Ganglion cells in the peripheral retina have lower density and larger receptive fields than in the fovea. Consequently, the visual signals relayed from the periphery have substantially lower resolution than those relayed by the fovea. The information contained in peripheral ganglion cell responses can be quantified by how well they predict the foveal ganglion cell responses to the same stimulus. We constructed a model of human ganglion cell outputs by combining existing measurements of the optical transfer function with the receptive field properties and sampling densities of midget (P) ganglion cells. We then simulated a spatial population of P-cell responses to image patches sampled from a large collection of luminance-calibrated natural images. Finally, we characterized the population response to each image patch, at each eccentricity, with two parameters of the spatial power spectrum of the responses: the average response contrast (standard deviation of the response patch) and the falloff in power with spatial frequency. The primary finding is that the optimal estimate of response contrast in the fovea is dependent on both the response contrast and the steepness of the falloff observed in the periphery. Humans could exploit this information when decoding peripheral signals to estimate contrasts, estimate blur levels, or select the most informative locations for saccadic eye movements.

Keywords: natural scene statistics, spatial vision, peripheral vision, retinal ganglion cells, contrast perception


Introduction

The retina is a major bottleneck of the primate visual system. The needs for a wide field of view and for resolving objects at large distances must be balanced against constraints on neuronal resources. The resulting evolutionary compromise is a high-resolution fovea, a larger, less densely sampled periphery, and a ballistic eye movement system capable of quickly deploying the fovea to points of interest within the visual scene. One consequence of this solution is that stable environmental properties give rise to neural signals that vary in quality with the direction of gaze. When the eyes move, objects in the world project to different retinal locations that encode the images of the objects with neural populations having different spatial resolution. The further in the periphery an image patch falls, the more information is lost due to increased spatial summation and decreased spatial sampling. However, the amount of information lost depends not only on the summation and sampling at a given retinal location but also on the statistical properties of the images being encoded. For example, if natural images varied smoothly in luminance (had no high-frequency content), then little information would be lost by increasing summation and decreasing sampling. Alternatively, if natural images were composed predominantly of high frequencies, then most of the information would be lost in the periphery. In the former case, the peripheral image is a good predictor of the foveal image, whereas in the latter case it is very poor. Since natural images fall between these extremes, it is an empirical question how well the foveal images can be predicted from the information available in the periphery.

Many natural tasks require interpreting signals in the peripheral retina. If peripheral images do contain statistically reliable information about foveal images, then it is possible that the human visual system exploits this...
information. Indeed, given that the environment tends to be stable over the short time intervals between fixations, every successive pair of fixations provides a readily available and potentially useful learning signal for relating peripheral and foveal images.

The aim of the current study was to better understand the information available in the output of the peripheral retina in natural environments. The approach was to analyze the responses of a simple model of the primate retina to natural images. The model is based on existing measurements of the optical quality of the human eye, the density of human retinal ganglion cells, and the response properties of macaque ganglion cells, all as a function of retinal eccentricity. The information available in the peripheral retina was measured by determining how accurately an ideal Bayesian observer can predict the foveal encoding of natural image patches from their encodings at peripheral locations. In principle, this approach can be applied to arbitrary properties of the retinal encoding. The relevant properties to consider will generally depend on the perceptual task. Here, we focus on the local power spectrum of the retinal outputs, which is particularly relevant to tasks such as contrast and blur/sharpness estimation in the periphery. In other words, we ask how accurately the local power spectrum of the foveal representation can be predicted from the local power spectrum of the peripheral representation (of the same image patch) at various retinal eccentricities.

Methods

To determine the ideal observer’s prediction accuracy, it is necessary to estimate the posterior probability distribution over the space of foveal power spectra, for any given observed peripheral power spectrum. To measure this posterior probability distribution, we processed 1000 luminance-calibrated natural images through a simple retinal model evaluated at each of 5 different retinal eccentricities between 0° and 15°. We then extracted 1040 patches tiling the mosaic of model ganglion cell responses to each image, for each retinal eccentricity. The power spectra of these samples were used to estimate the posterior probability distributions.

