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Radial frequency stimuli and sine-wave gratings seem to be processed by distinct contrast brain mechanisms

M.L.B. Simas[1], R.M.T.B.L. Nogueira[1] and N.A. Santos[2]

[1]Laboratório de Percepção Visual, Departamento de Psicologia, Universidade Federal de Pernambuco, Recife, PE, Brasil
[2]Laboratório de Processamento Visual, Departamento de Psicologia, CCHLA, Universidade Federal da Paraíba, João Pessoa, PB, Brasil

Abstract

An assumption commonly made in the study of visual perception is that the lower the contrast threshold for a given stimulus, the more sensitive and selective will be the mechanism that processes it. On the basis of this consideration, we investigated contrast thresholds for two classes of stimuli: sine-wave gratings and radial frequency stimuli (i.e., j_0 targets or stimuli modulated by spherical Bessel functions). Employing a suprathreshold summation method, we measured the selectivity of spatial and radial frequency filters using either sine-wave gratings or j_0 target contrast profiles at either 1 or 4 cycles per degree of visual angle (cpd), as the test frequencies. Thus, in a forced-choice trial, observers chose between a background spatial (or radial) frequency alone and the given background stimulus plus the test frequency (1 or 4 cpd sine-wave grating or radial frequency). Contrary to our expectations, the results showed elevated thresholds (i.e., inhibition) for sine-wave gratings and decreased thresholds (i.e., summation) for radial frequencies when background and test frequencies were identical. This was true for both 1- and 4-cpd test frequencies. This finding suggests that sine-wave gratings and radial frequency stimuli are processed by different quasi-linear systems, one working at low luminance and contrast level (sine-wave gratings) and the other at high luminance and contrast levels (radial frequency stimuli). We think that this interpretation is consistent with distinct foveal only and foveal-parafoveal mechanisms involving striate and/or other higher visual areas (i.e., V2 and V4).

Key words
- Sine-wave gratings
- Spatial frequency
- Radial frequency
- Bessel functions
- Multiple channels
- Contrast sensitivity

Correspondence
M.L.B. Simas
Laboratório de Percepção Visual
LabVis-UFPE, CFCH, UFPE, 9º andar
50670-901 Recife, PE
Brasil
Fax: +55-81-3441-7547
E-mail: mlbs@ufpe.br or mldbs@uol.com.br

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Introduction

In 1960, Kelly (1) proposed the use of images having a concentric configuration for studying visual mechanisms and properties where the contrast is modulated by a Bessel J_0 profile. Since Kelly's proposal, only few published reports have addressed the issue of contrast detection or sensitivity employing this kind of stimulus.

Among the few that did attempt to conduct experiments with these stimuli are Kelly and Magnuski (2) and Kelly (3). These investigators reported measurements of the modulation transfer function, or the contrast sensitivity function (CSF), for sine-wave gratings and for J_0 targets using psychophysical methods.

Kelly and Magnuski (2) reported that the human visual system is at least two times less sensitive to J_0 targets when compared to sine-wave gratings. This indicates that the amount of contrast necessary for the detection of sine-wave gratings is at least two times lower than the amount necessary to detect J_0 targets in its respective most sensitive range. The authors concluded that thresholds for sine-wave gratings, or cosine-wave circular targets could predict the responses to J_0 targets. Here we will call these stimuli radial (spatial) frequencies, use spherical Bessel function profile modulation, j_0, and name its response curve rCSF (radial (frequency) CSF) (4).

Kelly (3), reproduced part of the study of 1975 and also carried out experiments with stabilized images for both sine-wave gratings and J_0 targets. He found that both the CSF and rCSF had the same trend if their images were stabilized but reproduced previous trends if the images were presented in drifting motion. In his conclusion, Kelly reports on a mechanism that detects only "stationary, stabilized images..., whose existence can be inferred only by means of unchanging, high-contrast, achromatic patterns..." (p. 438), and questions its function.

The conclusion of Kelly and Magnuski (2) could imply that detection is mediated by only a single mechanism for sine-wave gratings and J_0 targets. On the other hand, Kelly's conclusion (3) suggests the existence of a sustained mechanism working at high levels of contrast.

Most of the work carried out in our laboratory has been to investigate mechanisms that are sensitive to steady stimulus presentations lasting at least 2000 ms. The main objective has been to look for spatial frequency filters that might be active in the detection and recognition of form, be the form sharp and detailed, or blurred and defocused. By filter we mean some sort of mechanism or channel represented by an assembly of neurons (some sort of neuronal network) that might show quasi-linear response characteristics, within specific ranges of time, location and spatial configuration, for given sets of visual stimuli. Also, we have been looking for such filters by measuring responses of the human visual system to angular frequency stimuli since 1989 (5), with earlier work beginning in 1985 (6,7).

