

Gain, noise, and contrast sensitivity of linear visual neurons

ANDREW B. WATSON

Vision Group, NASA Ames Research Center, Moffett Field

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Abstract

Contrast sensitivity is a measure of the ability of an observer to detect contrast signals of particular spatial and temporal frequencies. A formal definition of contrast sensitivity that can be applied to individual linear visual neurons is derived. A neuron is modeled by a contrast transfer function and its modulus, contrast gain, and by a noise power spectrum. The distributions of neural responses to signal and blank presentations are derived, and from these, a definition of contrast sensitivity is obtained. This formal definition may be used to relate the sensitivities of various populations of neurons, and to relate the sensitivities of neurons to that of the behaving animal.

Keywords: Contrast sensitivity, Maintained discharge, Noise, Signal detection theory, Linear systems, Power spectrum

Introduction

One of the fundamental goals of vision science is to relate the performance of the human observer to the behavior of visual neurons. Performance has many dimensions, but one of great importance is the capability to signal luminance contrast. Contrast sensitivity marks the border between blindness and sight, and is the necessary precursor to most other aspects of performance. It is therefore fitting that contrast sensitivity is a subject of intense psychophysical study. However, it is much more rarely the subject of electrophysiological experiments. Recordings from single visual neurons have traditionally examined only contrast gain, a measure of the spikes produced per unit contrast. Contrast sensitivity, on the other hand, is a measure of the ability to distinguish signal from noise. To provide a measure of contrast sensitivity, gain must be expressed relative to the noise in the output of the cell. One purpose of this paper is to provide a more precise formulation of the relationship between gain, noise, and contrast sensitivity of linear visual neurons.

Barlow and Levick (1969) first addressed the roles of gain and noise in determining sensitivity of retinal ganglion cells. More recently, a number of studies have directly measured contrast sensitivity of visual neurons, by estimating the contrast required to produce a response larger than the noise (Derrington & Lennie, 1982, 1984; Hawken & Parker, 1984; Troy, 1983*a, b*). A second goal of this paper is to set these experiments, which differed in various details, in a common theoretical context so that results may be more directly compared. This context also

suggests how these experiments might be made more efficient and complete.

The theoretical context is also designed to allow comparison of contrast sensitivities of neurons and of observers. This is an essential step towards the goal of explaining the sensitivity of the observer. Finally, the general theory may be applied to specific models of linear neurons, to examine how their sensitivity compares to that of actual neurons. In a later paper, these ideas will be applied to models of the linear cortical neuron.

Model of a stochastic linear neuron

Here we develop a simple model of a linear neuron whose response is perturbed by noise. The model has two parts: the deterministic spatiotemporal receptive field and the output noise.

Spatiotemporal receptive field

The *receptive field* $l(\mathbf{x}, t)$ describes the response at time t to an impulse of unit time-area-contrast product, located at $\mathbf{x} = (x, y)$. In practice, it is measured with pulses of small duration, area, and contrast, and normalized by the actual product. In this formulation, the spatial coordinate system is relative to the center of the receptive field. The expected response of the cell to an arbitrary signal $f(\mathbf{x}, t)$ is then

$$r(t) = \int \int_{-\infty}^{\infty} f(\mathbf{x}, t) l(\mathbf{x}, \tau - t) d\mathbf{x} d\tau. \quad (1)$$

A somewhat more convenient representation is the *impulse response*

$$h(\mathbf{x}, t) = l(-\mathbf{x}, -t), \quad (2)$$

Reprint requests to: Andrew B. Watson, MS 239-3, NASA Ames Research Center, Moffett Field, CA 94035, USA.

which allows us to express the cell response as

$$r(t) = h(\mathbf{x}, t) * f(\mathbf{x}, t)|_{\mathbf{x}=(0,0)} \quad (3)$$

where "*" indicates convolution over \mathbf{x}, t .

Neural responses in early vision may be either graded potentials or sequences of impulses. For simplicity, we will regard all responses as continuous functions. In the case of spike trains, the response is in units of impulses/second, and is to be regarded as a suitably smoothed measure of the instantaneous rate of discharge. Appendix 1 provides additional detail on the relation between a spike train and its smoothed counterpart.

The receptive field can also be characterized by the *transfer function*

$$H(\mathbf{u}, w) \leftrightarrow h(\mathbf{x}, t), \quad (4)$$

where the arrow indicates the Fourier transform* and where the variables \mathbf{u} and w represent spatial and temporal frequencies. It is useful to decompose the transfer function into *gain* and *phase* functions, i.e.

$$G(\mathbf{u}, w) = |H(\mathbf{u}, w)|, \quad (5)$$

$$P(\mathbf{u}, w) = \arg[H(\mathbf{u}, w)]. \quad (6)$$

For simplicity, we will occasionally omit the spatial-frequency argument \mathbf{u} from the contrast gain G . This is to be understood as the temporal contrast gain at a specific spatial frequency.

Noise

We represent the noise of a visual neuron as a stationary stochastic process $x(t)$ with *autocorrelation* function $n(t)$, which describes the degree of correlation between noise samples at time separation t . We assume that the noise is additive. This will certainly not be precisely true for all sources of noise (e.g. quantal fluctuations), but there is evidence that it is roughly true for the total output noise of ganglion cells in the presence of modest signals (Enroth-Cugell et al., 1983; Robson & Troy, 1987). It is a matter worthy of more extensive study.

The Fourier transform of the autocorrelation is the *power spectral density* (psd) $N(w)$. This describes the power per unit frequency bandwidth in the noise process. As we shall see, knowledge of the psd is essential to understanding contrast sensitivity.

Measurement of power spectral density

The variability of visual neural responses has been widely studied (Barlow & Levick, 1969; Dean, 1981; Frishman & Levine, 1983; Levine & Troy, 1986; MacGregor & Lewis, 1977;

*The definitions of the forward and inverse Fourier transforms used here are

$$F(w) = \int_{-\infty}^{\infty} f(t)e^{-i2\pi wt} dt,$$

$$f(t) = \int_{-\infty}^{\infty} F(w)e^{i2\pi wt} dt.$$

Multidimensional Fourier transforms are separable versions of this one-dimensional transform.

