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Modelling spatial contrast sensitivity functions for chromatic and luminance-modulated gratings

Jyrki M. Rovamo [a,*], Mia I. Kankaanpää [a], Heljä Kukkonen [a]

[a] *Department of Optometry and Vision Sciences, Redwood Building, University of Wales, College of Cardiff, PO Box 905, King Edward II Road, Cardiff CF1 3XF, UK*

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Abstract

We extended our detection model of achromatic spatial vision (Rovamo, J., Mustonen, J., & Näsänen, R. (1994a). Modelling contrast sensitivity as a function of retinal illuminance and grating area. *Vision Research*, *34*, 1301–1314) to colour vision by taking into account the fact that due to the spatio-chromatic opponency of retinal ganglion cells and dorsal lateral geniculate nucleus (dLGN) neurons, equiluminous chromatic gratings are not affected by precortical lateral inhibition. We then tested the extended model by using Mullen's experimental data (Mullen, K. J. (1985). The contrast sensitivity of human color vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology*, *359*, 381–400). The band-pass shape of the spatial contrast sensitivity function for luminance-modulated green and yellow gratings transformed to a low-pass shape, resembling the chromatic spatial contrast sensitivity function for red–green and blue–yellow equiluminous gratings, when the effect of precortical lateral inhibition on grating contrast was computationally removed by dividing luminance contrast sensitivities by spatial frequency (i.e. by af, where $a = 1°$). After the removal of this direct effect of lateral inhibition, there still remained a residual shape difference between the spatial contrast sensitivity functions for chromatic and luminance gratings. It was due to indirect reduction of grating visibility by quantal noise high-pass filtered by precortical lateral inhibition. When this indirect effect of quantal noise was also removed, contrast sensitivity for luminance gratings was about twice the sensitivity for chromatic gratings at all spatial frequencies. This was evidently due to the fact that the chromatic contrast of the equiluminous grating at the opponent stage (Cole, G. R., Hine, T. & McIihagga, W. (1993). Detection mechanisms in L-, M-, and S-cone contrast space. *Journal of the Optical Society of America A*, *10*, 38–51) was about half of the luminance contrast of either of its chromatic component. Thus, if the contrast of the equiluminous chromatic grating were not expressed as the Michelson contrast of one chromatic component grating against its own background (Mullen, K. J. (1985). The contrast sensitivity of human color vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology*, *359*, 381–400) but as chromatic contrast at the opponent stage, contrast sensitivity would be the same for chromatic and luminance gratings.

Keywords: Equiluminous chromatic gratings; Luminance gratings; Contrast sensitivity; Lateral inhibition; Modelling human spatial vision

1. Introduction

For luminance-modulated achromatic or monochromatic gratings contrast sensitivity refers to the inverse of Michelson contrast at threshold. The spatial contrast sensitivity function for luminance gratings has a band-pass shape: sensitivity is highest at medium spatial frequencies and decreases towards higher and lower frequencies (Campbell & Robson, 1968; Cohen, 1978). The low frequency decrease is believed to be due to lateral inhibition (e.g. Enroth-Cugell & Robson, 1966; Donner & Hemilä, 1996) which attenuates spatially slow luminance gradients, and thus contrast at low spatial frequencies. The high frequency decrease in sensitivity is caused by ocular optics whose point spread progressively attenuates contrast with increasing spatial frequency (Banks, Geisler & Bennet, 1987; Ijspreet, Van den Berg & Spekreijse, 1993; Rovamo, Mustonen & Näsänen, 1994b; Williams, Brainard, McMahon & Navarro, 1994).

* Corresponding author. Tel.: +44-1222-874000; fax: +44-1222-874859.

E-mail address: rovamo@cardiff.ac.uk (J.M. Rovamo)

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A chromatic equiluminous grating with red–green or blue–yellow modulation consists of the sum of red and green or blue and yellow luminance-modulated monochromatic gratings with a phase difference of 180° between them. For these chromatic gratings contrast sensitivity is calculated as the inverse of Michelson luminance contrast at threshold for one chromatic component grating against its own background luminance (Mullen, 1985). Spatial contrast sensitivity function for chromatic gratings is low-pass in shape: sensitivity is constant at low spatial frequencies but decreases at medium and high spatial frequencies (Mullen, 1985; Kelly, 1989). The result is similar even if chromatic modulation is expressed as purity percent[1] (Van der Horst & Bouman, 1969), relative distance in CIE chromaticity co-ordinates (Granger & Heurtley, 1973) or wavelength difference (Noorlander, Heuts & Koenderink, 1980).

Comparison between spatial contrast sensitivity functions for chromatic and luminance gratings reveals that Michelson contrast sensitivity is better for chromatic gratings at low spatial frequencies but for luminance gratings at high spatial frequencies (Mullen, 1985; Kelly, 1989).

The absence of a decrease in contrast sensitivity at low spatial frequencies has been suggested to be due to the lack of lateral inhibition in the visual system for chromatic stimuli (e.g. Cavanagh, 1991). One possible explanation for the difference in the magnitude of lateral inhibition between colour and luminance-modulated gratings could be the spatio-chromatic opponency (De Valois & De Valois, 1975, 1990) found in the receptive fields of P-type retinal ganglion cells and dLGN neurones (Kaplan, Barry & Shapley, 1990). De Valois and De Valois (1990) suggests that a typical receptive field (RF) with a spatiochromatic opponency receives an excitatory input from one cone type (e.g. medium wavelength, i.e. M-cone) and an inhibitory input from another cone type (e.g. long wavelength, i.e. L-cone) or possibly from both others (e.g. L-cone and short wavelength, i.e. S-cone). For a $+M-L$ cell, for example, the excitatory M-cone input may be concentrated in the RF centre while the inhibitory input from L-cones would cover the whole RF. This RF organisation results in very different RF properties when mapped either with luminance increment or pure chromatic stimulus: RF shows centre-surround antagonism for luminance, but not for chromatic stimulus. If the RF were mapped with a monochromatic or white light spot, an antagonistic centre-surround organisation would be revealed, because both cone types respond to the luminance increment. If, however, the RF were mapped with a green monochromatic light spot equiluminous to a large yellow background, there would be an excitatory response from all RF locations, because in this case the stimulus produces an increase in M-cone stimulation but a decrease in L-cone stimulation. On this basis, the $+M-L$ cell would produce a band-pass shaped spatial modulation transfer function (MTF) for achromatic or monochromatic gratings but a low-pass shaped spatial MTF for equiluminous red–green gratings.