In the paper by Simas et al. (5) we report results that are compatible with the existence of angular frequency filters and where the visual system is conceived as decomposing the visual information in terms of polar coordinates, the angular part being one of the components. The adoption of a polar coordinate system for visual system detection implies the existence of an orthogonal radial component. Besides Kelly's work, we found a more recent study (8) that also employed Bessel functions to measure contrast sensitivity and to estimate matched channels for radially symmetric patterns. But in this study the main focus was the center of the radial frequency stimulus.

In the present study, we report characteristic response functions for radial frequency filters at 1 and 4 cycles per degree of visual angle (cpd). We refer to a radial frequency filter as $F_r(R)$, where *r* stands for the radial test frequency (for the given radial frequency filter) and *R* refers to the varying background radial frequency. We used the same method, equipment and subjects as in the previous study to obtain estimations of angular frequency filter responses (5). As a control condition, we also measured the response to spatial frequency filters of 1.0 and 4.0 cpd, using the same equipment, method and subjects. We describe a spatial frequency filter as $F_s(S)$, with *s* standing for the test spatial frequency and *S* for the background spatial frequency.

In Experiment 1 we measured the CSF and the rCSF in the range of 0.2-9.0 cpd where observers had to differentiate between a stimulus containing either a spatial or a radial frequency and another stimulus at mean luminance in a forced-choice paradigm.

In Experiments 2 and 3 the psychophysical measures for the filter functions were obtained by the use of a suprathreshold summation method adapted and modified from Kulikowski and King-Smith (9) whereby the observer was asked to choose between two targets: one presenting the background frequency alone and the other containing the same background frequency plus the test frequency. Only the contrast of the specific test frequency was varied within each session.

Based on Kulikowski and King-Smith (9), we expected both spatial and radial frequency filters to show strong summation effects whenever test and background frequency were the same. We also expected a general summation effect in the neighborhood of the test frequency for each of the measured filters.

Experiment 1: CSF and rCSF measurements

This experiment measured absolute thresholds for sine-wave gratings and radial frequency stimuli using the same equipment and procedure as a preliminary standardizing study.

Subjects and Methods

Subjects. Seven students from the Psychology Department (20 to 30 years old) were the subjects in this experiment. They had either normal or corrected-to-normal acuity as assessed by an E of Rasquim Eye Chart.

Materials and procedures. A computer controlled a DT-2853 video board through which the visual stimuli were generated either on an RGBsync standard low contrast resolution TV monitor or on a high-contrast resolution Sony BVM-1910 RGBsync monitor. In each of 60-120 trials, the observer had to correctly choose the test stimulus contained in one of two presentation intervals lasting 2000 ms each, with an interstimulus interval (ISI) lasting 1000 ms. The test stimulus would be either the spatial or radial frequency stimulus (depending on the measured function, CSF or rCSF, respectively). The other presentation interval would contain only a constant homogeneous gray stimulus at mean luminance, i.e., 8.2 cd/m^2. After an error followed by three consecutive correct choices, the test stimulus contrast was lowered by 0.008, or 0.8%, and a maximum level (peak) value of contrast was recorded. After each error, contrast was increased by the same amount. A local minimum contrast level value (valley) was recorded every time an error was preceded by at least three consecutive correct choices. A total of 10 pairs of maximum-minimum were obtained in each experimental session run for each point estimate of the measured curves.

Examples of the stimuli detected during measurements of the CSF or rCSF are shown in Figure 1 (left columns). All stimuli were seen from a distance of 150 cm, subtending 7.25 degrees of visual angle. The other stimulus shown as comparison was the homogeneous gray circle. The spatial or radial frequencies used to obtain point estimates for each curve were 0.2, 0.3, 0.5, 0.8, 1.0, 2.0, 3.0, 4.0, 5.0, 6.0, and 9.0 cpd, each of these run in a separate experimental session, at least two sessions for each point, per observer.

A total of 22 curves were measured; nine for the CSF and 13 for the rCSF, for a total of about 242 experimental sessions of 15-25 min each.

Results

We report results obtained with the standard TV monitor (Figure 2A) and with the high-contrast resolution video monitor (Figure 2B).

Figure 2 shows the contrast sensitivity values derived from the measured mean contrast threshold amplitudes for both sine-wave gratings and radial frequency stimuli. The respective CSF and rCSF that are generally presented in the literature are the inverse function of contrast threshold amplitudes.

Each point estimate was obtained from the average of the peaks and valleys obtained across subjects for each given condition. Error bars of the mean are the 99% confidence interval corrected by the Student *t*-test distribution for sample size. Maximum sensitivity (i.e., corresponding to the minimum contrast threshold) occurred around 2-3 cpd for the CSF and around 0.8-1.0 cpd for the rCSF for both monitors used. Contrast sensitivity to sine-wave gratings was about 5 times higher than that for j_0 targets at their respective maximum sensitivity ranges.