Rodieck, 1967; Tolhurst et al., 1981; Tolhurst et al., 1983), but spectral methods have been applied less frequently (Derrington & Lennie, 1982, 1984; Robson & Troy, 1987; Troy, 1983a, b). A typical method (Derrington & Lennie, 1982) of estimating the psd of a cell is to capture a set of K records, each of duration T seconds, of the maintained discharge. Each record is then multiplied, point by point, by a cosine function of some frequency, and added up, to compute a cosine coefficient at that frequency. The same is done for a sine coefficient. These two numbers are squared and added to yield an estimate of the psd at that frequency. The same result may be obtained by taking the Discrete Fourier Transform of the record, and extracting the squared magnitude at the desired frequency. The process is repeated for each of the records, and the average and standard deviation of the resulting psd estimates are computed.

To derive the statistical distribution of power estimates obtained in this way, we note that sine and cosine coefficients are each weighted sums of zero mean, approximately Gaussian random variables, and are thus themselves approximately Gaussian and zero mean. Because the phase of the noise component at each frequency is random, sine and cosine coefficients are independent. Time stationarity implies that the two coefficients have equal variance σ . In the limit of long measurement interval T (which is all we consider here), this variance is given by

$$\sigma^2 = \frac{1}{2} N(w_0). \quad (7)$$

The power z , computed as the sum of two independent zero-mean Gaussians, is therefore equal to σ^2 times a chi-square random variable with two degrees of freedom, and therefore has mean and variance

$$\mu_z = \sigma_z = 2\sigma^2 = N(w_0). \quad (8)$$

Additional details on this derivation are given in Appendix 2.

Amplitude vs. power

Above we have assumed that the experimenter has used the power z at a frequency as the basic measure. An alternative empirical measure that is often used is the amplitude y equal to the square root of power. This will have a Rayleigh density (Papoulis, 1965),

$$f_y(y) = \frac{y}{\sigma^2} \exp\left[\frac{-y^2}{2\sigma^2}\right] u(y), \quad (9)$$

where $u(\)$ is the unit step function. This has mean and standard deviation

$$\mu_y = \sqrt{\frac{\pi}{2}} \sigma = \frac{\sqrt{\pi}}{2} \sqrt{N(w)}, \quad (10)$$

$$\sigma_y = \sqrt{2 - \frac{\pi}{2}} \sigma = \frac{\sqrt{4 - \pi}}{2} \sqrt{N(w)}. \quad (11)$$

It is interesting that the mean of this distribution does not equal the square root of N , but rather is biased downwards by the factor 0.886. Thus, if the estimate is to be used directly, or averaged with other like estimates, one should either use the un-

biased estimator of power, or correct the amplitude estimate by the appropriate factor. Note also that the standard deviation is proportional to the mean:

$$\sigma_y = \sqrt{\frac{4 - \Pi}{\Pi}} \mu_y \approx 0.523 \mu_y. \quad (12)$$

The ratios of mean to standard deviation of the amplitude estimates reported by Derrington and Lennie (1982) and Troy (1983a) are very close to this number, suggesting that our assumptions about the noise process are reasonable.

An example of a study using an amplitude measure is Troy (1983a). The author has kindly provided his raw distributions of estimates of amplitude at eight frequencies. In Fig. 1, these have been fit with Rayleigh distributions according to a maximum-likelihood criterion. A goodness-of-fit test rejects (at the 0.05 level) the Rayleigh distribution in one out of the eight cases (42 Hz). The chi-square goodness-of-fit statistic and degrees of freedom are indicated in each panel.

From each fit, we estimate σ (indicated by "s=" in each panel) and $N(w)$, via eqn. (7). The psd estimated in this way is shown in Fig. 2.

How long should T be?

In estimating the power spectrum, one must decide on the length of the measurement interval T . There is a trade-off between the size of T and the number of estimates we make. For example, suppose we have a fixed total time available of KT seconds. By setting $K = 1$, we can devote this time to one long measurement interval. By setting $K > 1$, we can subdivide the interval into several shorter segments. How should K be set?

First we note that the statistic z , on which we base our estimate of the psd, has a variance which does not depend on T ! This rather remarkable fact leads us to ask where the extra information derived from extending T is going, if not to reducing the variance? The answer is that it is increasing the frequency resolution of our estimate of the psd. We return to this observation momentarily.

