

Figure 3.10 Probability densities for the stimulus, given the firing rates shown in figure 3.9 and assuming the tuning curves of figure 3.8. The solid curve is $p[s|r]$ when the prior distribution of stimulus values is constant and the true value of the stimulus is $s = 0$. The dashed curve is for a Gaussian prior distribution with a mean of -2 and variance of 1 , again with the true stimulus being $s = 0$. The peaks of the solid and dashed curves are at $s = 0.0385$ and $s = -0.107$, respectively.

Note that the bias depends on the true value of the stimulus. An estimate is termed unbiased if $b_{\text{est}}(s) = 0$ for all stimulus values.

variance

The variance of the estimator, which quantifies how much the estimate varies about its mean value, is defined as

$$\sigma_{\text{est}}^2(s) = \langle (s_{\text{est}} - \langle s_{\text{est}} \rangle)^2 \rangle. \quad (3.39)$$

The bias and variance can be used to compute the trial-average squared estimation error, $\langle (s_{\text{est}} - s)^2 \rangle$. This is a measure of the spread of the estimated values about the true value of the stimulus. Because $s = \langle s_{\text{est}} \rangle - b_{\text{est}}(s)$, we can write the squared estimation error as

estimation error

$$\langle (s_{\text{est}} - s)^2 \rangle = \langle (s_{\text{est}} - \langle s_{\text{est}} \rangle + b_{\text{est}}(s))^2 \rangle = \sigma_{\text{est}}^2(s) + b_{\text{est}}^2(s). \quad (3.40)$$

In other words, the average squared estimation error is the sum of the variance and the square of the bias. For an unbiased estimate, the average squared estimation error is equal to the variance of the estimator.

Fisher Information

Decoding can be used to limit the accuracy with which a neural system encodes the value of a stimulus parameter because the encoding accuracy cannot exceed the accuracy of an optimal decoding method. Of course, we must be sure that the decoding technique used to establish such a bound is truly optimal, or else the result will reflect the limitations of the decoding procedure, not bounds on the neural system being studied. The Fisher information is a quantity that provides one such measure of encoding accuracy. Through a bound known as the Cramér-Rao bound, the Fisher information limits the accuracy with which any decoding scheme can extract an estimate of an encoded quantity.

Cramér-Rao bound The Cramér-Rao bound limits the variance of any estimate s_{est} according

to (appendix B)

$$\sigma_{\text{est}}^2(s) \geq \frac{(1 + b'_{\text{est}}(s))^2}{I_F(s)}, \quad (3.41)$$

where $b'_{\text{est}}(s)$ is the derivative of $b_{\text{est}}(s)$. If we assume here that the firing rates take continuous values and that their distribution in response to a stimulus s is described by the conditional probability density $p[\mathbf{r}|s]$, the quantity $I_F(s)$ in equation 3.41 is the Fisher information of the firing-rate distribution, which is related to $p[\mathbf{r}|s]$ (assuming the latter is sufficiently smooth) by

Fisher information

$$I_F(s) = \left\langle -\frac{\partial^2 \ln p[\mathbf{r}|s]}{\partial s^2} \right\rangle = \int d\mathbf{r} p[\mathbf{r}|s] \left(-\frac{\partial^2 \ln p[\mathbf{r}|s]}{\partial s^2} \right). \quad (3.42)$$

The reader can verify that the Fisher information can also be written as

$$I_F(s) = \left\langle \left(\frac{\partial \ln p[\mathbf{r}|s]}{\partial s} \right)^2 \right\rangle = \int d\mathbf{r} p[\mathbf{r}|s] \left(\frac{\partial \ln p[\mathbf{r}|s]}{\partial s} \right)^2. \quad (3.43)$$