The image set consisted of outdoor scenes collected in the Austin area with a Nikon D700 camera calibrated using a previously published procedure (Ing, Wilson, & Geisler, 2010). There were no man-made objects in the scenes, and the exposure was set to minimize clipping. The 14-bit images were converted to linear 8-bit gray scale. For more details on the image set, see Geisler and Perry (in press). The analysis reported here was also performed on images from another data set (van Hateren & van der Schaaf, 1998) and similar results were obtained.

Simple model of ganglion cell responses

To account for overall light adaptation, each calibrated image was first normalized by its mean luminance (Figure 1c). The optical properties of the eye were modeled using the modulation transfer functions (MTFs) of the human eye measured by Navarro, Artal, and Williams (1993). Figure 1a shows the MTFs for several different retinal eccentricities as specified by the formula published in Navarro et al. (see Appendix A). The neuronal properties of the model were estimated from data in the literature. The spacing between the ganglion receptive fields was based on midget ganglion cell densities measured in humans by Curcio and Allen (1990); the density expressed in on-center cells per degree is shown by the blue curve in Figure 1b (the density of off-center cells is assumed to be the same). The ganglion cell receptive fields were modeled as difference-of-Gaussian functions (DoGs) with shape properties based on the measurements of parvo cells (P cells) taken in the macaque LGN by Croner and Kaplan (1995). We focused on P cells because of their dominant role in spatial pattern vision (Merigan & Maunsell, 1993). Croner and Kaplan found that the width parameter of the surround was approximately six times larger than the center and the surround strength as approximately 55% of the center. This surround strength was based on responses to sinewave gratings drifting at 4 Hz. At lower drift rates, surround strength is likely to be greater; therefore, we also tested greater surround strengths. Very similar results were obtained but are not reported here. The center size was taken to be one cone diameter in the fovea and scaled in proportion to the ganglion cell spacing. (Note that the effective center size is larger than one cone diameter in the fovea because of the effect of the optical MTF.) Examples of the receptive fields (excluding the effects of the optical MTF) are shown by the red curves in Figure 1b.

The RMS amplitude of a signal (in this case, the standard deviation of the responses of a windowed patch of ganglion cells) can be directly related to the integral of the power spectrum of that same signal through Parseval’s theorem (Bracewell, 1978) and is therefore directly related to $\alpha$ and $\beta$. Here, we define the standard deviation of the windowed responses to be the “response contrast” $c$. (Note that the response contrast is not restricted to the range 0–1.) Thus, using any two parameters out of the three ($\alpha$, $\beta$, $c$) serves as a complete description of the power spectrum. Here, we used the response contrast ($c$) in lieu of $\alpha$ because it is a more intuitive property of the signal and is less correlated with the exponent $\beta$.

Estimation of posterior

The center of the fovea is the source of the best visual information to the brain. Thus, the posterior probability
distributions of interest are the joint probability distributions over foveal pairs, denoted as \((c_0, \beta_0)\), given each particular observed peripheral pair \((c, \beta)\) at an eccentricity \(e\) of interest: 

\[ P(c_0, \beta_0|c, \beta) = P(c, \beta|c_0, \beta_0)P(c_0, \beta_0) \frac{1}{K}, \]  

(1)

where \(K\) is the constant required for the posterior probabilities to sum to 1.0. First, we binned the foveal power spectra into quantiles containing approximately 1000 spectra, using a kd-tree algorithm (Press, Teukolsky, Vetterling, & Flannery, 2007) by recursively splitting at the median of the subcells’ data along alternating dimensions. These quantiles provide an approximation of the prior probability distribution, \(P(c_0, \beta_0)\), over the foveal power spectra. Next, we estimated the likelihood distributions, \(P(c, \beta|c_0, \beta_0)\). Note that each of the 1000 foveal power spectra falling within one of the discrete quantile bins maps onto a specific power spectrum \((c, \beta)\) at eccentricity \(e\). We fitted this sample of 1000 contrast and slope pairs at eccentricity \(e\) with a Gaussian distribution and used this Gaussian as the estimate of \(P(c, \beta|c_0, \beta_0)\). These estimated prior and likelihood distributions were combined using Equation 1 to obtain the estimated posterior distributions.