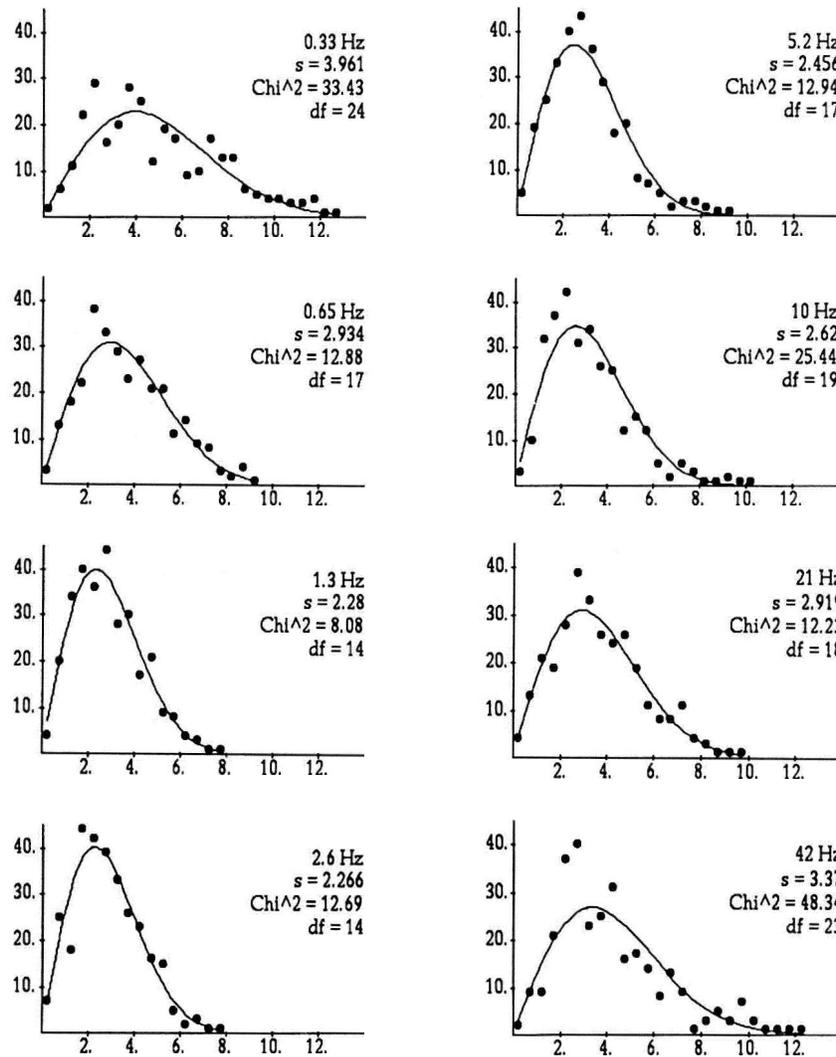


Fig. 1. Distributions of amplitude estimates at eight temporal frequencies, fitted with Rayleigh densities. The data are from Troy (1983a) (see Appendix 3).

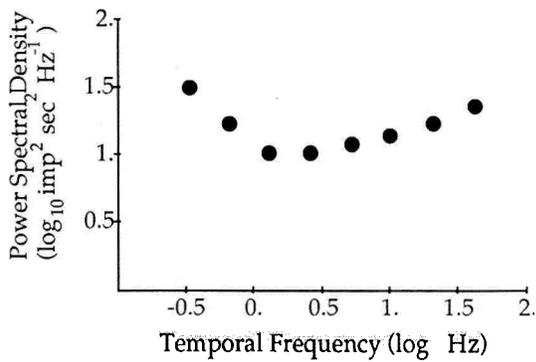


Fig. 2. Power spectral density of a cat LGN cell. Points are derived from fitted Rayleigh densities in Fig. 1.

Since extending T does not reduce the variance, this would seem to recommend partitioning the interval with $K > 1$. If the resulting K estimates are averaged, the variance of the mean will decline by K , thus increasing the accuracy of each estimate of the psd.

However, the duration T establishes the frequency resolution of the estimate of the psd as $1/T$. Furthermore, the estimator we employ is only *asymptotically* unbiased. This may be seen in eqn. (A8), wherein we assume that the psd is constant over the spectrum of the measurement window. This spectrum is roughly $2/T$ wide. Thus, the bias will be small provided that the psd does not vary much over this extent. Therefore as a practical guide, one must choose T based on the desired frequency resolution, and on prior information about the rate of change over frequency of the psd.

If the interval KT is long enough to allow subdivision and averaging, then there are in fact two ways to average. One, as we have described, is to subdivide by K and compute the mean. The second is to set $K = 1$, thus maximizing frequency resolution, and then to average K adjacent estimates in the frequency domain (Stremler, 1982). The former method assumes that the noise process is stationary over time, the latter that it is stationary over frequency. Both methods reduce both the variance and the frequency resolution by K . Finally, the averaging over time or frequency may employ a non-rectangular window, such as a Gaussian, to provide an estimate that is more localized in both time and frequency.

It is traditional to represent frequency spectra as functions of log frequency. This corresponds to a frequency resolution that increases in proportion to frequency. If this is desired, the value of K may be made proportional to frequency. Thus, for example, a noise record of 1 s might be subdivided by factors of {1,2,4,8,16,32,64} to give resolutions of {1,2,4,8,16,32,64} Hz at frequencies of {1,2,4,8,16,32,64} Hz. The same effect may be obtained without subdivision by averaging estimates over a frequency interval equal to {1,2,4,8,16,32,64} Hz at the corresponding frequencies.

Signal plus noise

Because we have assumed additive noise, it is clear that the signal will merely alter the means of the distributions of sine and cosine coefficients. If the input is a spatiotemporal sinusoid

with frequencies u, w and contrast k (a drifting grating with speed $w/|u|$),

$$f(x, t) = k \cos[2\pi(u \cdot x + wt)], \quad (13)$$

then the response of the cell will be

$$r(t) = a \cos(2\pi wt) + b \sin(2\pi wt), \quad (14)$$

where

$$a^2 + b^2 = k^2 G^2(u, w). \quad (15)$$

The new mean for the cosine coefficient will therefore be

$$\begin{aligned} h_c(t) * r(t)|_{t=T} &= \int_{-\infty}^{\infty} \frac{a}{\sqrt{T}} \cos(2\pi w_0 u) \text{rect}(u/T - 1/2) \\ &\quad \times \cos[2\pi w_0(T - u)] du, \\ &= \frac{a}{\sqrt{T}} \int_0^T [\cos(2\pi w_0 u)]^2 du, \\ &= \frac{a\sqrt{T}}{2}, \end{aligned} \quad (16)$$

where $h_c(t)$ is the cosine measurement filter defined in Appendix 2. Thus, the power z is now the sum of two Gaussians with means $\frac{a\sqrt{T}}{2}$ and $\frac{b\sqrt{T}}{2}$, and variance σ^2 , which is σ^2 times a non-central chi-square with two degrees of freedom and non-centrality parameter

$$\begin{aligned} \tau &= \left(\frac{a\sqrt{T}}{2\sigma}\right)^2 + \left(\frac{b\sqrt{T}}{2\sigma}\right)^2, \\ &= \frac{T(a^2 + b^2)}{4\sigma^2}, \\ &= \frac{Tk^2 G^2(w_0)}{2N(w_0)}. \end{aligned} \quad (17)$$

If the amplitude, rather than power, is estimated, then the resulting distribution is a "non-central Rayleigh" (Papoulis, 1965).