The Cramér-Rao bound sets a limit on the accuracy of any unbiased estimate of the stimulus. When $b_{\text{est}}(s) = 0$, equation 3.40 indicates that the average squared estimation error is equal to σ_{est}^2 and, by equation 3.41, this satisfies the bound $\sigma_{\text{est}}^2 \geq 1/I_F(s)$. Provided that we restrict ourselves to unbiased decoding schemes, the Fisher information sets an absolute limit on decoding accuracy, and it thus provides a useful limit on encoding accuracy. Although imposing zero bias on the decoding estimate seems reasonable, the restriction is not trivial. In general, minimizing the decoding error in equation 3.40 involves a trade-off between minimizing the bias and minimizing the variance of the estimator. In some cases, biased schemes may produce more accurate results than unbiased ones. For a biased estimator, the average squared estimation error and the variance of the estimate are not equal, and the estimation error can be either larger or smaller than $1/I_F(s)$.

The limit on decoding accuracy set by the Fisher information can be attained by a decoding scheme we have studied, the maximum likelihood method. In the limit of large numbers of encoding neurons, and for most firing-rate distributions, the ML estimate is unbiased and saturates the Cramér-Rao bound. In other words, the variance of the ML estimate is given asymptotically (for large N) by $\sigma_{\text{ML}}^2(s) = 1/I_F(s)$. Any unbiased estimator that saturates the Cramér-Rao lower bound is called efficient. Furthermore, $I_F(s)$ grows linearly with N , and the ML estimate obeys a central limit theorem, so that $N^{1/2}(s_{\text{ML}} - s)$ is Gaussian distributed with a variance that is independent of N in the large N limit. Finally, in the limit $N \rightarrow \infty$, the ML estimate is asymptotically consistent, in the sense that $P[|s_{\text{ML}} - s| > \epsilon] \rightarrow 0$ for any $\epsilon > 0$.

efficiency

asymptotic consistency

As equation 3.42 shows, the Fisher information is a measure of the expected curvature of the log likelihood at the stimulus value s . Curvature is

important because the likelihood is expected to be at a maximum near the true stimulus value s that caused the responses. If the likelihood is very curved, and thus the Fisher information is large, responses typical for the stimulus s are much less likely to occur for slightly different stimuli. Therefore, the typical response provides a strong indication of the value of the stimulus. If the likelihood is fairly flat, and thus the Fisher information is small, responses common for s are likely to occur for slightly different stimuli as well. Thus, the response does not as clearly determine the stimulus value. The Fisher information is purely local in the sense that it does not reflect the existence of stimulus values completely different from s that are likely to evoke the same responses as those evoked by s itself. However, this does not happen for the sort of simple population codes we consider. Shannon's mutual information measure, discussed in chapter 4, takes such possibilities into account.

The Fisher information for a population of neurons with uniformly arrayed tuning curves (the Gaussian array in figure 3.8, for example) and Poisson statistics can be computed from the conditional firing-rate probability in equation 3.31. Because the spike-count rate is described here by a probability rather than a probability density, we use the discrete analog of equation 3.42,

$$I_F(s) = \left\langle -\frac{d^2 \ln P[\mathbf{r}|s]}{ds^2} \right\rangle = T \sum_{a=1}^N \langle r_a \rangle \left(\left(\frac{f'_a(s)}{f_a(s)} \right)^2 - \frac{f''_a(s)}{f_a(s)} \right). \quad (3.44)$$

If we assume that the array of tuning curves is symmetric, like the Gaussian array of figure 3.8, the second term in the parentheses of the last expression sums to 0. We can also make the replacement $\langle r_a \rangle = f_a(s)$, producing the final result

$$I_F(s) = T \sum_{a=1}^N \frac{(f'_a(s))^2}{f_a(s)}. \quad (3.45)$$

In this expression, each neuron contributes an amount to the Fisher information proportional to the square of its tuning curve slope and inversely proportional to the average firing rate for the particular stimulus value being estimated. Highly sloped tuning curves give firing rates that are sensitive to the precise value of the stimulus. Figure 3.11 shows the contribution to the sum in equation 3.45 from a single neuron with a Gaussian tuning curve, the neuron with $s_a = 0$ in figure 3.8. For comparison purposes, a dashed curve proportional to the tuning curve is also plotted. Note that the Fisher information vanishes for the stimulus value that produces the maximum average firing rate, because $f'_a(s) = 0$ at this point. The firing rate of a neuron at the peak of its tuning curve is relatively unaffected by small changes in the stimulus. Individual neurons carry the most Fisher information in regions of their tuning curves where average firing rates are rapidly varying functions of the stimulus value, not where the firing rate is highest.