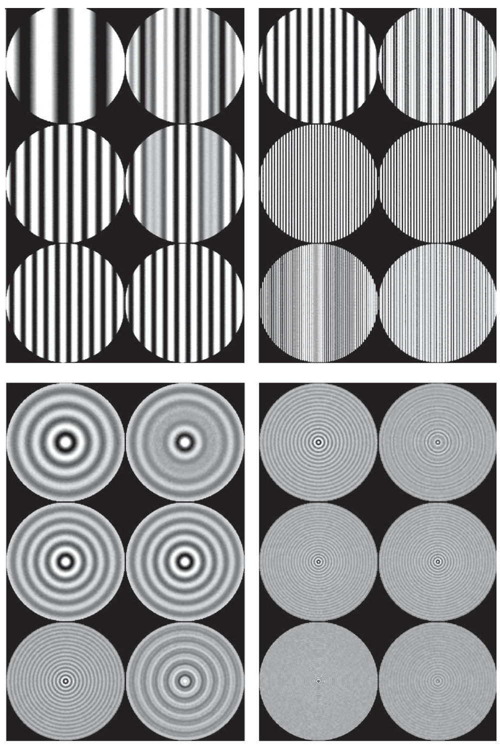

Figure 1. Example of pairs of stimuli used to measure $F_1(S)$ (or FSIN01cpd, top, left), $F_4(S)$ (or FSIN04cpd, top right), $F_1(R)$ (or FBES01cpd, bottom left) and $F_4(R)$ (or FBES04cpd, bottom right). For each function we present three pairs: for FSIN01cpd the pairs are: 0.3 cpd (top), 0.8 cpd (center) and 1.0 cpd (bottom); for FSIN04cpd: 1.0 cpd (top), 4.0 cpd (center), and 6.0 cpd (bottom); for FBES01cpd: 0.8 cpd (top), 1.0 cpd (center) and 3.0 cpd (bottom), and for FBES04cpd: 3.0 cpd (top), 4.0 cpd (center) and 6.0 cpd (bottom). For each function, on the left are the background frequencies only. On the right side are the summed stimuli (i.e., background plus test frequency). All stimuli were generated originally to be seen at a distance of 150 cm. cpd = cycles per degree of visual angle.

On the other hand, mean contrast sensitivities (obtained with the high-contrast resolution monitor) within the range of 0.2-9.0 cpd varied from about 3.9 to 48.6 (arbitrary units) for sine-wave gratings whereas for j_0 targets, within the same range, they varied between 2.8-5.8. Thus, the dynamic contrast amplitude range was about 14.9 higher for sine-wave gratings, given the same spatial frequency range. For the low-contrast resolution monitor this range was about 7.0 times higher for sine-wave gratings.

The results obtained with the Sony BVM-1910 monitor as well as with the standard TV monitor show that the contrast range of the latter monitor, being too high (with low dynamic range), was inadequate to correctly measure absolute thresholds for sine-wave gratings at their peak sensitivity (Figure 2).

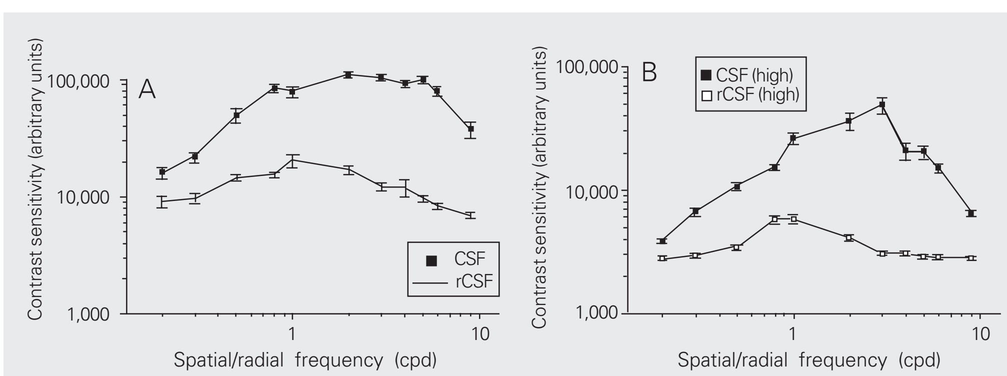

Figure 2. Contrast sensitivity for sine-wave gratings and radial frequency stimuli. Grand mean of contrast sensitivity values observed in the measurement of both CSF (contrast sensitivity function) and rCSF (radial contrast sensitivity function). These are measurements made on the standard low-contrast resolution monitor (A) and on a Sony BVM-1910 RGB-TV-video monitor, a high-contrast resolution monitor (B). In *A*, the CSF maximum sensitivity occurs around 2.0-3.0 cpd whereas that for the rCSF occurs around 1.0 cpd. In *B*, CSF maximum sensitivity occurs around 3.0 cpd whereas that for the rCSF occurs around 0.8-1.0 cpd. Error bars are standard errors of the mean at the 99% confidence level interval. All the differences between respective point estimates of each function were statistically significant at P < 0.01 (*t*-test for correlated samples).