To summarize, the distribution of the power estimate for noise alone is $N(w_0)/2$ times a chi-square with two degrees of freedom. When a sinusoid is present, the distribution is $N(w_0)/2$ times a non-central chi-square with two degrees of freedom and a non-centrality parameter that is determined by gain, by contrast, by duration, and by noise power. Similar expressions, involving Rayleigh distributions, can be given for amplitude rather than power estimates.

Contrast sensitivity

Contrast sensitivity is a measure of the ability to distinguish signal and noise. Above we have derived distributions for signal and noise and we are therefore in a position to construct a definition of contrast sensitivity. However, there is no single number that uniquely describes this ability. In fact, the most complete

description is given by the contrast transfer function and the psd. A particular experimental procedure or psychophysical task defines just one particular measure of contrast sensitivity. Hence, there are as many measures as there are tasks and procedures. However, if our model is an accurate representation of the situation, then many of these measures are derivable from one another. We shall illustrate this point by constructing two measures, one that is analogous to a "yes/no" procedure, the other to a "two-alternative forced-choice" procedure.

Yes/no

We first consider an experiment designed to measure contrast sensitivity, then we put this experiment in a theoretical context. The experiment is adapted from (Derrington & Lennie, 1982). The essence of the yes/no procedure is to determine the contrast that yields a specified proportion correct p_h when the signal is present (the hit rate), and a specified proportion incorrect p_f when the signal is absent (the false alarm rate). A trial is scored "yes" when the response exceeds some criterion λ .

Within certain limits, the selection of λ is arbitrary (see below). However, a tradition with some sense is to select a value that yields a small, but measurable false alarm rate, 0.05 for example. To locate this value of λ , we first collect a number of estimates of power z from the maintained discharge, as described above. From these, and knowledge of the underlying distribution, we select a criterion power λ such that the probability of it being exceeded by noise alone is $p_f = 0.05$.

We next select a spatial and temporal frequency. During the course of repeated presentations, the contrast of the signal is adjusted to find a level that yields 50% of the values of z larger than λ . The inverse of this contrast is a measure of contrast sensitivity.

In the context of our theory, let the cumulative noise-alone distribution be $F_n(z)$, and let the signal-plus-noise distribution, expressed as a function of the non-centrality parameter τ , be $F_s(\tau|z)$. Then the criterion λ is given by

$$\lambda = F_n^{-1}(1 - p_f). \tag{18}$$

For example, when $p_f = 0.05$, $\lambda = 5.99$ as shown in Fig. 3.

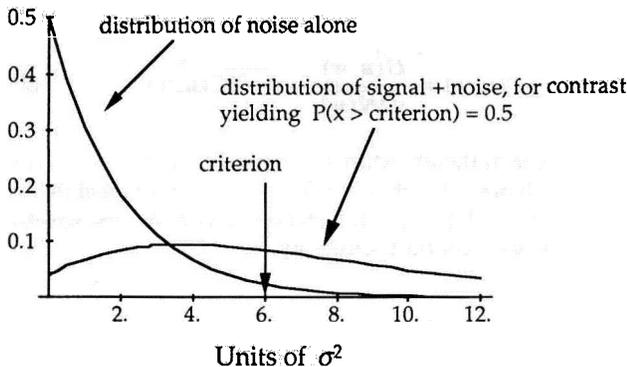


Fig. 3. Distributions of power estimates for noise and signal plus noise at threshold in the yes/no procedure. False alarm rate is 0.05, hit rate is 0.5.

Table 1. Values of τ for the yes/no procedure for various hit and false alarm rates

False alarm	Hit	
	0.5	0.75
0.05	4.957	8.591
0.10	3.556	6.770

The distributions for signal and noise at threshold in the yes/no procedure are illustrated in Fig. 3. The noise density is chi-square with two degrees of freedom, and the signal-plus-noise density is non-central chi-square with two degrees of freedom and non-centrality parameter of 4.96. The criterion at 5.99 is also shown. The horizontal axis is in units of σ^2 .

The non-centrality parameter τ that yields an estimate greater than the criterion λ on p_h of the signal trials is given by

$$\tau = F_s^{-1}[1 - p_h|F_n^{-1}(1 - p_f)]. \tag{19}$$

Continuing the example pictured in Fig. 3, if $p_f = 0.05$, and $p_h = 0.5$, then $\tau = 4.96$. Table 1 gives values of τ for various hit and false alarm rates.[†]

We now rearrange eqn. (17) to express contrast sensitivity $1/k$ in terms of G and N :

$$1/k = \frac{\sqrt{TG}(w_0)}{\sqrt{2\tau N}(w_0)}. \tag{20}$$

This result is sufficiently important that we restate it in slightly different terms, expressing contrast sensitivity explicitly as a function of spatial and temporal frequency, and re-introducing the spatial-frequency variable to the expression for contrast gain.

$$C(u, w) = \frac{\sqrt{TG}(u, w)}{\sqrt{2\tau N}(w)}. \tag{21}$$

This expression shows that contrast sensitivity is essentially a signal/noise ratio G/\sqrt{N} , scaled by constants T and τ that reflect the measurement duration and the criterion performance (Table 1). The dependence upon duration illustrates that contrast sensitivity will increase with time, as we expect. It also shows that to relate theoretical and empirical measures of contrast sensitivity, one must specify the value of T used.