**Results**

After fitting the power spectra (as shown in Figure 2) to each of the 1,040,000 filtered image patches, we formed histograms of the values of \(c\) and \(\beta\) for each eccentricity. These histograms are plotted in Figure 3 for several eccentricities. The figure shows that the primary change with eccentricity is in the distribution of the slope parameter \(\beta\) indicated by the horizontal shift of the distributions. On the other hand, the distribution of
response contrast, indicated by the vertical position, remains relatively constant. This shows that despite the removal of high spatial frequencies due to spatial summation by the peripheral ganglion cells, the simultaneous reduction in the spatial sampling rate of the ganglion cells tends to preserve the average variation of the responses within the image patch (i.e., the response contrast).

Since these distributions reflect the statistics of ganglion cell responses to a large population of natural images, they capture the full range of cortical inputs. Thus, these distributions represent the baseline probability of a ganglion cell response to an unknown image. The visual system could, in principle, improve its estimate of a peripheral image patch by learning the statistical relationship between the signals generated by the same image patches presented to the periphery and the fovea. Here, we measured that statistical relationship.

As described in the Methods section, the first step was to estimate the prior probability distribution of $c$ and $\beta$ in the fovea, $P(c_0, \beta_0)$, by quantile binning. The resulting distribution is shown in Figure 4 (note that this is the same data as in Figure 3a replotted with quantile binning). The

response contrasts vary from approximately 0.02 to 20, and the spectral falloff parameter varies from approximately 0.2 to 0.45.

The second step is to estimate the likelihood distributions (i.e., the probability distribution of power spectra at each eccentricity given a power spectrum in the fovea). As described in the Methods section, we did this by analyzing how the 1000 power spectra in each bin of the estimated prior distribution (Figure 4) change when the same image patches are encoded at a peripheral location. Figure 5b shows the likelihood distributions for the four colored bins indicated in Figure 5a. The symbols in Figure 5b show the samples (a small fraction of the 1000 samples) and the solid curves show the 95% confidence ellipses of the fitted Gaussian functions (the slight distortion of the ellipses is due to the logarithmic axes).

The figure shows that the distributions become broader with increasing eccentricity. It also demonstrates that changes in the foveal falloff parameter $\beta_0$ do not correspond to large changes in the peripheral likelihood distributions. For example, the cyan and blue bins map to highly overlapping distributions at all eccentricities. This means that little information about $\beta_0$ is carried by the peripheral power spectrum. On the other hand, differences in the foveal response contrast $c_0$ are preserved in the likelihood distributions, although the separation diminishes with eccentricity. Finally, the distributions tilt as eccentricity increases. This means that knowledge of the falloff parameter of the peripheral power spectrum $\beta_2$ is informative about the contrast of the corresponding foveal power spectrum. For example, in Figure 5b, the patches indicated by the arrows have an equal observed response contrast but different falloff values. Clearly, the point indicated by the left arrow is more likely to have come from the cyan bin than from the red bin. Thus, the falloff steepness of the spatial power spectrum of a small patch of peripheral ganglion cell responses is informative about the response contrast that the same small image patch would generate had it been projected to the fovea. Further, this becomes more relevant at greater eccentricities.