The previous attempts to explain the shape difference between the spatial contrast sensitivity functions for chromatic and luminance gratings have been based on preneural (Geisler, 1989) as well as neural (Ingling & Martinez-Uerigas, 1983; Lennie & D'Zmura, 1988; Rohaly & Buschbaum, 1988; Kelly, 1989; Sekiguchi, Williams & Brainard, 1993) factors. However, preneural factors affecting signal transmission from the front surface of the cornea up to the quantal absorption taking place in the outer segments of photoreceptors cannot explain the sensitivity difference at low spatial frequencies (Geisler, 1989). The results of Sekiguchi et al. (1993) based on the use of isoluminant and isochromatic interference fringes to avoid the blurring caused by ocular optics and corrected for other preneural factors by using the ideal-observer analysis (Geisler, 1989) showed that neural factors are needed to explain the shape difference between the spatial contrast sensitivity functions for chromatic and luminance gratings. The retinal ganglion cells and dLGN neurones with spatiochromatic opponency carry both luminance and colour information, and their output can be decomposed to a luminance pathway with a band-pass spatial MTF and a chromatic pathway with a low-pass spatial MTF (Ingling & Martinez-Uerigas, 1983; Lennie & D'Zmura, 1988; Rohaly & Buschbaum, 1988; Kelly, 1989). At least in principle this decoding could explain the shape difference between the spatial contrast sensitivity functions for chromatic and luminance gratings, but Ingling and Martinez-Uerigas (1983) and Lennie and D'Zmura (1988) do not advance this idea any further. Rohaly and Buschbaum (1988) developed the idea further by modelling the shape difference between the spatial contrast sensitivity functions for red–green and yellow gratings (Mullen, 1985) by means of a receptive field with a spatiochromatic opponency and Gaussian point spread functions (PSFs) for both centre and surround but without taking into account the effect of quantal noise. When we used their parameters to predict Mullen's data, the success was only moderate. Kelly (1989) analysed his luminance and chromatic contrast sensitivity data by also assuming spatiochromatic opponency but found that the MTFs of the excitatory and inhibitory mechanisms were band-pass and thus not compatible with the Gaussian or exponential MTFs of the centre and surround in the RFs of retinal ganglion cells and dLGN neurones. Hence, none

[1] Purity percent indicates how far in relative terms a given colour is displaced from a white point towards its dominant wavelength.

of the previous attempts to explain the shape difference between the spatial contrast sensitivity functions for chromatic and luminance gratings have been very successful.

According to our detection model of human achromatic spatial vision (Rovamo, Mustonen & Näsänen, 1994a) a visual signal first goes through the ocular optics. This is followed by quantal absorption, processing in the retina and subsequent neural visual pathways, and addition of neural noise, before detection takes place in the human brain. The model describes accurately how contrast sensitivity for luminance-modulated gratings depends on spatial frequency, grating area, stimulus complexity, exposure time, external additive spatial noise, quantal noise, and average level of retinal illuminance (Rovamo, Luntinen & Näsänen, 1992, 1993; Näsänen, Kukkonen & Rovamo, 1994; Rovamo et al., 1994a; Rovamo et al., 1994b; Rovamo, Ukkonen, Thompson & Näsänen, 1994c; Luntinen, Rovamo & Näsänen, 1995; Rovamo, Mustonen & Näsänen, 1995; Näsänen, Syväjärvi & Rovamo, 1997). An analogous model, where retinal receptors perform the low-pass filtering, has been designed for achromatic temporal vision (Rovamo, Raninen, Lukkarinen & Donner, 1996; Rovamo, Raninen & Donner, 1999).

The aim of this study is to investigate whether the model of human achromatic spatial vision successfully describing the detection of luminance-modulated gratings (Rovamo et al., 1994a) can be extended to describe the detection of equiluminous chromatic gratings by just taking into account the grating-type specific difference in precortical lateral inhibition. We tested the extended model on the spatial contrast sensitivity functions measured by Mullen (1985) for equiluminous chromatic red–green and blue–yellow gratings as well as for monochromatic green and yellow luminance-modulated gratings.

2. The model

According to the model of Rovamo et al. (1994a) human visual system is described as a simple spatial image processor (Fig. 1). First a visual signal is spatially low-pass filtered by the optical modulation transfer function (O) of the eye. Then light-dependent noise (N_q) is added at the event of quantal absorption that takes place in the outer segments of photoreceptors. Thereafter the visual signal together with quantal noise is high-pass filtered by the spatial modulation transfer function (P) of the retina and subsequent neural visual pathways. This is followed by the addition of internal neural noise (N_i) before detection by a local, spatially windowed, suboptimal matched filter in the human brain.

In the detection model of human achromatic spatial vision (Rovamo et al., 1994a) the high-pass filtering in the retina and subsequent neural visual pathways can be assumed to result from subtractive lateral inhibition produced by the centre-surround antagonism of the receptive fields (e.g. Enroth-Cugell & Robson, 1966; Donner & Hemilä, 1996) producing attenuation at low spatial frequencies for luminance-modulated stimuli. We have shown that the modulation transfer function (MTF) of the retina and subsequent neural visual pathways measured psychophysically for luminance gratings (i.e. P_L) is directly proportional to spatial frequency (Rovamo et al., 1994a, 1995), thus attenuating low spatial frequencies more than high.

The experimental contrast sensitivity data of Enroth-Gugell and Robson (1966) recorded from X-type ganglion cells in the cat retina indicates that MTF is proportional to spatial frequency: in their plots of logarithmic sensitivity as a function of logarithmic spatial frequency the slope of increase up to the sensitivity maximum is very close to one. Both Enroth-Gugell and Robson (1966) and Donner and Hemilä (1996) modelled the MTF by assuming (i) that the point spread functions (PSF) of the antagonistic centre and surround mechanisms in the ideal receptive field (RF) of retinal ganglion cells and dLGN neurones are Gaussians with effective radius r_c for centre and r_s for surround, and (ii) that the response of the centre weighed by k_c is subtracted by the response of the surround weighed by k_s. Enroth-Gugell and Robson (1966) allowed the ratio $k_c r_c^2/k_s r_s^2$ to vary (range 0.73–0.96) in order to obtain the best possible fit to the experimental data. This means that the MTF gets a non-zero value at zero frequency. Hence, lateral inhibition would not eliminate information at very low spatial frequencies, as it should, by filtering out spatially slow luminance

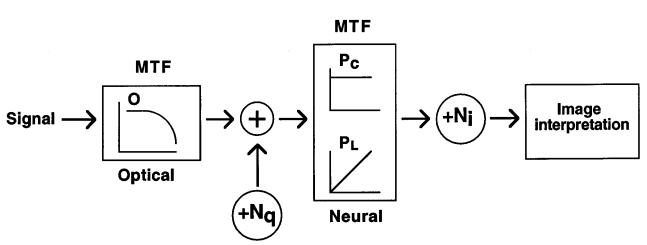

Fig. 1. Description of the human visual system as a simple image processor. First the visual signal is spatially low-pass filtered by the optical modulation transfer function (O) of the eye. Then light-dependent noise (N_q) is added at the event of quantal absorption that takes place in the outer segments of photoreceptors. Thereafter the visual signal + noise is filtered by the spatial modulation transfer function (P_L or P_C) of the retina and subsequent neural visual pathways. Due to lateral inhibition P_L is high-pass for luminance-modulated gratings but due to the lack of lateral inhibition P_C is constant for chromatic equiluminous gratings. Then comes addition of internal neural noise (N_i) before image interpretation (detection, discrimination etc.) takes place in the human brain.