[†]A traditional alternative to selecting a criterion based on particular hit and false alarm rates is to select a criterion that is a certain number of standard deviations above the mean of the noise-alone samples. This number is then analogous to d' , the detectability measure of signal detection theory (Green and Swets, 1966). A common choice is $d' = 2$. From eqn. (8) above, this gives

$$\lambda = \mu_z + d'\sigma_z = 2\sigma^2 + 2(2\sigma^2) = 6\sigma^2.$$

The distribution of z is σ^2 times χ_2^2 , so the false alarm rate is

$$p_f = 1 - \int_0^6 \chi_2^2(x) dx = 0.0498.$$

Forced choice

In a forced-choice procedure, no prior estimate is made of the psd. Each trial consists of two presentations, one of contrast k and the other of zero contrast. A value of z is computed for each presentation, and if the larger corresponds to the high contrast presentation, the trial is a "success," otherwise, a "failure." During repeated trials, the contrast is varied to find the "threshold" contrast yielding a specified proportion of successes, p_s . A number of methods exist for searching efficiently for the threshold (Cornsweet, 1962; Watson & Pelli, 1983; Wetherill & Levitt, 1965), or a less efficient method of constant stimuli may be used (Watson & Fitzhugh, 1990). If we write $f_s(z|\tau)$ for the density of signal plus noise, given non-centrality parameter τ , then the expected proportion correct will be

$$P(\tau) = \int_{-\infty}^{\infty} f_s(z|\tau) F_n(z) dz. \quad (22)$$

Then the value of τ corresponding to a particular p_s is simply

$$\tau = P^{-1}(p_s). \quad (23)$$

Once again we can compute values of τ for several interesting values of the proportion correct, as shown in Table 2. The value of 0.816 is the conventional threshold probability for a Weibull psychometric function (Weibull, 1951; Watson, 1979). As in the yes/no method, eqn. (21) states the relationship between τ and contrast sensitivity. This means that if the theoretical framework is correct, then one can measure contrast sensitivity equally well by either forced-choice or yes/no methods, and indeed, that one should be able to predict one from the other.

Amplitude vs. power

As noted above, the basic measure used in these procedures may be either power or amplitude (z or \sqrt{z}). The preceding derivations for yes/no and forced-choice methods used a power measure, which leads to expressions involving chi-square distributions. The derivations may also be done with amplitude measures, in which case Rayleigh distributions result. However, it is simple to show that the square-root transformation has no effect on the derivations, so that eqn. (21) remains a general description of contrast sensitivity. The only caution is that one must determine the value of τ corresponding to the task in question. For example, Derrington and Lennie (1984) use an amplitude criterion equal to the mean plus two standard deviations. From eqns. (10) and (11) this criterion is

$$\begin{aligned} \sqrt{\lambda} &= \mu_y + 2\sigma_y, \\ &= \left[\sqrt{\frac{\Pi}{2}} + 2\sqrt{2 - \frac{\Pi}{2}} \right] \sigma, \\ &= 2.5636\sigma. \end{aligned} \quad (24)$$

This criterion, applied to amplitude measures, will be functionally equivalent to its square applied to a power measure. Thus, we observe that the false alarm rate in this situation is $p_f = 1 - F_n[\lambda]$, or 0.0374. Next, Derrington and Lennie found that contrast for which 50% of the measured amplitudes y were

Table 2. Values of τ for the forced-choice procedure for various proportions correct

P(correct)	τ
0.75	2.78
0.816	4.00

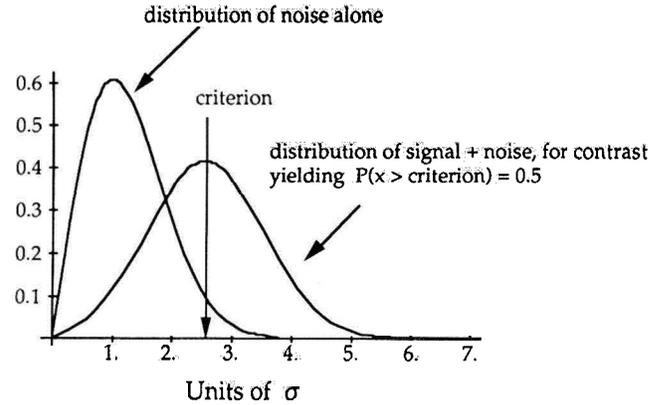


Fig. 4. Distributions of amplitude for signal and noise at threshold in the yes/no procedure.

greater than $\sqrt{\lambda}$. If $y > \sqrt{\lambda}$, then $z > \lambda$. Thus, we can substitute $\lambda = 2.5636^2 = 6.5720$ into eqns. (18) and (19) to obtain $\tau = 5.541$.

This situation is pictured in Fig. 4. On the left is the Rayleigh density describing the distribution of amplitudes for noise alone, and on the right is the distribution of amplitudes when contrast is sufficient to produce 50% amplitudes greater than the criterion $\sqrt{\lambda}$.

Normalized contrast sensitivity

Note that for a single cell with unchanging behavior, one can obtain many different estimates of contrast sensitivity, depending on the conditions of measurement and their reflection in the values of T and τ . To allow comparisons that are unconfounded by these values, it may be useful to consider a normalized contrast sensitivity,

$$C^*(u, w) = \frac{G(u, w)}{\sqrt{2N(w)}} = \sqrt{\tau/TC(u, w)}. \quad (25)$$

As a rule of thumb, when $T = 1$ s and proportion correct in a forced-choice (2AFC) task is 0.816 (the conventional threshold for a Weibull function), then normalized contrast sensitivity is just twice contrast sensitivity.

Neurometric functions

The complete description of signal and noise distributions allows the construction of "neurometric functions" (Tolhurst et al., 1983) which describe the probability of a criterion response as a function of contrast. The yes/no neurometric function may be derived from eqns. (18) and (19). The forced-choice neuro-

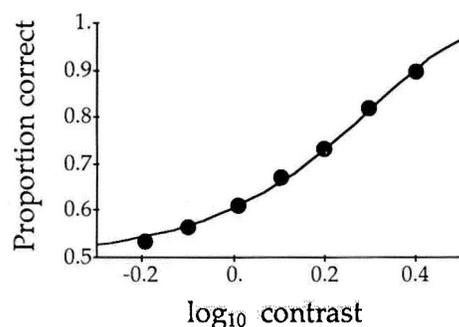


Fig. 5. Simulated 2AFC neurometric function. Points are values calculated from eqn. (22). The curve is the best-fitting Weibull function ($\beta = 2.090$).

metric function is given by eqn. (22), and an example is shown in Fig. 5.