The Fisher information can be used to derive an interesting result on the optimal widths of response tuning curves. Consider a population of neu-

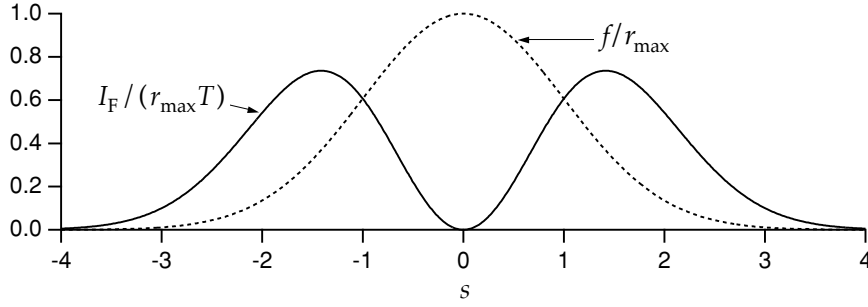


Figure 3.11 The Fisher information for a single neuron with a Gaussian tuning curve with $s=0$ and $\sigma_a=1$, and Poisson variability. The Fisher information (solid curve) has been divided by $r_{\max}T$, the peak firing rate of the tuning curve times the duration of the trial. The dashed curve shows the tuning curve scaled by r_{\max} . Note that the Fisher information is greatest where the slope of the tuning curve is highest, and vanishes at $s=0$, where the tuning curve peaks.

rons with tuning curves of identical shapes, distributed evenly over a range of stimulus values as in figure 3.8. Equation 3.45 indicates that the Fisher information will be largest if the tuning curves of individual neurons are rapidly varying (making the square of their derivatives large), and if many neurons respond (making the sum over neurons large). For typical neuronal response tuning curves, these two requirements are in conflict with one another. If the population of neurons has narrow tuning curves, individual neural responses are rapidly varying functions of the stimulus, but few neurons respond. Broad tuning curves allow many neurons to respond, but the individual responses are not as sensitive to the stimulus value. To determine whether narrow or broad tuning curves produce the more accurate encodings, we consider a dense distribution of Gaussian tuning curves, all with $\sigma_a = \sigma_r$. Using such curves in equation 3.45, we find

$$I_F(s) = T \sum_{a=1}^N \frac{r_{\max}(s - s_a)^2}{\sigma_r^4} \exp\left(-\frac{1}{2} \left(\frac{s - s_a}{\sigma_r}\right)^2\right). \quad (3.46)$$

This expression can be approximated by replacing the sum over neurons with an integral over their preferred stimulus values and multiplying by a density factor ρ_s . The factor ρ_s is the density with which the neurons cover the range of stimulus values, and it is equal to the number of neurons with preferred stimulus values lying within a unit range of s values. Replacing the sum over a with an integral over a continuous preferred stimulus parameter ξ (which replaces s_a), we find

sums \rightarrow integrals

$$\begin{aligned} I_F(s) &\approx \rho_s T \int_{-\infty}^{\infty} d\xi \frac{r_{\max}(s - \xi)^2}{\sigma_r^4} \exp\left(-\frac{1}{2} \left(\frac{s - \xi}{\sigma_r}\right)^2\right) \\ &= \frac{\sqrt{2\pi} \rho_s \sigma_r r_{\max} T}{\sigma_r^2}. \end{aligned} \quad (3.47)$$

We have expressed the final result in this form because the number of neurons that respond to a given stimulus value is roughly $\rho_s \sigma_r$, and the Fisher

information is proportional to this number divided by the square of the tuning curve width. Combining these factors, the Fisher information is inversely proportional to σ_r , and the encoding accuracy increases with narrower tuning curves.