changes. Donner and Hemilä (1996) solved this problem by assuming that the ideal RF is balanced, i.e. $k_c r_c^2 = k_s r_s^2$. For luminance-modulated gratings, how-ever, this leads to a neural modulation transfer function (MTF) that is proportional to the spatial frequency squared up to the MTF maximum (Donner & Hemilä, 1996), which is, however, not in agreement with the neurophysiological data of Enroth-Gugell and Robson (1966) or our psychophysical data (Rovamo et al., 1994a, 1995). For a *balanced RF* the neural modulation transfer function can be made proportional to spatial frequency by assuming that the MTF of the surround is exponential. Appendix A shows that the corresponding point spread function (PSF) of such surround can be approximated quite accurately by a Gaussian down to a tenth of its maximum as the main difference from a Gaussian shape is the slowly decreasing outskirts of the PSF. Appendix A also shows that the PSFs of the RF centres and surrounds can be chosen in such a way that for luminance-modulated gratings the MTF of the RF up to its maximum can be described as $P_L(f) = af$, where $a = 1°$ for all receptive field sizes[2].

Due to the spatio-chromatic opponency (De Valois & De Valois, 1975, 1990) found in the P-type retinal ganglion cells and dLGN neurones (Kaplan et al., 1990), equiluminous chromatic gratings are not affected by precortical lateral inhibition. Appendix A shows that the MTFs of the RF centres and surrounds can be chosen in such a way that the MTF of their combination for equiluminous chromatic gratings is $P_C(f) = 1$ for all receptive field sizes. With this accepted, the band-pass shape of luminance contrast sensitivity $S_L(f)$ as a function of spatial frequency (f) can be changed to a low-pass shape by dividing it by (af) to produce $S_L(f)/(af)$, while the low-pass shape of chromatic contrast sensitivity $S_C(f)$ can be changed to a band-pass shape by multiplying it by (af) to produce $S_C(f)(af)$. In the former case the MTF of the achromatic system (P_L) proportional to spatial frequency will be computationally replaced by the constant MTF of the chromatic system (P_C) while in the latter case the reverse takes place.

According to our model (Rovamo et al., 1994a) it is the signal-to-noise ratio at the output of the detector that determines performance. The quantal noise is added to the signal before lateral inhibition, and hence, the effect of quantal noise[3] on contrast sensitivity at various spatial frequencies depends on the MTF of the retina and subsequent neural visual pathways. Because the chromatic and luminance MTFs are different in shape, also the effect of quantal noise has to be taken into account in order to explain fully the shape difference between spatial contrast sensitivity functions for equiluminous chromatic and monochromatic or achromatic luminance gratings.

Human visual performance obeys DeVries–Rose law (DeVries, 1943; Rose, 1948) at low light levels but Weber's law at higher light levels. The two laws mean that at low levels of retinal illuminance grating contrast sensitivity increases in direct proportion to the square root of average luminance but at higher illuminances sensitivity is independent of light level (Van Nes & Bouman, 1967; Kelly, 1977; Mustonen, Rovamo & Näsänen, 1993). The illuminance marking the transition between the laws is known to increase with spatial frequency. In addition, performance falls between DeVries–Rose and Weber's laws at intermediate light levels (Kelly, 1972; Koenderink, Bouman, Bueno de Mesquita & Slappendel, 1978; Savage & Banks, 1992). Mustonen et al. (1993) recently derived an equation for contrast sensitivity (S) that combines the two laws and also explains the non-abrupt transition between them:

$$S = S_{max}(1 + I_c/I)^{-0.5}, \quad (1)$$

where S_{max} is the maximum contrast sensitivity obtainable in bright light at the particular exposure duration, grating area, and spatial frequency used, I is retinal illuminance, and I_c is the critical retinal illuminance marking the transition between the DeVries–Rose and Weber's laws. Eq. (1) is a mathematical description of certain properties of the model shown in Fig. 1 and can also be derived directly from it (Rovamo et al., 1994a). For further details see Appendix B.

For luminance modulated gratings I_c depends on spatial frequency so that the higher the spatial frequency, the higher the critical retinal illuminance where the transition between the two laws occurs (Van Nes & Bouman, 1967; Kelly, 1977). According to Van Nes–Bouman law critical retinal illuminance (I_c) for luminance-modulated gratings is directly proportional to spatial frequency (f) squared:

$$I_c = I_0 f^2 \quad (2)$$

(Van Nes et al., 1967; Mustonen et al., 1993), where the proportionality constant $I_0 = 12$ phot. td. (Kankaanpää, Rovamo & Hallikainen, 1996) is in agreement with the range of 5.2–21 phot. td. reported previously for I_0 (Mustonen et al., 1993; Rovamo et al., 1995). With $I_0 = 12$ phot. td accepted, I_c increases from 0.12 td at 0.1 c/deg to 1200 td at 10 c/deg.

[2] If spatial frequency were expressed e.g. in c/rad or c/min of arc, the corresponding value of a would be $\pi/180$ rad or 60 min, respectively.

[3] The effect of quantal noise on contrast sensitivity also depends on grating area (e.g. Banks et al., 1987). This aspect is not considered here, however, as there was no size difference between equiluminous chromatic and monochromatic luminance-modulated gratings in Mullen's (1985) experiments.

Van Nes–Bouman law described by Eq. (2) is in complete agreement with the amplification of quantal noise produced by the filtering[4] through the MTF of the retina and subsequent neural visual pathways for luminance-modulated gratings, as $P_L(f)$ increases in proportion to spatial frequency. Thus, Van Nes–Bouman law can be derived directly from our model (Rovamo et al., 1994a). For further details see Appendix B.

For chromatic equiluminous red–green and blue–yellow gratings I_c has been found to be independent of spatial frequency (Kankaanpää et al., 1996):

$$I_c = I_0, \tag{3}$$

where $I_0 = 165$ phot. td. This is in agreement with the fact that $P_C(f)$ is constant and thus independent of spatial frequency for equiluminous chromatic gratings.

3. Results

In Fig. 2 the spatial contrast sensitivity functions for equiluminous red–green and blue–yellow gratings and for luminance-modulated green and yellow gratings have been replotted from Mullen (1985). Sensitivities for luminance-modulated gratings at very high spatial frequencies have been excluded because there are no corresponding sensitivities for chromatic gratings. As Fig. 2 shows, spatial contrast sensitivity function has a low-pass shape for chromatic gratings but a band-pass shape for luminance-modulated gratings. Contrast sensitivity was better for chromatic gratings at low spatial frequencies ($f < 0.3$ c/deg) but better for luminance-modulated gratings at higher spatial frequencies.

According to the extended detection model the spatial MTF of the retina and subsequent neural visual pathways is proportional to spatial frequency (i.e. $P_L(f) = af$, where $a = 1°$) for luminance-modulated gratings but constant (i.e. $P_C(f) = 1$) for chromatic gratings, reflecting the fact that precortical lateral inhibition in the visual system is strong for luminance stimuli but absent for chromatic stimuli. Thus, the band-pass shape of the spatial contrast sensitivity function for luminance-modulated gratings should transform to a low-pass shape when the effect of lateral inhibition, i.e. $P_L(f)$ on grating signal is computationally removed by dividing contrast sensitivities with spatial frequency, i.e. with (af), where $a = 1°$.