Discussion

We were able to measure the range of maximum sensitivity for sine-wave gratings with the high-resolution monitor. For radial frequency stimuli the trends were similar for both monitors. Following this preliminary study we proceeded to measure the spatial and radial frequency filter.

Experiment 2: Spatial and radial frequency filter measurements of 1 and 4 cpd using the standard TV monitor with low-contrast resolution

Originally, we were only able to run the spatial and radial frequency filter measurements using a low-contrast resolution monitor (the same used for the angular frequency filter measurements reported by Simas et al., 5). We report these in Experiment 2. Later, we were able to replicate these experiments in part using a higher contrast resolution monitor. These additional measurements are reported in Experiment 3.

Experiments 2 and 3 were run using a suprathreshold summation method, a variation of the method of Kulikowski and King-Smith (9). This was done within a forced-choice procedure (10). In the original study, Kulikowski and King-Smith employed 1/2 of the contrast needed for the test frequency to attain threshold as the background stimulus contrast value. These investigators thought that the test frequency contrast summed with the background frequency contrast, would be sufficient for the test frequency to reach detection threshold, if processed by the same underlying mechanism. This was done instead of the detectable contrast value attributed to the background stimuli that we used in our experiments.

Subjects and Methods

Subjects. Five observers from the UFPE student population (20-30 years old) participated in this study. They had either normal or corrected-to-normal visual acuity.

Materials and procedures. In these experiments, we used both 6 and 42% contrast levels for the background spatial or radial frequency stimuli. These were suprathreshold contrast levels. The background spatial and radial frequency values were the same as for the measurement of the CSF and rCSF point estimates. The test stimulus was either a 1- or a 4-cpd spatial or radial frequency stimulus depending on the filter being tested. Thus, for $F_1(S)$ and for $F_4(S)$ the test stimulus was a 1- or a 4-cpd sine-wave grating, respectively, whereas for $F_1(R)$ and for $F_4(R)$ these were a 1- and a 4-cpd radial frequency stimulus, respectively.

We measured the amount of test frequency contrast needed for detection of the test frequency summated to each of the background frequencies. That is, observers had to consistently choose the sum of the test plus the background frequency from the background frequency presented alone. In all trials, the background stimulus had fixed contrasts at either 6 or 42% during all presentations. So, on the one hand, when test and background spatial or radial frequencies were identical, discrimination was made based on contrast alone. On the other hand, in any other experimental condition, observers could make discriminations based on contrast as well as on spatial or radial frequency of the background. Nevertheless, according to the original paradigm (9), the strongest contrast summation effect should theoretically occur when the spatial or radial frequencies of test and background stimuli were similar or identical. This should be so due to the selectiveness of the mechanisms processing each stimulus.

Both stimuli were again presented for 2000 ms, having an ISI of 1000 ms and an intertrial interval lasting 3000 ms.

A total of 32 curves (each having 11 point estimates) were measured to estimate $F_1(S)$,

F_1(R), F_4(S) or F_4(R), where the background frequency was always at a contrast level of 42%. Thus, we measured 7 curves for F_1(S), 10 curves for F_1(R), 9 curves for F_4(S), and 6 curves for F_4(R).

Similarly, a total of 15 curves (each having 11 point estimates) were measured with the background set at 6%. Thus, 3 curves were measured for F_1(S), 5 curves were measured for F_1(R) and F_4(S) and two curves were measured for F_4(R).

Figure 1 shows examples of pairs of stimuli used in the experiments. Observers had to differentiate the background plus test frequency from the background frequency alone. The test stimulus for the various measured filters is the one in the right columns for each pair of stimuli. Thus, for F_1(S) we show pairs for points at 0.3 (top), 0.8 (center) and 1.0 (bottom) cpd; for F_1(R) we show 0.8, 1.0, and 3.0 cpd; for F_4(S) we illustrate points at 1.0, 4.0, and 6.0 cpd, and for F_4(R) we present points at 3.0, 4.0, and 6.0 cpd.

About 517 sessions were run to obtain all of these curve estimates, with each session held to measure each point estimate lasting about 15-25 min, depending on the number of trials needed for reaching criterion, i.e., 10 pairs of peaks and valleys, with the number of trials ranging from about 60 to 125.

Results

Point estimates as well as the standard error bars of the mean for the 99% confidence interval (corrected for the sample size by the Student *t*-test distribution) for each measured function are shown in Figure 3. For easier identification in the figures, we decided to name the filter curves after each stimulus test: FSIN01cpd, FBES01cpd, FSIN04cpd, and FBES04cpd for F_1(S), F_1(R), F_4(S), and F_4(R), respectively.

Each point estimate represents contrast summation effects that are the actually obtained grand mean (averaged across subjects) of contrast thresholds for detecting contrast of the test frequency in the summated stimuli.

