned out, the lowest sum of distances was almost without exception obtained when a and b were set equal to the measured contrast thresholds for the components by themselves. (This would certainly not have occurred were there several compound grating thresholds scattered throughout the summation square rather than concentrated on the positive diagonal.)

Note 2. About the theoretical predictions shown in Fig. 5

(*a*) *Definition of the effective extent of spatial pooling.* For the curves shown in Fig. 5, the function relating sensitivity to spatial position was assumed to be a Gaussian centered at the fixation point. The effective extent of the spatial-pooling is taken to be twice the standard deviation (twice the distance at which sensitivity has fallen to about 61% of maximum or 1.414 times the distance at which sensitivity has fallen to 37% of maximum).*

The exact form of the function relating sensitivity to position is relatively unimportant (Quick *et al.*, 1978). The curves predicted from an exponential function or from one with quite sharp edges are very similar to those shown in Fig. 3 as long as effective extent has been properly defined and equated for. Examples can be found in Fig. 2 of Quick *et al.* (1978). Two functions are defined to have the same effective spatial-pooling extent when the integral of each raised to the fourth power is the same (when each has been normalized to have the same peak height). The fourth power is used because that was the exponent used in Quick's formula for probability summation when making these predictions. More generally, the definition of effective extent would use whatever exponent was used in the probability-summation calculations.

(*b*) *Comparing the effective spatial-pooling extents of Guassian and exponential fall-offs.* It is sometimes convenient to describe non-uniformity in the retina in terms of log units of decrease per unit of distance. This kind of description implies that sensitivity is an exponential function of position: i.e.

$$\exp(-|x/a|).$$

The integral of this exponential function raised to the fourth power is

$$\int_{-\infty}^{+\infty} [\exp(-|x/a|)]^4 \,dx = a/2.$$

On the other hand, the integral of the Gaussian function with standard deviation s normalized to have height one at $x = 0$ is

$$\int_{-\infty}^{+\infty} \{\exp[-(x^2/2s^2)]\}^4 \,dx = 0.5(2\pi)^{1/2}s \approx 1.25s.$$

Thus for a Gaussian and an exponential to have the same effective extent,

$$a = (2\pi)^{1/2}s \approx 2.51s.$$

When the effective spatial pooling extent is 12 periods (as in the predictions of the bottom panels of Fig. 5) s is 6 periods and the exponential function of equivalent extent has a equal to 15 periods. That represents a fall-off in sensitivity of 0.028 log units per period, which is consistent with the sensitivity functions measured across the fovea by Robson and Graham (1981) in conditions very close to those used here.

(*c*) *Independence of lower spatial frequency in top panels of Fig. 5.* It is perhaps somewhat surprising that a single theoretical curve (as in the top panels of Fig. 5) is the correct prediction when assuming constant spatial-pooling extent (measured in degrees of visual angle) independent of the lower spatial frequency. For, although the size of the beat period (in degrees of visual angle) is independent of the lower spatial frequency, the structure within a beat period is quite different. As it turns out, however, the sharp fall-off in sensitivity due to spatial probability summation depends almost entirely on the relationship of the envelope of the compound grating to the effective extent of spatial pooling—that is, on the relationship of the beat period to the pattern of sensitivity across the visual field (e.g. Quick *et al.*, 1978). For very close spatial frequencies, neither the precise spatial frequencies nor the exact phase between the spatial frequencies makes much difference. This can be contrasted with the difference made by the phase relationship between components with frequencies a factor of three apart in the predictions shown in Fig. 5 of Graham *et al.* (1978).

(*d*) *Value of the exponent.* The exact value of the exponent (4.0) used by Quick *et al.* (1978) is not crucial to the shape of predicted relative-sensitivity functions but does affect the asymptotic value of relative sensitivity at very far-apart spatial frequencies predicted in the absence of channel–bandwidth limitations (that is, the horizontal asymptote of the dotted curves in Fig. 5). See, for example, the predictions for frequencies a factor of three apart in Fig. 5 of Graham *et al.* (1978). For values of the exponent between 2 and 5, the asymptotic relative sensitivity at large spatial-frequecy differences due to spatial probability summation will vary between about 1.4 and 1.67. An exponent of 3.5 was used to fit the results in Robson and Graham (1981). This is slightly lower than the exponent of 4 used in the predictions reproduced here and, therefore, predicts a slightly lower asymptote. However, results such as those reported here could never distinguish between such asymptotes, as the decline in sensitivity due to channel–bandwidth limitations effectively disguises the asymptote.

(*e*) *Comparison of experimental conditions.* The measurements of sensitivity as a function of spatial position (across the fixation point and in a strip 42 periods above the fixation point), that have been invoked in the discussions here, were published in Robson and Graham (1981). They were collected on the same two observers under conditions very similar, but not quite identical to those of the present experiments. While the differences should matter little they are described here for the sake of completeness.

The time-course of the stimuli used in the two studies was identical. The mean luminance was slightly less here (340 cd/m^2) than previously (500 cd/m^2) although both levels are high enough for there to be very little difference in contrast thresholds.

The edges of the patterns were shaped very similarly in the two studies but the bar length in the present study was somewhat shorter (about 3 periods) than previously (about 4). Sensitivity may decrease a little *faster* with distance from the fixation point with the shorter bars used here. Compensating for this difference, however, sensitivity may decrease a little *more slowly* in the horizontal direction away from the fixation point (as used here because of equipment limi-

*Choosing this measure of the effective extent rather than some other measure has the following good feature. Note that the theoretical curve in the top panel of Fig. 3 asymptotes beginning at a spatial-frequency difference of 0.5 c/deg which corresponds to a beat period of 2 deg and the effective extent of the spatial-pooling area for this curve was 2 deg. Similarly, the curves in the bottom asymptote beginning at a relative frequency of about 0.083 c/deg which corresponds to a beat period of 12 cycles, equal in extent to the effective spatial-pooling area.

tations) than in the vertical direction (measured previously) although the pattern changes across spatial frequency are very similar in both directions (J. G. Robson, unpublished observations).

The psychophysical procedure used here was a yes–no staircase procedure rather than the forced-choice staircase procedure used previously in order to increase somewhat the rate at which we could gather results.