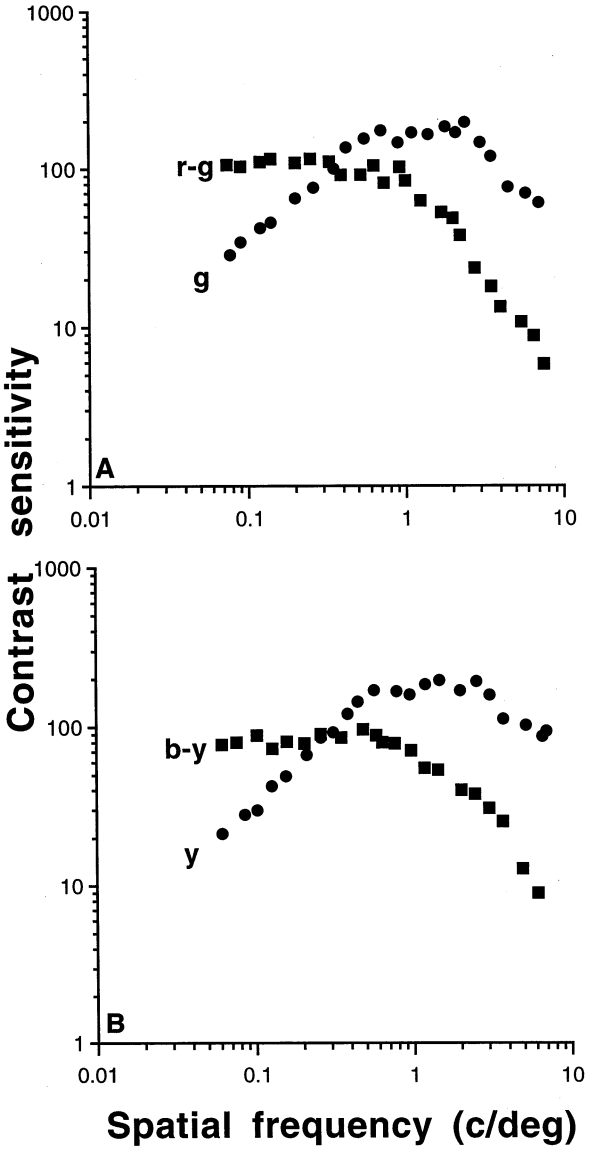

Fig. 2. Contrast sensitivity for equiluminous red–green (r–g) and blue–yellow (b–y) gratings and luminance-modulated green (g) and yellow (y) gratings as a function of spatial frequency from Mullen (1985).

To test the above prediction the original contrast sensitivities for chromatic gratings were replotted in Fig. 3 together with the contrast sensitivities for luminance-modulated gratings divided by spatial frequency (i.e. by af, where $a = 1°$) to remove the effect of lateral inhibition on grating signal. According to our model (see Fig. 1) the shape of neither contrast sensitivity function is now directly affected by precortical lateral inhibition. Thus, if the direct effect of lateral inhibition on grating contrast were the only reason for the shape difference between the spatial contrast sensitivity functions for chromatic and luminance-modulated gratings,

[4] The effect of filtering is calculated as $N_q P_L^2(f) = N_q f^2$ because the spectral density (N_q) of quantal noise expressed in contrast terms is proportional to the square of its rms-contrast. This relationship is easily explained (Rovamo et al., 1994a): The effective spectral density of quantal noise is inversely proportional to retinal illuminance, i.e. $N_q = K/I$. Let retinal illuminance (I) correspond to n quanta on average. One standard deviation from the mean is then equal to $\sqrt{n}$, because light quanta obey Poisson distribution. By definition, the rms-contrast of noise (c) is equal to standard deviation divided by the mean, i.e. $\sqrt{n}/n = 1/\sqrt{n} = 1/\sqrt{I}$. Hence, $N_q = kc^2$.

the curves should have the same shape. However, as Fig. 3 shows, this is not strictly true.

Although the two sensitivity functions in Fig. 3 are quite parallel at low spatial frequencies, the decrease of contrast sensitivity as a function of spatial frequency is faster at higher spatial frequencies for luminance-modulated than chromatic gratings. Consequently, the superiority of contrast sensitivity for luminance gratings practically disappears with increasing spatial frequency. In comparison to the clear-cut shape difference between the spatial contrast sensitivity functions for chromatic and luminance-modulated gratings shown in Fig. 2, the difference remaining in Fig. 3 is small, however. According to the model of Fig. 1 this residual shape difference is due to low retinal illuminance, or in fact due to the effect of lateral inhibition on the masking effect of quantal noise.

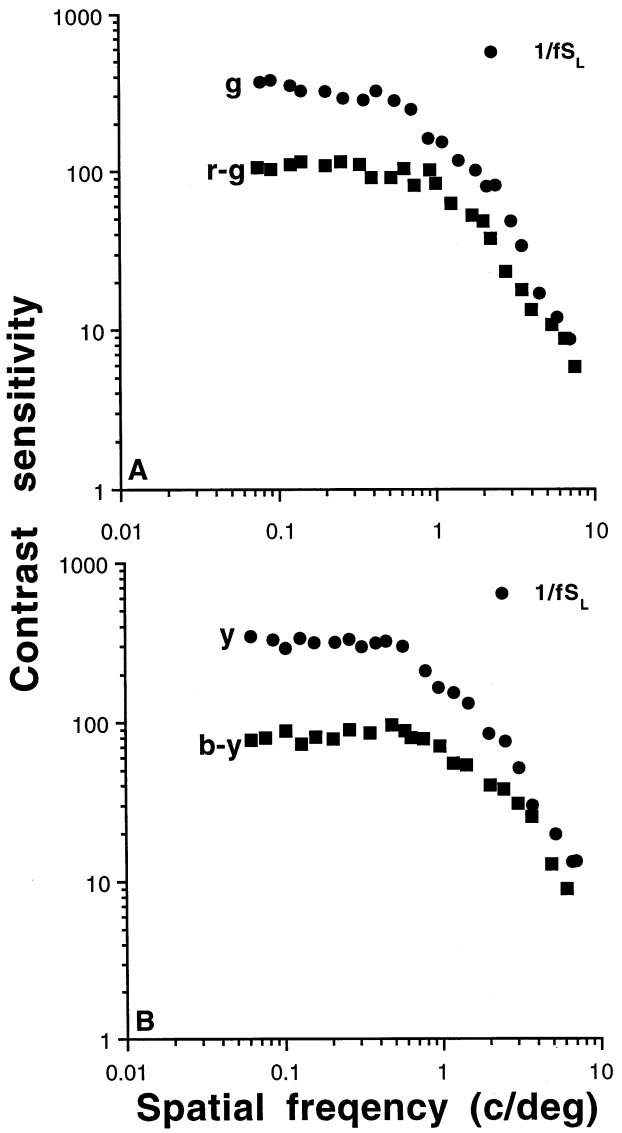

Fig. 3. Spatial contrast sensitivity functions for equiluminous red–green and blue–yellow gratings from Fig. 2A and B presented together with contrast sensitivities for luminance-modulated green and yellow gratings from Fig. 2A and B first divided by spatial frequency (i.e. by af, where $a = 1°$) to remove the effect of lateral inhibition on grating signal and then plotted as a function of spatial frequency.