The Weibull function

$$P(k) = 1 - (1 - \gamma)\exp[-(k/\alpha)^\beta] \quad (26)$$

is a widely used template for both psychometric and neurometric functions (Nachmias, 1981; Quick, 1974; Tolhurst et al., 1983; Watson, 1979; Weibull, 1951). For comparison, the best-fitting Weibull function (with $\gamma = 0.5$) is also shown. The slope of the Weibull function has been a subject of some study. For ideal detection in Gaussian noise, it should have a value of about 1.4. Higher values may reflect uncertainty about the signal (Pelli, 1986). Typical psychophysical estimates are about 3.5. The curve in Fig. 5 has a slope of $\beta = 2.090$.

Unfortunately, the only published study of neurometric functions is for cortical cells, and for a measure consisting of total spikes during an interval, rather than the power of a Fourier component (Tolhurst et al., 1983). The slope in this one case was $\beta = 1.29$.

Psychophysical sensitivity

Consider an observer who must detect a spatiotemporal sinusoid based only on the response of a single neuron. Theoretically, optimal performance, characterized by a so-called "ideal observer," depends upon the prior knowledge assumed of the observer. If the observer is certain as to the temporal frequency, but uncertain as to the phase of the signal, then the ideal procedure is to compute the power (or amplitude) at the signal frequency, as we have done above. Thus, if the observer acts as this type of ideal observer, psychophysical contrast sensitivity will be exactly as described by eqn. (21). This provides a rigorous means of predicting psychophysical sensitivity from the responses of single neurons.

There are a number of caveats to this direct prediction. First, the observer may be less than completely uncertain as to phase, particularly for a signal of extended duration, and may thus perform better than the direct prediction. Second, the observer may be less than completely certain as to temporal frequency, thus reducing performance. Both of these effects are likely to be modest in size. Limited vigilance or memory would preclude ideal performance at very long durations.

Of potentially greater consequence is the role of other neurons. Other neurons may help or hinder, depending upon

whether they respond to the signal in question. If the observer attends to neurons that do not respond, performance will be degraded. For example, if 100 neurons are attended to, of which only one responds to the signal, sensitivity may be reduced by about 2.8 (Pelli, 1986). But if the other neurons do respond to the signal, they may improve performance, through either summation of responses or of probabilities. Probability summation would arise if each neuron individually decided whether the signal was there, and these decisions were pooled (Green & Luce, 1975; Robson & Graham, 1981; Watson, 1979). If the responses are independent, probability summation would increase sensitivity by a factor of roughly $n^{1/4}$, where n is the number of cells. Again if $n = 100$, this factor is 3.16. Signal summation would arise if the responses of the several neurons are linearly combined by a cell later in the visual pathway. This sort of summation produces large improvements in sensitivity, essentially proportional to $n^{1/2}$, which in turn is proportional to the width of the summation area. The process of signal summation is dealt with at greater length in a forthcoming paper (Watson, 1990).

The two effects likely to produce the largest increments in sensitivity over the direct prediction, signal summation, and probability summation, can occur only if the signal extends over an area larger than a single receptive field. Thus, we should expect the direct prediction to be most accurate when the signal is of the same size as the receptive field.

Discussion

In the preceding sections, we have derived expressions for estimates of the power spectral density of the response of a linear neuron. For noise alone, these estimates follow a chi-square distribution with two degrees of freedom. For signal plus noise, they are non-central chi-square with two degrees of freedom. Knowledge of these distributions enabled us to then construct an equation formally relating contrast sensitivity to contrast gain, noise power spectral density, signal duration, and a factor of τ that depends upon the measurement method. Values of τ were provided for several common methods. We also derive an equation for the "neurometric function" of a cell, describing the probability of a given percent correct as a function of contrast. We note that these equations allow direct comparison of contrast sensitivity of cells and observers, although various caveats must be observed.

Although contrast sensitivity is a useful and widely used measure of visual performance, it is not a complete description of the behavior of the cell. First, it confounds gain and noise by taking their ratio. A more complete description would keep these two functions separate, and we may hope that future physiological experiments will take this step. Second, the complete contrast transfer function is composed of both gain and phase, but only the former is retained in measures of contrast sensitivity. Again, a more complete measurement would be that of the complete transfer function. Some recent studies have made the necessary phase measurements (Enroth-Cugell et al., 1983; Hamilton et al., 1989), and we may hope this trend continues. When the complete psd and transfer function are available, predictions of contrast threshold for arbitrary stimuli and arbitrary response criteria become possible.

One goal of this work was to provide a formal basis on which to relate the sensitivity of cells at various levels in the visual pathway. For example, how does the contrast sensitivity of

a population of ganglion cells constrain the contrast sensitivity of geniculate and cortical cells? The equations derived in this paper provide the basis for answering this question, and these answers are presented in a forthcoming paper (Watson, 1990).

Acknowledgments

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Appendix 1

The conversion from a spike train to power spectrum may be done in either of two ways. Consider the train as a sequence of impulses at times t_k . This has a transform that is the sum of complex exponentials:

$$\sum_k \delta(t - t_k) \leftrightarrow \sum_k e^{-i2\pi w t_k}. \quad (\text{A1})$$

Expanding the exponential into more familiar sine and cosine terms, the power density estimate at a frequency w can be written as

$$\left[\sum_k \cos(2\pi w t_k) \right]^2 + \left[\sum_k \sin(2\pi w t_k) \right]^2. \quad (\text{A2})$$

The first method is a direct implementation of this expression, wherein sine and cosine functions are evaluated at the occurrence times of the spikes, accumulated, squared, and added.

The second method is to accumulate spikes within bins of duration D , and to regard this sequence of counts as a measure of instantaneous rate. This is equivalent to convolving the spike train with a pulse of duration D and sampling at intervals of D . In the frequency domain, this is equivalent to multiplying the Fourier transform of the spike train by a sinc function whose first zero is at D^{-1} . This will produce some attenuation for higher frequencies relative to the first method, but for small D , the effect will be modest. For example, Derrington and Lennie (1982, 1984) and Troy (1983*a,b*) used $D = 6$ ms, so $D^{-1} = 167$ Hz. This leads to an attenuation of about 10% at the highest time frequency they used (42 Hz). Likewise sampling at intervals of D will replicate the spectrum at intervals of D^{-1} , but with a 6-ms bin effects from this source will be negligible.