The use of 99% confidence intervals shows most of the significant differences without need for specific tests. Nevertheless, to illustrate this point, we carried out a *t*-test for correlated samples for points 0.8, 1.0, 2.0, and 3.0 cpd for FBES01cpd in Figure 3A and found a significant difference between 0.8 and 1.0 cpd, $P < 0.001$ (d.f. = 150, t = 15.067) and between 1.0 and 3.0 cpd, $P < 0.001$ (d.f. = 147, t = -6.535). We found no significant difference between 1.0 and 2.0 cpd.

We used the absolute threshold contrast values for 1- and 4-cpd sine-wave gratings or radial frequency stimuli as the reference baseline values for the filter measurements. Thus, to better observe the summation effects we included straight lines in the grand mean obtained for detecting the test stimulus used for measuring curve estimates of each filter.

The figures were organized so as to allow direct comparisons between FSIN01cpd and FBES01cpd, as well as between FSIN04cpd and FBES04cpd. Thus, Figure 3A and C compares FSIN01cpd and FBES01cpd with background stimulus contrasts at 42 and 6%, respectively, while Figure 3B and D is the equivalent comparing FSIN04cpd and FBES04cpd.

Summation effects are easily observed with respect to the horizontal lines which indicate absolute thresholds for each of the test frequencies. Points below the absolute threshold line indicate summation effects. If a point value is at the absolute threshold line, it may illustrate independent detection, whereas if it is above it, it shows interdependence and inhibition.

Thus, in all figures we observe relative summation effects for FBES01cpd (with respect to neighboring frequencies) and FBES04cpd at the test frequencies. The effects are present for both background stimulus contrasts, i.e., at both 42 and 6%. In