The mean retinal illuminance (I) in Mullen's (1985) experiments was 200 phot. td for green luminance-modulated and red–green equiluminous gratings and 60 phot. td for yellow luminance-modulated and blue–yellow equiluminous gratings. At light levels of 60–200 phot. td contrast sensitivity (S) for luminance-modulated green and yellow gratings is reduced progressively with increasing spatial frequency (see Eq. (1) and Eq. (2)) by quantal noise amplified by $P_L = af$ (where $a = 1°$) resulting from lateral inhibition (Rovamo et al., 1994a). This effect is negligible at low spatial frequencies (f) where $I_c \ll I$ ($I = 60$ or 200 phot. td.) (see Eq. (2)) so that $S = S_{max}$ (see Eq. (1)). The amplification of quantal noise by P_L is reflected in the increase of I_c-values with spatial frequency. For $I_c \gg I$, $S = S_{max}(I/I_c)^{0.5}$ (see Eq. (1)). For equiluminant chromatic gratings, on the other hand, there is no difference in noise amplification between spatial frequencies, because $P_C = 1$ due to the lack of lateral inhibition in the human visual system for equiluminous gratings. Therefore, contrast sensitivity for chromatic gratings (see Eq. (1)) is reduced at light levels of 60–200 phot. td by quantal noise similarly at all spatial frequencies, because $I_c = 165$ phot. td, i.e. a constant independent of spatial frequency. Hence, it seems probable that the low level of retinal illuminance could explain why the decrease of contrast sensitivity with increasing spatial frequency is steeper for luminance gratings at higher spatial frequencies in Fig. 3.

To test the above prediction, we corrected the contrast sensitivities (S) of Fig. 3 for the effect of quantal noise by replacing them by the corresponding values of S_{max} calculated across spatial frequencies (f) from Eq. (1) solved for S_{max} and using $I_c = 12f^2$ for luminance gratings and $I_c = 165$ phot td for chromatic gratings. The corrected sensitivities have been plotted in Fig. 4.

As Fig. 4 shows, the spatial contrast sensitivity functions for luminance modulated monochromatic and equiluminous chromatic gratings became quite similar in shape. The two functions are parallel across the spatial frequency range studied, and their sensitivity ratio appears to be independent of spatial frequency. However, contrast sensitivity was now about two times higher for luminance-modulated than chromatic gratings at all spatial frequencies.

In the context of our extended detection model of human spatial vision (Fig. 1) there are various possible explanations for the sensitivity difference in Fig. 4. For example, the spectral density of internal neural noise could be greater for chromatic than luminance-modulated gratings or the detection efficiency could be smaller for chromatic than luminance-modulated grat-

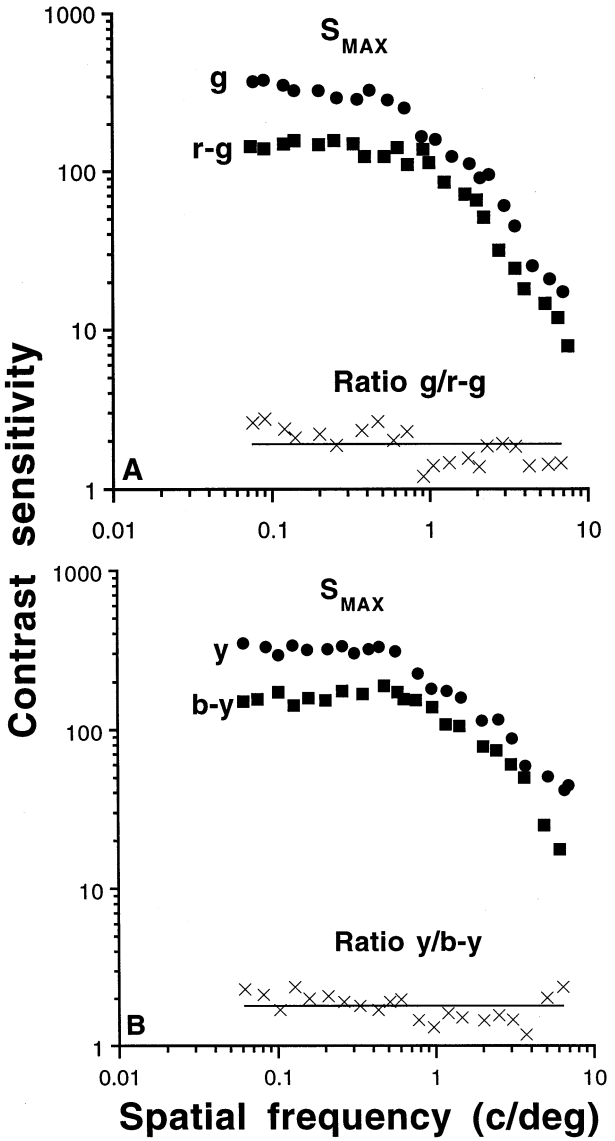

Fig. 4. The spatial contrast sensitivity functions of Fig. 3 A and B after removing the effect of quantal noise, i.e. luminance level on contrast sensitivity. Crosses indicate the contrast sensitivities for luminance gratings divided by the contrast sensitivities for chromatic gratings and lines refer to their means.

ings. The latter alternative can be readily rejected on the basis of the experimental results (Gegenfurtner & Kiper, 1992) showing that detection efficiency is the same for chromatic and luminance gratings, while the former alternative would add another constant to the model. Therefore, a more plausible explanation could be the ad-hoc measure of colour contrast based on the luminance contrast of either of the two chromatic components in equiluminous gratings (Mullen, 1985). When Mullen (1985) in the Appendix of her paper expressed the contrast of the red–green equiluminous grating in terms of contrasts in L (long-wave-length) and M (medium-wave-length) cones, the cone contrasts c_L and c_M varied depending on what percentages of red and green light were needed to nullify the subjective achromatic contrast in the equiluminous gratings. However, their difference $(c_L - c_M)$, i.e. chromatic contrast at the opponent stage (e.g. Cole, Hine & McIlhagga, 1993) was found to be 57% of the luminance contrast of either of the two chromatic component gratings, irrespective of the red–green ratio needed for subjective equiluminance. Mullen's (1985) grating was equiluminous, which means that grating signals in L- and M-cone arrays were in opposite phase. Hence, the difference $c_L - c_M$ was calculated by adding together the absolute cone contrast values. The fact that the contrast of the red–green chromatic grating at the opponent stage was about half of the luminance contrast of either chromatic component grating explains the finding that contrast sensitivity for chromatic gratings was about half of the contrast sensitivity for luminance gratings. Thus, the contrast sensitivity difference between green and red–green gratings is the result of the ad-hoc definition of chromatic contrast, and there would be no sensitivity difference, if chromatic contrast were expressed as $c_L - c_M$. This suggests that the contrast of the blue–yellow grating in the corresponding opponent channel is also half of the luminance contrast of either chromatic component grating. Another possible explanation for the difference in contrast sensitivity between yellow and blue–yellow gratings could be the low blue cone density in the retina (Geisler, 1989)