Appendix 2

Measurement of power spectral density is a standard topic in engineering texts (Parzen, 1962; Stremmer, 1982). Here we provide a derivation suited to electrophysiological measurement.

We define a cosine measurement filter with impulse response

$$h_c(t) = \frac{1}{\sqrt{T}} \cos(2\pi w_0 t) \text{rect}(t/T - 1/2). \quad (\text{A3})$$

This is a cosine function multiplied by a rectangular pulse that starts at time 0 and ends at time T . The pulse represents the measurement interval. We arrange that T is an integer multiple of $1/w_0$, the period of the cosine function.

Let the noise be a stationary process $x(t)$ with psd $N(w)$. Create a new process $c(t)$ by filtering $x(t)$, i.e.

$$c(t) = h_c(t) * x(t) \quad (\text{A4})$$

The mean of a linear filtering of a stationary process is the mean of the input times the integral of the filter impulse response. Since T is an integral number of cycles of the cosine, this integral and hence the mean of $c(t)$ are zero.

The psd of a filtered process is the psd of the input times the squared gain of the filter, so this new process will have psd

$$N_c(w) = N(w) |H_c(w)|^2. \quad (\text{A5})$$

The variance of a zero-mean process is the integral of the psd, so we have

$$\begin{aligned} \sigma^2 &= \int_{-\infty}^{\infty} N_c(w) dw, \\ &= \int_{-\infty}^{\infty} N(w) |H_c(w)|^2 dw. \end{aligned} \quad (\text{A6})$$

The squared gain of the filter is given by

$$|H_c(w)|^2 = \frac{T}{4} \{ \text{sinc}[T(w - w_0)] + \text{sinc}[T(w + w_0)] \}^2. \quad (\text{A7})$$

The first zero of the sinc(\cdot) function is a distance $1/T$ from w_0 . If T is large, then each lobe of H_c will be narrow, and N will be effectively constant over the integral, in which case

$$\sigma^2 = N(w_0) \int_{-\infty}^{\infty} |H_c(w)|^2 dw. \quad (\text{A8})$$

From Parseval's Theorem,

$$\sigma^2 = N(w_0) \int_{-\infty}^{\infty} |h_c(t)|^2 dt. \quad (\text{A9})$$

Substituting for $h_c(t)$ [eqn. (A3)], and making use of the rect(\cdot) function to set the limits of integration,

$$\sigma^2 = N(w_0) \frac{1}{T} \int_0^T |\cos(2\pi w_0 t)|^2 dt. \quad (\text{A10})$$

For Tw_0 integer, this reduces to

$$\sigma^2 = \frac{1}{2} N(w_0). \quad (\text{A11})$$

We produce a second process $s(t)$ identical to $c(t)$ except that it uses a sine filter. It will also have the same mean (zero) and variance as $c(t)$. Because the phase of the component at frequency w_0 is random, $c(t)$ and $s(t)$ are independent.

When we make a measurement, we take samples c and s from the filtered processes. We now take the sum of squared sine and cosine coefficients,

$$z = c^2 + s^2. \quad (\text{A12})$$

Since both c and s are linear combinations of random variables, they are likely to be approximately Gaussian,[†] and z will be the sum of two squared zero-mean Gaussians with variance σ^2 , which is σ^2 times a chi-square with two degrees of freedom. The mean and standard deviation are then

$$\mu_z = \sigma_z = 2\sigma^2 = N(w_0). \quad (\text{A13})$$

Appendix 3

The following are some notes on specific reports that have used a signal/noise method to estimate contrast sensitivity in visual neurons.

Derrington and Lennie (1982)

This study estimated the psd and spatial and temporal contrast sensitivity of X and Y ganglion cells in the cat. They used a measuring interval of 3.1 s, divided into 512 bins, each of 6 ms, to examine frequencies in octave steps between 0.33 and 42 Hz. They used an amplitude, rather than power measure, so their psd estimates are biased [eqn. (10)]. Estimates are based on 30 replications. In three X cells and two Y cells, they fit a Gaussian to the distribution of 100 amplitudes. The fit failed in two of five cases. This is perhaps to be expected since from the above analysis this distribution should be Rayleigh, rather than Gaussian. However, the Rayleigh is not so different from the Gaussian (see Fig. 4) as to reject all five cases. They note that the psd, hence the criterion, hence the contrast sensitivity, all depend on T . While they use several values of T in measuring contrast sensitivity, they normalize all results to a T of 1.5 s. They also point out that prediction of psychophysical results requires an assumption about T .

They found that the mean of psd is approximately constant at about 4 impulses/s/Hz. The s.d. is also approximately constant at about 0.57 times the mean. This is close to the predicted value of 0.523 [eqn. (12)]. Psd's for X and Y cells are essentially identical, although mean rate is quite different (51.6 impulse/s for X cells, 30.8 impulses/s for Y cells). Contrast sensitivities were measured using the yes/no technique, with the criterion set to the mean plus two standard deviations.

Troy (1983a,b)

In these studies of cat LGN cells, complete psds were reported for five X cells and five Y cells. As in Derrington and Lennie (1982), psds for X and Y cells were almost identical, and the ratio of standard deviation to mean is about 0.57, close to the predicted value of 0.52 [eqn. (12)]. In addition, distributions of power spectrum amplitudes for eight temporal frequencies in the maintained discharge were collected (reproduced in Fig. 1 of this paper). Fit of a Gaussian was rejected in all but one case. An amplitude measure and a yes/no method were used. Other methods are generally as in Derrington and Lennie (1982).

Derrington and Lennie (1984)

This study examined spatial and temporal contrast sensitivity in macaque geniculate cells. Complete psds are not reported. Con-

trast sensitivity was measured by the same method as in Derrington and Lennie (1982). For most cells criterion was close to 10 impulses/s. Frequencies between 0.16 and 41.8 Hz were used. The measurement duration T is not stated.