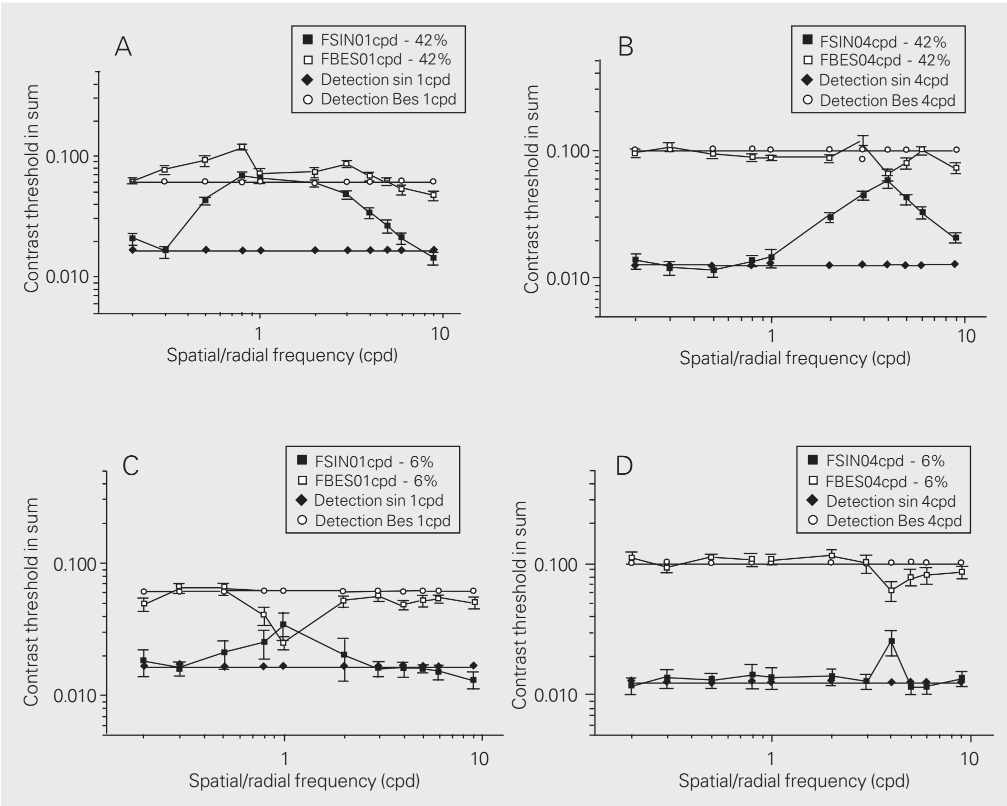

Figure 3. Contrast thresholds of test frequency in the summed stimuli obtained with the standard low-contrast resolution monitor. *A*, Grand mean of contrast at threshold in sum for the test frequency used to estimate FSIN01cpd and FBES01cpd with background frequency contrast fixed at 42%. Horizontal lines are detection thresholds for the 1.0 cpd sine-wave grating and for the 1.0 cpd radial frequency. Note the difference in trends. While most FSIN01cpd points fell significantly above the 1.0 cpd sine-wave grating absolute detection threshold, point estimates for the FBES01cpd showed small local summation effects at 1.0 cpd radial frequency and inhibitory effects at neighboring frequencies, i.e., at 0.8 and 3.0 cpd. The differences among 1.0, 0.8 and 3.0 cpd were statistically significant. *B*, Grand mean of contrast at threshold in sum for the test frequency used to estimate FSIN04cpd and FBES04cpd with background frequency contrast fixed at 42%. Horizontal lines are detection thresholds for the 4.0 cpd sine-wave grating and for the 4.0 cpd radial frequency. While all FSIN04cpd point estimates in the neighborhood of the test frequency fell significantly above the 4.0 cpd sine-wave grating absolute detection threshold, point estimates for the FBES04cpd showed a significant summation effect at 4.0 cpd test radial frequency and, again, relative and significant inhibitory effects at neighboring frequencies, i.e., at 3.0 and 6.0 cpd. *C*, Grand mean of contrast at threshold in sum for the test frequency used to estimate FSIN01cpd and FBES01cpd with background frequency contrast fixed at 6%. While the central point estimates for FSIN01cpd fell above the 1.0 cpd sine-wave grating absolute detection threshold, showing inhibition, point estimates for the FBES01cpd showed significantly larger summation effects with a maximum at 1.0 cpd radial frequency, and still showed significant inhibitory effects at neighboring frequencies, i.e., at 0.5 and 2.0 cpd. *D*, Grand mean of contrast at threshold in sum for the test frequency used to estimate FSIN04cpd and FBES04cpd with background frequency contrast fixed at 6%. While most point estimates for FSIN04cpd fell nearby the 4.0 cpd sine-wave grating absolute detection threshold, inhibition was observed at 4 cpd. On the other hand, point estimates for the FBES04cpd showed significant summation effects at 4.0 cpd test radial frequency and at its high frequency neighborhood. For FBES04cpd, the inhibitory effects at neighboring frequencies, i.e., at 3.0 and 6.0-9.0 cpd, are still present. All error bars are standard errors of the mean and corrected for the sample size to be at the 99% level of confidence interval. All inhibitory effects are reported relative to the test frequencies. cpd = cycles per degree of visual angle.

contrast, for FSIN01cpd and FSIN04cpd, we found inhibitory effects at the test frequencies, also present at 6% background stimulus contrast.

On the other hand, a tendency to inhibitory effects, also found previously for angular frequencies (5,7), appears to be present for radial frequency stimuli in the neighborhood of the test frequency.

We found no summation effects for FSIN01cpd and FSIN04cpd. Inhibition for the latter curves was still present at a 2% background stimulus contrast for at least one subject (i.e., JTF:2).

For all curves, but FSIN04cpd (in the 6% condition), the summation or inhibition effects were larger than 25% as compared to either neighboring or more remote spatial or radial background frequencies.

It is interesting to compare Figure 3B to 3C. There were effects of similar magnitude for FSIN04cpd and FBES04cpd (42% condition) and FSIN01cpd and FBES01cpd (6% condition). This is consistent with larger summation/inhibition effects at higher contrast levels at 4 cpd, and at lower contrast levels for 1 cpd.

Since summation effects reflect linearity, Figure 3 shows linear effects for radial frequency stimuli only. Clear out-of-linearity-range effects were detected for sine-wave gratings in all measurements.

Discussion

We were able to measure narrow-band filters for sine-wave gratings as well as for radial frequency stimuli. The effects appear to be reversed for the former as compared to the effects observed for the latter. The suprathreshold contrast present in the background stimuli seems to have caused inhibitory effects in the detection of the test sine-wave gratings. We obtained these results even when we lowered the amount of the contrast of the background stimuli to 6%. In the next experiment, we proceeded to measure such filters using the high-contrast resolution monitor.

Experiment 3: Spatial and radial frequency filter measurements of 1 and 4 cpd using the high-contrast resolution monitor

Experiment 3 was a repetition, in part, of Experiment 2 (only using background stimulus contrast fixed at 42%) on a monitor having much higher contrast resolution. The method we used is described above and also in detail by Simas and Dodwell (7) and by Simas et al. (5,11).

Subjects and Methods

Subjects. Three subjects having normal or corrected-to-normal visual acuity participated in the study.

Materials and procedures. Except for the fact that these were run on the high-contrast resolution monitor Sony BVM-1910, all the materials and equipment were the same as used for the first set of experiments. By high-contrast resolution we mean that the rate of increase in brightness was very slow for the same given digital steps as entered for a standard TV-RGB-video monitor. In the latter, the steps of increase in brightness are much larger. Thus, a 0.008 or 0.8% step increase implies different rates of increase for the two monitors used. The correct comparison is made if we measure the maximum and the minimum contrast levels. For the standard TV-RGB-video monitor these are within about 13.7 and 2.7 cd/m^2, respectively, whereas for the Sony BVM-1910, these are within about 9.6 and 6.9 cd/m^2. The mean luminance was always kept at 8.2 cd/m^2.