Having computed the likelihood distributions, the posterior distributions can now be calculated using Equation 1. Of particular interest are the mean values of the posterior distributions, because they correspond to the optimal minimum mean squared error (MMSE) estimates of the foveal values ($c_{opt}, \beta_{opt}$), given observed peripheral values ($c_i, \beta_i$). Figure 6 illustrates the systematic behavior of the means of the posterior distributions. In each panel, the points on the right represent a regular grid spanning the distribution of ($c_{opt}, \beta_{opt}$) values. For each grid point, the mean of the posterior distribution is indicated by the corresponding point on the left side of the panel (marked with a solid line). There are two obvious trends visible in the plots. First, for any given peripheral response contrast, the optimal estimate of foveal response contrast is, on average, approximately constant. Specifically, the average orientation of the solid lines for any
given peripheral response contrast is approximately horizontal. Second, for any given peripheral response contrast, the optimal estimate of foveal response contrast varies systematically with the falloff parameter $\beta_e$, especially at larger eccentricities. Specifically, the optimal estimate of foveal response contrast tends to decrease as the magnitude of $\beta_e$ increases (this is related to the tilt of the likelihood distributions in Figure 5). These two trends are illustrated more fully in Figure 7a, which plots the optimal estimate of foveal response contrast for a large set of image patches randomly sampled at 15° eccentricity.

Interestingly, the trends between the optimal estimate of the foveal falloff ($\beta_{opt}$) and the peripheral values ($c_e, \beta_e$) are much weaker. This may be related to the observation...
that the variation in the peripheral falloff is much greater than in the foveal falloff. The weaker trends are illustrated in Figure 7b, which plots the optimal estimate of foveal falloff for image patches randomly sampled at 15° eccentricity. The estimated falloff increases with observed contrast from about 0.3 to 0.35, and there is an even weaker effect of the observed falloff. We conclude that a rational strategy for estimating the foveal power spectrum from a peripherally encoded power spectrum is to take into account both the peripheral response contrast and the falloff in estimating the foveal response contrast but only take into account the peripheral response contrast in estimating the foveal falloff. Given this conclusion, we attempted to find a descriptive function that summarizes the relationship between the peripheral response contrast and falloff values.

Figure 5. Projection of likelihood distributions at various eccentricities. (a) An overhead view of the binned distribution in Figure 4. The colored bins indicated by arrows are the foveal values that project to the corresponding distributions in the other plots. (b) The grayscale histograms are the same as Figure 3 and plotted for reference. The scatters of colored points are the parameters fit to the power spectra at the peripheral eccentricity for the same patches that had foveal values contained within the similarly colored bin in (a). For ease of visualization, only a random 5% of the data in each bin is plotted. The solid curves show 95% confidence intervals for the Gaussian fit to the scatters. The arrows in (b) show an example where two patches, with an equivalent measured response contrast at 15°, are clearly likely to have come from substantially different foveal response contrasts based solely on the peripherally measured falloff in the power spectrum.

Figure 6. Peripheral measurements mapped to MMSE posterior estimates. These plots show the mapping from a measured peripheral power spectrum to the mean of the posterior distribution over foveal power spectra. The gray distributions are the same as in Figure 3 and are plotted for reference. The distribution to the left is the foveal distribution, while the distribution on the right corresponds to the eccentricity indicated in the corner. The lines show the mapping from the peripheral power spectrum (point on the right) to the mean of the posterior distribution (point on the left). The fanning out of these lines shows the effect of peripheral falloff on estimated foveal response contrast.
and the optimal estimate of the foveal response contrast. At a given eccentricity, we found that the log of the optimal estimate of foveal contrast was approximately a linear function of the falloff and of the log of the peripheral contrast. More precisely, we found that the mapping was well described by the following equation:

\[
\ln(\hat{c}_{\text{opt}}) = f(e)\beta_e + k\ln(c_e) + g(e),
\]

where \( f \) is a hyperbolic function of eccentricity, \( g \) is a quadratic function of eccentricity, and \( k \) is a constant. The full six-parameter function, as well as the fitted parameter values, is given in Appendix A.

Our most surprising finding is that the optimal estimate of foveal response contrast depends on the falloff of the power spectrum measured in the periphery. Although the finding is clear, an obvious question is whether taking into account the falloff significantly increases the accuracy of the foveal response contrast estimates.