4. Discussion

The analysis of Mullen's (1985) data (Fig. 1) in the context of our extended model showed that the difference in the shape of luminance and chromatic contrast sensitivity functions can be explained by the difference in lateral inhibition produced by these two types of stimuli. The two functions became almost similar in shape when the direct effect of lateral inhibition on grating contrast was computationally removed by dividing luminance contrast sensitivities by spatial frequency (i.e. by af, where $a = 1°$). After the removal of the direct effect of lateral inhibition, there still remained a residual shape difference between the spatial contrast sensitivity functions. The residual shape difference was explained in terms of indirect reduction of the visibility of luminance-modulated gratings caused by quantal noise high-pass filtered by lateral inhibition. When this indirect effect of quantal noise was also removed, contrast sensitivity for luminance gratings was about twice the sensitivity for chromatic gratings at all spatial frequencies. This was evidently due to the fact that the chromatic contrast of the equiluminous grating at the opponent stage (Cole et al., 1993) was about half of the luminance contrast of either of its chromatic compo-

nent. Thus, if the contrast of the equiluminous chromatic grating were not expressed as the Michelson contrast of one chromatic component grating against its own background (Mullen, 1985) but as chromatic contrast at the opponent stage, contrast sensitivity would be the same for chromatic and luminance gratings and contrast sensitivity functions would superimpose.

According to our extended model of human spatial vision the shape difference between the spatial contrast sensitivity functions for luminance-modulated and chromatic gratings in Mullen's (1985) data was mainly due to a difference in the strength of lateral inhibition that affected grating contrast. A further support for this hypothesis is provided by the finding that the light level at which the increase of contrast sensitivity with retinal illuminance saturates is constant and thus independent of spatial frequency for chromatic gratings (Kankaanpää et al., 1996) but increases in direct proportional to spatial frequency squared for luminance-modulated gratings (Van Nes, Koenderink, Nas & Bouman, 1967; Mustonen et al., 1993; Rovamo et al., 1995). In the context of our model of human spatial vision (Rovamo et al., 1994a) these experimental results mean that the spatial modulation transfer function (MTF) of the retina and subsequent neural visual pathways (P) is proportional to spatial frequency for luminance-modulated gratings but a constant independent of spatial frequency for chromatic gratings.

The mean retinal illuminance (I) in Mullen's (1985) experiments was at all spatial frequencies 200 phot. td for green luminance-modulated and red–green equiluminous gratings and 60 phot. td for yellow luminance-modulated and blue–yellow equiluminous gratings. Contrast sensitivity for luminance-modulated gratings is at these light levels reduced according to Eq. (1) especially at high spatial frequencies by quantal noise that is amplified by $P_L = af$ ($a = 1°$) resulting from lateral inhibition (Rovamo et al., 1994a). The amplification is reflected in the increase of I_c-values with spatial frequency according to Eq. (2). On the other hand, there is no difference in noise amplification between spatial frequencies for chromatic gratings as $P_C = 1$ due to the lack of precortical lateral inhibition in the human visual system for equiluiminous gratings. Therefore, contrast sensitivity for chromatic gratings is reduced according to Eq. (1) at the light levels of 60–200 phot. td by quantal noise similarly at all spatial frequencies because $I_c = 165$ phot. td, i.e. a constant independent of spatial frequency. In complete agreement with the above reasoning, the residual shape difference between the spatial contrast sensitivity functions for luminance-modulated and chromatic gratings, remaining after the removal of the direct effect of lateral inhibition on grating contrast, was found to be solely due to the spatial-frequency dependent reduction of monochromatic luminance grating visibility caused by quantal noise high-pass filtered by lateral inhibition.

The above finding that the shape difference between the spatial contrast sensitivity functions for chromatic and luminance gratings in Mullen's (1985) data could be completely attributed to lateral inhibition and its effect on quantal noise indicates that Mullen (1985) in her experiments managed to minimise the effects of various chromatic aberrations (Bradley, Zhang & Thibos, 1992) on contrast sensitivity. The finding also supports the view that spatial integration is similar for chromatic and luminance-modulated gratings (Noorlander et al., 1980; Sekiguchi et al., 1993) and also suggests that the dependence of detection efficiency (Tanner & Birdsall, 1958) on grating area (Näsänen et al., 1994) is similar for the two grating types. Moreover, Gegenfurtner and Kiper (1992) have shown experimentally that efficiency is the same for chromatic and luminance-modulated gratings.

Our detection model of human spatial vision is a single-channel model although there are both psychophysical results (Campbell & Robson, 1968; Bradley, Switkes & De Valois, 1988; Losada & Mullen, 1994) and neurophysiological evidence from visual cortex (De Valois, Albrecht & Thorell, 1982; Thorell, De Valois & Albrecht, 1984; Lennie, Krauskopf & Sclar, 1990) suggesting that spatial contrast sensitivity functions for luminance-modulated as well as chromatic gratings comprise an upper envelope for a range of spatial band-pass mechanisms. This implies that at the cortical level not even equiluminous chromatic stimuli are immune to lateral inhibition resulting for example from the centre-surround antagonism of double-opponent cells (Michael, 1978). However, if the dominant source of neural noise is precortical then any subsequent filtering (e.g. band-pass in the visual cortex) of spatially narrow-bandwidth stimuli (e.g. gratings) taking place after the addition of white internal neural noise leaves detection unaffected, because detection mediated by a matched filter is based on signal-to-noise ratio and both the grating and noise at the spatial frequency of the grating signal are attenuated/amplified in the filtering process by the same factor, which keeps the signal-to-noise ratio unchanged. Hence, our model is not able to discriminate the presence or absence of multiple spatial filters.

The existence of band-pass mechanisms implies that the retinal image coding is based on local spatial frequency components (Watson, 1990). This can be taken into account by constructing a local matched filter in the code domain (see Myers & Barrett, 1987), instead of using a filtered retinal image directly as we did. In this case detection is based on matching (cross-correlating) the model with the coded stimulus plus noise. Thus, our model based on a local sub-optimal matched filter is in harmony with current knowledge of visual physiology

and theories of early visual information processing. The model should be taken as representing for the performance envelope of multiple filters, if they exist.

Our finding that after the removal of the effects of lateral inhibition and quantal noise, contrast sensitivity was about two times better for luminance-modulated than chromatic gratings at all spatial frequencies is evidently due to the fact that the chromatic contrast of the equiluminous grating at the opponent retinal stage (Cole et al., 1993) was about half of the luminance contrast of either component grating. Thus, if the contrast of the equiluminous chromatic grating were not expressed as the luminance contrast of one chromatic component grating against its own background (Mullen, 1985) but as chromatic contrast at the opponent stage, contrast sensitivity would be the same for chromatic and luminance gratings and contrast sensitivity functions would superimpose.