A total of 12 curves were obtained with the suprathreshold summation procedure for F_1(S), F_1(R), F_4(S), and F_4(R) using the background stimulus contrast level of 42%. Thus, three curves were measured for each of the filters; F_1(S), F_1(R), F_4(S), and F_4(R).

Results

In Experiment 3 we ran the same conditions as in Experiment 2, but using a higher contrast resolution monitor with background contrast at 42% for all conditions.

Thus, Figure 4 shows the curves obtained with the Sony BVM-1910 monitor. All details are similar to the explanations for Experiment 2. Consistent with the lower range of contrast in this monitor, we found for the 42% condition results that were similar to those of the 6% condition in the high-contrast range monitor (standard TV monitor). It is interesting to observe that, again, for the lower contrast range, the larger summation and inhibition effects were obtained in the 1-cpd range rather than around 4 cpd.

Discussion

We were able to repeat the results of Experiment 2 for both sine-wave gratings and radial frequency stimuli. Replication at 1.0 cpd showed larger effects than at the 4.0-cpd range. Nevertheless, for FSIN04cpd and FBES04cpd, the test sine-wave grating at 4.0 cpd was above its absolute threshold when summated with each of the tested background frequencies, whereas the test radial frequency stimulus at 4.0 cpd was below its absolute threshold under similar conditions.

General Discussion

In Experiment 1 (CSF and rCSF meas-

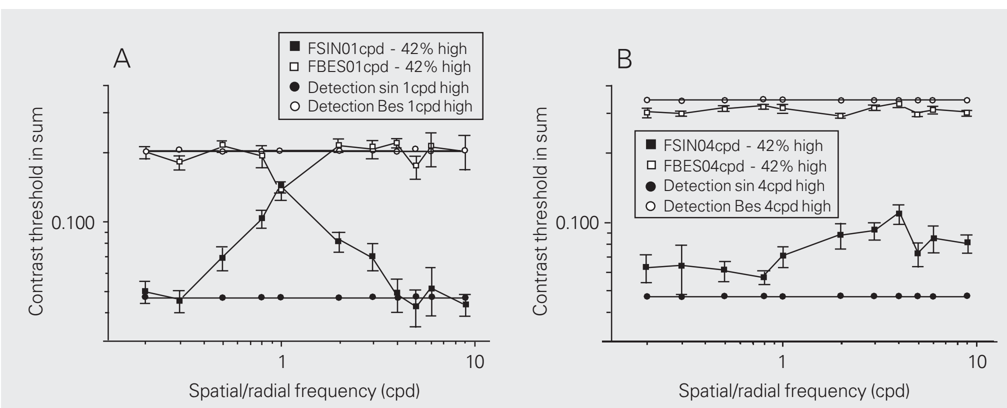

Figure 4. Contrast thresholds of test frequency in the summed stimuli obtained with the high-contrast resolution monitor. *A*, Grand mean of contrast at threshold in sum for the test frequency used to estimate FSIN01cpd and FBES01cpd. These are measurements using the high-contrast resolution monitor (please, note the higher ordinate values at low luminance). Again the background frequencies had contrast fixed at 42%. Horizontal lines are detection thresholds for the 1.0-cpd sine-wave grating and for the 1.0-cpd radial frequency. Again, observe the difference in trends (refer also to Figure 3A and C). For FSIN01cpd, the test frequency of 1.0 cpd fell significantly above the 1.0-cpd sine-wave grating absolute detection threshold. Neighboring point estimates at 0.5, 0.8, 2.0, and 3.0 cpd also showed significant inhibition. On the other hand, point estimates for the FBES01cpd showed a significant summation effect at 1.0-cpd radial frequency (the test frequency), and still showed significant inhibitory effects at neighboring frequencies, i.e., at 0.5-0.8 and 2.0-4.0 cpd. *B*, Grand mean of contrast at threshold in sum for the test frequency used to estimate FSIN04cpd and FBES04cpd with background stimulus contrast at 42%. Horizontal lines are detection thresholds for the 4.0-cpd sine-wave grating and for the 4.0-cpd radial frequency. While all point estimates for FSIN04cpd fell above the 4.0-cpd sine-wave grating absolute detection threshold, showing general inhibition with a maximum significant effect at 4.0 cpd, point estimates for the FBES04cpd fell all below the absolute contrast threshold value for the 4.0-cpd radial frequency. At that low luminance level, summation was stronger at 2.0 instead of 4.0 cpd with a secondary minimum at 5.0 cpd. All error bars are standard errors of the mean and corrected for the sample size to be at the 99% level of confidence interval. All inhibitory effects are reported relative to the test frequencies. cpd = cycles per degree of visual angle.

urements), the results as shown in Figure 2 present the trend of previous findings (2,3) for the CSF and rCSF. Much lower contrast levels are needed to detect sine-wave gratings than for radial frequency stimuli. On the other hand, the amplitude contrast range is much steeper for sine-wave gratings than for radial frequency stimuli. We see the increased difference in contrast sensitivity between the CSF and rCSF within their respective maximum sensitivity ranges as procedure dependent. The forced-choice procedure is a far better and less biased method than the adjustment procedure used by Kelly and Magnuski (2).