To address this question, we computed the optimal (MMSE) estimate of the foveal contrast for a random sample of 1000 patches using both parameters of the peripheral power spectrum and using only the peripheral response contrast. We then calculated the error between the actual foveal response contrast and the predicted foveal response contrasts, for each of the 1000 patches at each eccentricity. Figure 8 plots the average percent error of the predicted response contrast for the two cases. The percent error using both response contrast and falloff is shown by the red line (the dashed line is the performance of the summary function in Equation 2), while the error using response contrast alone is shown by the blue line. Clearly, knowledge of peripheral beta improves the estimate of foveal response contrast, and the improvement increases with eccentricity (e.g., at an eccentricity of 15°, use of peripheral falloff reduces the average percent error from 19% to 10%).

Exploiting the peripherally measured falloff not only shifts (improves) the estimate of foveal contrast but reduces the variance of the posterior distribution. This is illustrated in Figure 7a.

Figure 7. Relationship between observed and predicted spectra. (a) This plot shows the systematic relationship between the two parameters of power spectra observed at 15° in the periphery and the corresponding MMSE estimate of foveal response contrast. The unity line is plotted for reference. Data falling along the unity line would suggest that foveal contrast is perfectly predicted by peripheral contrast. The systematic deviations from unity indicate that the observed peripheral falloff is informative about foveal response contrast. (b) This plot shows the relationship between the two parameters of power spectra observed at 15° in the periphery and the corresponding MMSE estimate of foveal falloff. The slight upward trend with contrast is to be expected from the slight correlation between contrast and falloff seen in Figure 5a.

Figure 8. Accuracy with and without falloff. This plot shows the average percent error in predicted response contrast when using only response contrast, response contrast plus the falloff, and the summary model provided in Equation 2. Clearly, taking the falloff into account provides a substantial improvement.
in Figure 9, which plots the posterior distribution of foveal response contrast for typical patches at 15° eccentricity. Again, the blue bars show the posterior distribution based on using only peripheral response contrast, while the red bars show the posterior distribution based on both peripheral response contrast and falloff. Both red distributions are significantly shifted, while the distribution in Figure 9b is also substantially narrower. On average, at 15° eccentricity, the standard deviation of the posterior distribution over foveal response contrasts is reduced by about 15% when the peripheral falloff is taken into account.

Discussion

Natural images have many statistical regularities (Geisler, 2008; Simoncelli & Olshausen, 2001). In this study, we investigated how these statistical regularities might be exploited by the visual system to better interpret ganglion cell responses in the periphery. Specifically, we processed a large set of calibrated natural images through a simple model of the midget ganglion cells (P cells) in the human visual system and then analyzed the responses. The model combined existing measurements of (i) the optical quality of the human eye, (ii) the sampling density of human midget ganglion cells, and (iii) the receptive field parameters of P cells in the primate. Using this model, we simulated the responses of the retina to the same natural image patches (~10⁶ patches of width 2°) presented at various retinal eccentricities.

We found that the spatial power spectra of the responses (excluding the value at a spatial frequency of zero, i.e., the mean response) were accurately summarized by a two-parameter exponential function. One parameter was the response contrast (the standard deviation of the P-cell responses within the patch) and the other was the rate of falloff in response amplitude as a function of spatial frequency. Thus, for each patch, at each retinal eccentricity, the responses of the P-cell population under the patch were summarized with these two parameter values.

Given these ~10⁶ pairs of parameter values for each retinal eccentricity, we then asked the following question: Given the observed neural responses to a stimulus presented in the periphery, how accurately could the brain predict what the neural responses would be to that stimulus if it were presented in the fovea? In other words, we asked how accurately one can predict the pair of parameter values in the fovea from the pair of values observed in the periphery. Obviously, the more accurate the prediction, the less uncertainty there is about the peripheral stimulus, and the less the need to fixate the peripheral stimulus (Raj, Geisler, Frazor, & Bovik, 2005).

To address this question, we first characterized the probability distributions of the parameter values and then used those distributions to determine the Bayes’ optimal (MMSE) estimates of foveal parameters given observed peripheral parameters. We found that the optimal estimate of the response contrast in the fovea was dependent on both the response contrast and the falloff observed in the periphery and that the optimal estimate of the falloff in the fovea was weakly dependent on the response contrast observed in the periphery and largely independent of the falloff observed in the periphery.