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Appendix A

A.1. The MTF of a RF with a subtractive Gaussian-exponential centre-surround organisation

Let us assume (i) that the modulation transfer functions (MTF) of the antagonistic centre and surround mechanisms in the ideal receptive field (RF) of retinal ganglion cells and dLGN neurones are Gaussian and exponential, respectively and (ii) that the response of the centre is reduced (Enroth-Cugell & Robson, 1966) by the response of the surround by means of subtraction. Let the MTF of the RF surround be

$$Z_s(f) = (2\pi b/a)^{-1} \exp(-2\pi bf), \quad \text{(A1)}$$

where $\exp(u)$ refers to e^u, $a = 1°$, b is a measure of receptive field surround size in degrees[5], and $f = \sqrt{(f_x^2 + f_y^2)}$ is the radial spatial frequency (c/deg), where f_x and f_y are its orthogonal (e.g. horizontal and vertical) component spatial frequencies (Näsänen et al., 1994). For a simple cosine grating its spatial frequency f refers to the spatial frequency measured across the bars, as its orthogonal component spatial frequency measured along the bars is zero. The corresponding MTF of the RF centre in a balanced ganglion-cell with a Gaussian point spread function (PSF) is then

$$Z_c(f) = (2\pi b/a)^{-1} \exp[-(\pi r_0 f)^2], \quad \text{(A2)}$$

where r_0 is the effective radius of the RF centre (Donner & Hemilä, 1996). Then the MTF of the receptive field is

$$P_L(f) = Z_c(f) - Z_s(f) = (2\pi b/a)^{-1}\{\exp[-(\pi r_0 f)^2] - \exp(-2\pi bf)\}. \quad \text{(A3)}$$

The Taylor series approximation for an exponential function is know to be

$$e^u = 1 + u + u^2/2! + u^3/3! + \ldots \quad \text{(A4)}$$

Hence, at spatial frequencies below the maximum of MTF, $\exp[-(\pi r_0 f)^2]$ is approximately equal to unity while $\exp(-2\pi bf)$ can be approximated by $1 - 2\pi bf$

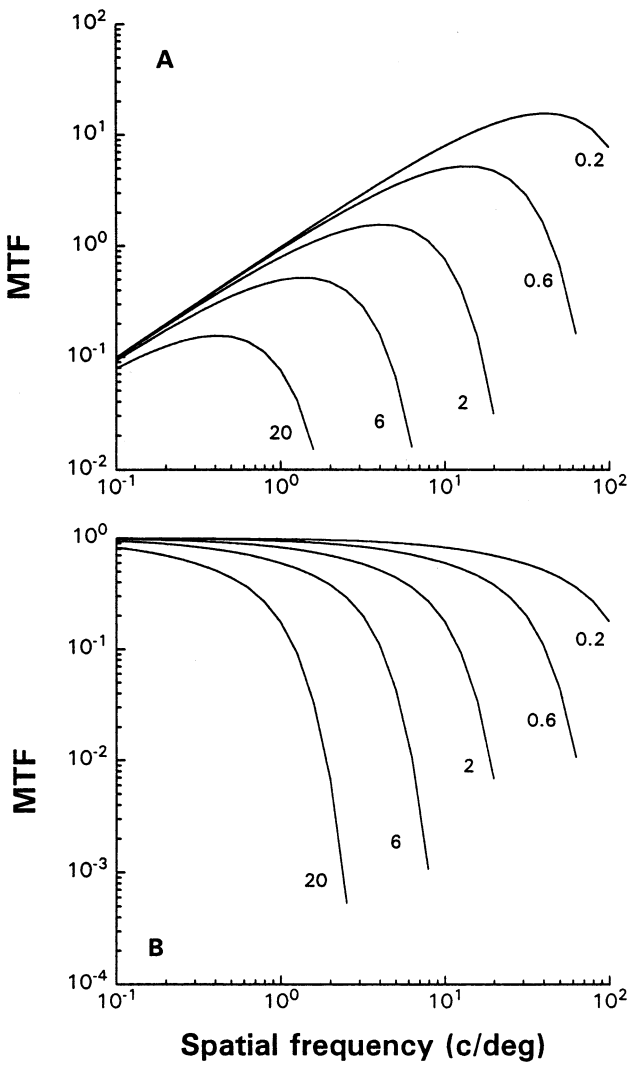

Fig. 5. (A) The MTFs of ganglion cells with spatiochromatic opponency for luminance-modulated gratings were calculated according to Eq. (A3) under the assumption that $b/r_0 = 2$. (B) The MTFs for equiluminous chromatic gratings were calculated according to Eq. (A10) under the assumption that $[w_c - w_s]/2 = \pi b/a$. The values of r_0 in min of arc are shown close to curves.

[5] If the unit of spatial frequency were c/rad or c/min of arc, then b would be expressed in rad or min and a would be $\pi/180$ rad or 60 min, respectively.

and thus the value of Eq. (A3) becomes approximately equal to $P_L(f) = (2\pi b/a)^{-1}(1 - 1 + 2\pi bf) = af$ for all receptive field surround sizes b.

The spatial frequency corresponding to the peak of MTF is determined by the RF size. As Fig. 5A, calculated according to Eq. (A3) under the assumption[6] that $b/r_0 = 2$ and $r_0 = 0.2$, 0.6, 2, 6, or 20 min of arc, shows, the MTF of the ganglion cell with the greatest centre radius starts to decrease first but the MTFs of smaller RFs still continue to rise as $P_L(f)$, which is in fact the envelope of the MTFs of ganglion cells. This view of ours about $P_L(f)$ is in complete agreement with the experimental finding that $I_c = I_0 f^2$ up to the resolution limit irrespective of visual field location (Rovamo et al., 1995), which implies that $P_L(f)$ is the same at all eccentricities. The radius of 0.2 min of arc for the smallest RF centre corresponds (Kaplan et al., 1990) to the cone diameter of 0.4 min of arc, which is 90% (Stacey & Pask, 1997) of the average of the foveal cone separations reported by Poylak (1957) and Liang, Williams & Miller (1997): 1.78 and 2.6 μm equivalent to 0.367 and 0.536 min of arc in the schematic eye with a nodal distance of 16.7 mm, where 1° is equal to 291 μm. Thus, Fig. 5A is in agreement with our experimental finding that I_c is proportional to the spatial frequency squared in the fovea at all spatial frequencies (0.125–30 c/deg) studied (Rovamo et al., 1994b).