In Experiments 2 and 3 (filter measurements), we were surprised to find inhibition for spatial frequency filters using this supra-threshold summation method. We did not expect this based on the results of Kulikowski and King-Smith (9) or based on established results using adaptation methods (see, e.g., 12,13). On the other hand, our procedure cannot be compared to masking as most masking procedures use time intervals of up to 300 ms; our study used durations of 2000 ms for stimulus presentation. The ISI of 1000 ms was sufficient to ensure absence of masking.

Thus, we observed spatial frequency filters that, probably due to high contrast levels, went out of their linearity range and, instead of summating, suffered inhibition around the test spatial frequency.

On the other hand, it is interesting to note that radial frequency filters tend to behave linearly at high contrast ranges. Though they show a more restricted range as compared to spatial frequencies, they appear to work well and linearly at relatively high-contrast threshold levels.

On the basis of Figures 3 and 4, we are led to infer that at least two different mechanisms are acting in the detection of sine-wave gratings and radial frequency stimuli. To reach this conclusion we need to consider various aspects. First, we have to discuss the meaning of summation or inhibition and when to consider a filter as having filtering characteristics.

From electronic engineering and physics we learn that in order to be considered to be filtering frequencies, a mechanism should present selectively increased or decreased effects for a range or interval (that is, to have selective band-pass characteristics) where it shows a maximum or a minimum (depending on the measurement procedure) that is at least about 25% higher, or lower, when compared to neighboring and distant frequencies.

In our procedure, a summation effect would occur when both the test and background frequencies add contrast levels linearly and become much easier to detect with respect to neighboring frequencies. In other words, with very little addition of contrast it would be very easy to differentiate between the background alone and the summated stimulus. In that case, the amount of contrast necessary to allow this differentiation is much smaller than the amount of contrast needed to detect the test frequency alone. This could also happen for detection within a small range around the test frequency value. In that case, we would assume that the same mechanism is detecting both stimuli.

When the amount of contrast needed for distinguishing the test frequency in the summated stimulus from the background stimulus alone is about the same amount as needed for the absolute detection of the test frequency, then one can assume independent mechanisms. But one cannot infer linearity.

However, if the amount of contrast needed to make the same distinction is many times the amount needed for detecting the test frequency alone, then inference about having the same mechanism is not so readily possible. One can infer that there is interdependence because the added background frequency is making it difficult to detect the test frequency, but one can no longer infer that there is a single mechanism. More than one single mechanism may be implied.

When looking at Figures 3 and 4, one can observe that summation effects, selective and not so selective, are occurring for most results for radial frequency. The interesting part is the fact that summation effects can be observed at high, sometimes very high, contrast levels (e.g., Figure 3B-D).

On the other hand, except for the effects shown in Figure 3D, widespread inhibition was found for sine-wave gratings. Furthermore, the amplitude detection ranges between sine-wave gratings and radial frequency stimulus test frequencies were quite large. This can already be observed in the measurement of the CSF and rCSF.

But, instead of abandoning radial frequencies (j_0 targets) as stimuli to which the visual system is not highly selective, we choose to infer the existence of two or more separate mechanisms involved in the detection of spatial and radial frequencies.

Thus, a new look at our results will lead us to infer the existence of mechanisms that appear to function linearly at medium-high and high contrast levels, the former tending to peak at radial frequencies around 1 cpd, the latter at radial frequencies around 4 cpd.

On the other hand, sine-wave gratings seem to be detected at much lower contrast levels than the ones we employed since we could not observe any summation effect as did Kulikowski and King-Smith (9). Furthermore, according to Figure 3A-C, there are larger inhibitions at spatial frequencies around 1 cpd. This would be consistent with a lower contrast mechanism working better in the low spatial frequency range.

We think that these results are quite consistent with foveal-parafoveal detection mechanisms as well as with the many physiological findings related to striate and extrastriate areas involved in form processing. We may refer, for instance, to the studies by Gallant and colleagues (14,15) that show preferences for radial frequency stimuli in area V2 and V4 of macaque monkeys. We can also mention some recent work using functional magnetic resonance imaging in humans (16) showing extra-striate areas involved in the processing of radial (we call these angular frequency stimuli) and concentric gratings (we call these radial frequency stimuli).

In addition, there are inherent differences in the contrast profiles of spatial and radial frequencies. These could explain, at least in part, the present results. And it is precisely this point that we contend. The fact that linearity existed only at very low levels of contrast has been used frequently in the literature arguing against spatial frequency filters. The present results show the existence of linearity at high levels of contrast for radial frequency stimuli, possibly implying the existence of radial frequency filters.

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