Some aspects of the results are not surprising. For example, it is not surprising that higher response contrast in the periphery is predictive of higher response contrast in the fovea. A bit more surprising is that, on average, the response contrast observed in the periphery is similar to that observed in the fovea. Presumably, this is because the increase in receptive field size with eccentricity is matched by a corresponding increase in receptive field spacing. Given that natural images are approximately scale invariant (Field, 1987; van Hateren & van der Schaaf, 1998), holding the ratio of receptive field size to receptive field spacing fixed should give statistically similar responses. In other words, shifting a stimulus into the periphery is approximately analogous to moving the stimulus further away in the fovea.

Perhaps the most surprising result is that the optimal estimate of foveal response contrast is strongly dependent on the falloff observed in the periphery. Specifically, for the same peripheral response contrast, the steeper the peripheral falloff, the less the expected foveal response contrast. The most likely hypothesis is that those peripheral input image patches producing a steeper falloff are dominated by low spatial frequency content, and image patches dominated by low-frequency content should be less attenuated by spatial summation in the periphery. In fact, for sufficiently low-frequency image patches, one would expect response contrast to increase in the periphery due to the decreased sampling rate and better match of the receptive size to the low-frequency content. We verified this intuition by inspecting a large number of randomly sampled patches having the same peripheral response contrast but different falloff (e.g., see Figure 10). Patches with steeper falloff tend to contain large relatively uniform subregions or tend to be defocused to a noticeable degree.

In this study, we focused on how well the neural responses to a foveal stimulus can be predicted from the responses to that stimulus when it is presented in the periphery. We chose to address this question because it is the relationship between these responses that would be most easily learned by the visual system. Specifically, across the timespan of a saccade, the visual scene is, on average, very stable, and thus, the statistical relationship between responses to the same stimulus at different eccentricities could be learned via a mechanism that compares the responses from the same scene location before and after an eye movement.

On the other hand, a perhaps more natural question might be how well the retinal image itself can be predicted from the responses of the peripheral retina. However, it is intuitively plausible that the statistics
relevant for predicting the retinal image are closely related to those for predicting the foveal responses. To test this intuition, we computed the correlation between the foveal response contrast and retinal image contrast and between the foveal response falloff parameter and the image falloff parameter and found both correlations to be very high, $r = 0.99$ and $r = 0.88$, respectively. In other words, it appears that learning to optimally estimate the retinal image in the periphery can be accomplished in large part by learning to optimally estimate what would be the foveal responses to the peripheral retinal image.

It should be possible to test whether the human visual system exploits the statistical relationships shown in Figures 6 and 7. The most direct test would be to measure points of subjective equality (PSE) for the same natural image patches presented in the fovea and periphery by varying the contrast of the foveal patch. If the observers are using knowledge of the natural image statistics, they should judge a foveal and peripheral test patch to match in contrast when the observed foveal response contrast matches the foveal contrast predicted by the peripheral observation. As implied by Figures 8 and 9, the predictions for PSE differ substantially depending on whether humans base their estimates on only the peripheral response contrast or on both the peripheral falloff and response contrast. Note that in the latter case their estimates are expected to be more veridical. If observers are not using knowledge of image statistics at all, then they might judge the patches to match when the response contrasts match, which would make yet different predictions.

Although there have been no systematic studies of contrast matching between natural image patches in the fovea and periphery, there have been a number of studies using simpler stimuli. Georgeson and Sullivan (1975) found a substantial degree of contrast constancy for sinewave gratings as a function of retinal eccentricity. Georgeson (1991) found evidence for overconstancy (a tendency to perceive the contrast of the peripheral stimulus as somewhat greater), for spatial frequencies above 3 cpd. More recently, Galvin, O’Shea, Squire, and Govan (1997) found evidence for sharpness overconstancy in the periphery for Gaussian-blurred edge stimuli. An obvious question is whether optimal decoding of peripheral ganglion cell responses to natural image patches might explain some of these results. We found that, in fact, it was not possible to generate predictions for these experiments. Sinewave stimuli do not produce a ganglion cell response power spectrum anything like that of a natural image patch. Specifically, the power spectra cannot be described by response contrast and falloff parameters, because there is no meaningful falloff parameter for a single sinewave. On the other hand, the power spectra of ganglion cell responses to Gaussian-blurred edge stimuli are well described by response contrast and falloff parameters. However, the parameters fall well outside the range produced by our natural images, and hence, the only possible predictions involve