A.2. The PSF of the RF surround with an exponential MTF

The PSF of the radially symmetric RF surround corresponding to the MTF of Eq. (A1) can be calculated by means of an inverse Hankel (i.e. radially symmetric Fourier) transform (Bracewell, 1986). It becomes the following:

$$z_s(r) = (4\pi^2 b^3/a)^{-1}(1 + (r/b)^2)^{-3/2}, \quad \text{(A5)}$$

where r refers to the radial distance from the receptive field centre.In addition, we found that for $0 < r < 2b$ Eq. (A5) can be quite accurately approximated by the following:

$$z'_s(r) = (4\pi^2 b^3/a)^{-1} \exp[-(r/r_a)^2], \quad \text{(A6)}$$

where r_a is $1.15b$. At about $r = 2b$, $z_s(r)$ has already decreased below one tenth of its maximum. Hence, it is difficult in practice to discriminate whether the PSF of the RF surround obeys (A5) or (A6), as the main difference between surrounds with Gaussian and exponential MTFs is in the outskirts of the response function.

[6] The exact value of b/r_0 is not critical: any value within $1 \leq b/r_0 \leq 3$ would produce graphs very similar to those in Fig. 5A.

A.3. The MTF of the composite RF with a spatiochromatic opponency

The MTF of a spatiochromatically opponent RF with a Gaussian MTF at the centre and exponential MTF in the surround is the following:

$$P(f) = w_c Z_c(f) - w_s Z_s(f), \quad \text{(A7)}$$

where weights depend on the types of cones in the RF centre and surround as well as on the wavelength composition of the grating stimulus. Eq. (A7) can be rearranged (Ingling & Martinez-Uerigas, 1983; Lennie & D'Zmura, 1988; Rohaly & Buschbaum, 1988; Kelly, 1989) to be a sum of two components as follows:

$$P(f) = [w_c - w_s][Z_c(f) + Z_s(f)]/2 + [w_c + w_s][Z_c(f) - Z_s(f)]/2 \quad \text{(A8)}$$

For an achromatic luminance-modulated grating it is reasonable to assume that the weights of the centre and surround are close to equal, i.e. RF is balanced. Hence, the MTF of the chromatically opponent RF for a luminance modulated grating can be approximated as

$$P_L(f) = [w_c + w_s][Z_c(f) - Z_s(f)]/2. \quad \text{(A9)}$$

Under the assumption that $[w_c + w_s]/2$ is close to unity, i.e. $w_c = w_s = 1$, Eq. (A9) can be approximated by Eq. (A3), i.e. $P_L(f) = af$.

For an equiluminous chromatic grating it is reasonable to assume that the weights of the centre and surround are again close to equal in magnitude but have an opposite sign as the chromatic component gratings are in opposite phase. Hence, the MTF of the chromatically opponent RF for a colour modulated grating can be approximated as

$$P_C(f) = [w_c - w_s][Z_c(f) + Z_s(f)]/2. \quad \text{(A10)}$$

As explained in the context of Eq. (3), $\exp[-(\pi r_0 f)^2]$ is approximately equal to unity while $\exp(-2\pi bf)$ can be approximated by $1 - 2\pi bf$ at spatial frequencies below the maximum of MTF. Hence, the sum $Z_c(f) + Z_s(f)$ is approximately equal to $(2\pi b/a)^{-1}(1 + 1 - 2\pi bf)$, which is approximately equal to $(\pi b/a)^{-1}$, i.e. constant at low spatial frequencies. Under the assumption that $[w_c - w_s]/2$ is close to $(\pi b/a)$, i.e. $w_c = -w_s = (\pi b/a)$, $P_C(f) = 1$.

As Fig. 5B, calculated according to Eq. (A10) under the assumption that $b = 2r_0$ and $r_0 = 0.2$, 0.6, 2, 6, or 20 min of arc, shows, the MTF of ganglion cell with the greatest centre radius starts to decrease first but the MTFs of smaller RFs still continue as $P_C(f) = 1$, which is in fact the envelope of the MTFs of ganglion cells. This view of ours about $P_C(f)$ is in complete agreement with the experimental finding that for chromatic equiluminous gratings $I_c = 165$ phot. td at all spatial frequencies studied (Kankaanpää et al., 1996), which implies that $P_C(f)$ is constant irrespective of spatial frequency.

Appendix B

B.1. Modelling contrast sensitivity as a function of retinal illuminance

Assuming that the limiting factor for the detection of a signal is the signal-to-noise ratio (R) calculated here as the signal contrast divided by the square root of the sum of the variances of the two independent sources of noise, we get

$$R = c_{th}/(N_i + N_q)^{0.5}, \quad \text{(B1)}$$

where c_{th} is the external contrast of the signal at detection threshold, and N_i and N_q are the external (or equivalent; Pelli, 1990) spectral densities of neural and quantal noises, respectively. N_i is assumed to be independent of light level. The spectral density of effective quantal noise is inversely proportional to retinal illuminance (e.g. Pelli, 1990; Rovamo et al., 1994a). Thus,

$$N_q = K/I. \quad \text{(B2)}$$

By substituting c_{th} by $1/S$, where S is contrast sensitivity, and applying elementary algebra to Eq. (B1) we get

$$S^{-1} = (RN_i^{0.5})(1 + N_q/N_i)^{0.5}. \quad \text{(B3)}$$

By substituting Eq. (B2) to Eq. (B3) solved for S and by replacing $(RN_i^{0.5})^{-1}$ by S_{max} and K/N_i by I_c, we get Eq. (1).

B.2. Modelling the dependence of I_c on spatial frequency for luminance-modulated gratings

If we want to compare external effective quantal noise (N_q) and neural noise inside the brain (N_i') properly, the comparison have to take place at the same location in the human visual system. Hence, we have to transfer quantal noise through the MTFs of ocular optics and neural visual pathways into the brain. Individual light quanta cannot be blurred by the optical point spread function, and hence, quantal noise is unaffected by ocular optics. In other words, optical blur does not introduce correlations among neighbouring points, and therefore, it does not attenuate high spatial frequencies in the quantal noise (Graham & Hood, 1992), although blur is known to redistribute light so that high spatial frequencies (f) in the image are attenuated more than low frequencies. On the other hand, at the event of quantal absorption, quantal noise is transformed into neural noise and is therefore filtered by the MTF of neural visual pathways. According to our model of human spatial vision (Rovamo et al., 1994a) the MTF for achromatic and monochromatic gratings is $P_L(f) = af$, where $a = 1°$. Hence, the spectral density of quantal noise inside the brain is

$$N_q' = P_L(f)N_q = N_q f^2. \quad \text{(B4)}$$

Comparison of Eqs. (1) and (B3) reveals the first equivalence in Eq. (B5):

$$I_c/I = N_q/N_i = N_q'/N_i', \quad \text{(B5)}$$

The second equivalence is just reflecting the fact that it does not matter where (at the cornea or inside the brain) we compare quantal and neural noises provided that we compare them at the same location. By solving Eq. (B5) for I_c and substituting Eqs. (B2) and (B4) we get the following:

$$I_c = N_q' I/N_i' = Kf^2/N_i' = I_0 f^2, \quad \text{(B6)}$$

where $I_0 = K/N_i'$. Eq. (B6) means that I_c is proportional to spatial frequency squared for monochromatic and achromatic gratings.

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