Hawken and Parker (1984)

A yes/no method was used to measure contrast sensitivity of macaque cortical cells. The authors appear to have used an amplitude measure, although this is not explicitly stated. The noise-alone psd was estimated from 16 samples. The oldest sample was replaced after each stimulus trial. The measurement interval is described as equal to the stimulus duration, but is not otherwise specified. They used a criterion of mean plus two standard deviations. They examined temporal frequencies from 0.75–6.0 Hz. Evidently not all measures were of contrast sensitivity as defined here, since the response measure was “the component modulated in synchrony with the passage of the bars of the drifting grating or in terms of the overall elevation of the maintained discharge, as was appropriate for each particular cell.” Analysis of contrast sensitivity of cortical cells must consider output nonlinearities and small or absent maintained discharges, neither of which was considered here.

Appendix 4

To supplement the mathematical content of this paper, this Appendix contains Mathematica expressions for several of the formulae used in the text. Mathematica is a program and language for manipulating mathematical ideas (Wolfram, 1988). It is available for many computers in wide use. To conserve space, only definitions and expressions are shown; results of most evaluations, including graphics, are omitted.

Probability densities and distributions

Chi-square density

In the following, $df =$ degrees of freedom.

`chiDens[x_,df_] := 0 /; x < 0`

`chiDens[x_,df_] := 1/2 /; (x == 0 && df == 2)`

`chiDens[x_,df_] := 1/(2^(df/2) Gamma[df/2])
(x^((df/2) - 1)) * Exp[-x/2] /; x > 0`

Chi-square distribution

`chiDist[x_,df_] := Block[{u}, 1/(2^(df/2) Gamma[df/2]) *
NIntegrate[(u^((df/2) - 1)) Exp[-u/2], {u,0,x}]`

Non-central chi-square density

In the following, $df =$ degrees of freedom and $t =$ non-centrality parameter.

`nChiDens[x_,df_,t_] := Block[{j}, (1/(Sqrt[Pi] 2^(df/2))) *
Exp[-(t + x)/2] x^(df/2 - 1) *
NSum[(t x)^j / (2 j!) Gamma[j + 1/2] /
Gamma[j + df/2]
,{j, 0, Infinity}]] /; x > 0`

`nChiDens[x_,df_,t_] := nChiDens[.0000001,df,t] /; x == 0`

`nChiDens[x_,df_,t_] := 0 /; x < 0`

[†]If the original process $x(t)$ is Gaussian, then c and s will be exactly Gaussian.

Non-central chi-square distribution

```
nChiDist[x_,df_,t_] := Block[ {j} , Exp[-t/2]
  Apply[Plus,Table[ (((t/2)^j)/(j!)) ChiDist[x, df + 2 j]
    , {j,0,10}]] ] /; x > 0
nChiDist[x_,df_,t_] := 0 /; x <= 0
```

Rayleigh density

In the following, s is the standard deviation of the underlying Gaussians.

```
rayDens[x_, s_] := (x / s^2) Exp[-(x/s)^2 / 2] /; x > 0
rayDens[x_, s_] := 0 /; x <= 0
```

Non-central Rayleigh density

The argument t is the square root of the sum of squared means of the underlying Gaussians.

```
nRayDens[x_,s_,t_] :=
  (x/s^2) Exp[-(x^2 + t^2)/(2 s^2)] Bessell[0,x t / s^2] /;
  x >= 0
nRayDens[x_,s_,t_] := 0 /; x < 0
```

Yes/no method

This function finds the criterion (λ) that generates a particular false-alarm rate (pf).

```
findLambda[pf_,goal_] := x /. FindRoot[ chiDist[x,2] ==
  1-pf
  , {x,{1,2},0,10} , AccuracyGoal->goal]
```

This function finds the value of tau corresponding to a particular hit rate (ph) and false-alarm rate (pf).

```
findTauYN[ph_,pf_,goal_] :=
tau /. FindRoot[ nChiDist[(findLambda[pf,goal]),2,tau] ==
  1-ph
  , {tau,{1,2},0,10} , AccuracyGoal->goal ]
```

2AFC method

Here we compute the probability correct in a 2AFC task where the assumed underlying noise distribution is Chi-Square with 2 df, and that of signal is non-central Chi-Square with 2 df and non-centrality parameter tau.

2AFC percent correct vs. tau

This function returns proportion correct in a 2AFC task as a function of the non-centrality parameter tau and accuracy goal.

```
tafc[tau_,goal_] := Block[ {x},
  NIntegrate[nChiDens[x,2,tau] ChiDist[x,2]
    , {x,0,Infinity}
    ,AccuracyGoal->goal] ]
SetAttributes[tafc,Listable]
```

Tau vs. 2AFC percent correct

This routine finds the value of tau corresponding to a particular 2AFC proportion correct.

```
findTauFC[p_,goal_] :=
tau /. FindRoot[ tafc[tau,goal] == p
  , {tau,{2.78,2.79},0,10} , AccuracyGoal->goal ]
```

The neurometric function

We create a set of contrasts increasing in $\frac{1}{3}$ octave steps.

```
contrast = Table[2^(i/3),{i,-2,4}] //N
{0.629961, 0.793701, 1., 1.25992, 1.5874, 2., 2.51984}
```

We generate a "neurometric function." Note that tau is proportional to contrast squared.

```
neuro = tafc[contrast^2,3]
{0.532044, 0.568983, 0.608901, 0.662451, 0.733404,
  0.816094, 0.897546}
```

We define a Weibull function.

```
weibull[x_,a_,b_,g_] := 1 - (1-g) Exp[- (x/a)^b] //N
```

```
SetAttributes[weibull, Listable]
```

We find the best fitting Weibull function, using a simple least-squares fit.

```
FindMinimum[
  Apply[Plus, ( neuro - weibull[contrast,alph,bet,0.5] )
    ^2 ]
  , {alph,{2,2.1},.5,3} , {bet,{2,3},0,4} ]
{0.000167506, {alph -> 1.99878, bet -> 2.07002}}
```

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