Figure 9. Variability with and without falloff. This plot shows some examples of the variability that can be expected in the posterior distribution for a particular response contrast and falloff at 15°. The blue bars show the posterior distribution over contrasts estimated using only the contrast of the peripheral power spectrum. The red bars show the posterior distribution over contrasts estimated using both the contrast and the falloff of the peripheral power spectrum. (a) An example where the variability remains roughly constant, but conditioning on only the response contrast introduces a significant bias in the posterior estimate of foveal response contrast. (b) An example where conditioning on only the response contrast introduces a bias and reduces the precision of the posterior estimate. Both of these examples have the same peripheral response contrast.
extrapolation to parts of the parameter space where we have no data.

This is an important result because it demonstrates that laboratory stimuli can easily fall outside the natural range of stimulus parameters. It is likely that circuits in the visual system are matched to the natural parameter ranges, and thus, it is crucial to measure the relevant natural image statistics and to test with at least some stimuli that fall within the natural parameter ranges (Barlow, 1961).

Of course, testing with stimuli outside the natural ranges can be valuable for testing hypotheses about the underlying mechanisms, but the results could be misleading about mechanism if they are considered in isolation. For example, it is possible that contrast and sharpness overconstancy may be reduced (better constancy holds) for natural or artificial stimuli having response contrast and falloff parameters within the normal range for natural images. These important experiments are an obvious next step.

**Appendix A**

**Modulation transfer measured by Navarro et al.**

The following function can be found in Navarro et al. (1993) under Table 2. It is worth noting that the parameters used were for the radial profile, not the upper or lower bounds:

\[
M = (1 - c_1 + c_2) e^{-a_1 f e^{b_1 e}} + (c_1 - c_2) e^{-b_1 f e^{b_2 e}},
\]

\[
\begin{align*}
a_1 &= 0.1743 \\
a_2 &= 0.0392 \\
b_1 &= 0.0362 \\
b_2 &= 0.0172 \\
c_1 &= 0.215 \\
c_2 &= 0.00294
\end{align*}
\]  

\[
\text{(A1)}
\]

**Detailed explanation of the summary function in Equation 2**

Equation 2 shows a summary of an equation fit to the data describing the behavior of the optimal estimate of foveal response contrast as a function of the given peripheral slope, response contrast, and eccentricity. The summary describes this relationship with six fit parameters.

One parameter, \( k \), was used to describe the strong relationship between an observed peripheral response contrast and an estimated foveal response contrast. Two parameters were used to describe the changing impact on the estimated foveal contrast of the measured peripheral slope with eccentricity:

\[
f(e) = \left( \frac{1}{(e+f_1)} \right) - f_2.
\]

Three parameters were used to capture the effect of eccentricity on the prior over response contrast:

\[
g(e) = -g_1 e^2 + g_2 e - g_3.
\]

Thus, Equation 2 can be rewritten as

\[
\ln(c_{opt}) = \left( \frac{1}{(e+f_1)} \right) - f_2 \beta e + k \ln(c_e) - g_1 e^2 + g_2 e - g_3,
\]

where

\[
\begin{align*}
f_1 &= 0.2877 \\
f_2 &= 0.5559 \\
k &= 0.9524 \\
g_1 &= 0.0010 \\
g_2 &= 0.1049 \\
g_3 &= 0.2680
\end{align*}
\]  

\[
\text{(A2)}
\]  

\[
\text{(A3)}
\]  

\[
\text{(A4)}
\]  

\[
\text{(A5)}
\]  

\[
\text{(A6)}
\]
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