The advantage of using narrow tuning curves goes away if the stimulus is characterized by more than one parameter. Consider a stimulus with D parameters and suppose that the response tuning curves are products of identical Gaussians for each of these parameters. If the tuning curves cover the D -dimensional space of stimulus values with a uniform density ρ_s , the number of responding neurons for any stimulus value is proportional to $\rho_s \sigma_r^D$ and, using the same integral approximation as in equation 3.47, the Fisher information is

$$I_F = \frac{(2\pi)^{D/2} D \rho_s \sigma_r^D r_{\max} T}{\sigma_r^2} = (2\pi)^{D/2} D \rho_s \sigma_r^{D-2} r_{\max} T. \quad (3.48)$$

This equation, which reduces to the result given above if $D = 1$, allows us to examine the effect of tuning curve width on encoding accuracy. The trade-off between the encoding accuracy of individual neurons and the number of responding neurons depends on the dimension of the stimulus space. Narrowing the tuning curves (making σ_r smaller) increases the Fisher information for $D = 1$, decreases it for $D > 2$, and has no impact if $D = 2$.

Optimal Discrimination

In the first part of this chapter, we considered discrimination between two values of a stimulus. An alternative to the procedures discussed there is simply to decode the responses and discriminate on the basis of the estimated stimulus values. Consider the case of discriminating between s and $s + \Delta s$ for small Δs . For large N , the average value of the difference between the ML estimates for the two stimulus values is equal to Δs (because the estimate is unbiased) and the variance of each estimate (for small Δs) is $1/I_F(s)$. Thus, the discriminability, defined in equation 3.4, for the ML-based test is

$$d' = \Delta s \sqrt{I_F(s)}. \quad (3.49)$$

The larger the Fisher information, the higher the discriminability. We leave as an exercise the proof that for small Δs , this discriminability is the same as that of the likelihood ratio test $Z(\mathbf{r})$ defined in equation 3.19.

Discrimination by ML estimation requires maximizing the likelihood, and this may be computationally challenging. The likelihood ratio test described previously may be simpler, especially for Poisson variability, because, for small Δs , the likelihood ratio test Z defined in equation 3.19 is a linear function of the firing rates,

$$Z = T \sum_{a=1}^N r_a \frac{f'_a(s)}{f_a(s)}. \quad (3.50)$$

ML
discriminability

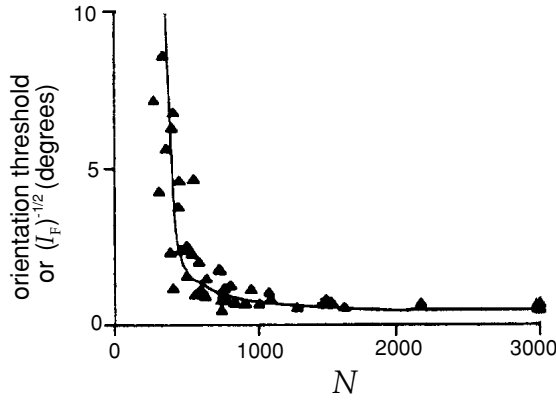


Figure 3.12 Comparison of Fisher information and discrimination thresholds for orientation tuning. The solid curve is the minimum standard deviation of an estimate of orientation angle from the Cramér-Rao bound, plotted as a function of the number of neurons (N) involved in the estimation. The triangles are data points from an experiment that determined the threshold for discrimination of the orientation of line images by human subjects as a function of line length and eccentricity. An effective number of neurons involved in the task was estimated for the different line lengths and eccentricities, using the cortical magnification factor discussed in chapter 2. (Adapted from Paradiso, 1988.)

Figure 3.12 shows an interesting comparison of the Fisher information for orientation tuning in the primary visual cortex with human orientation discrimination thresholds. Agreement like this can occur for difficult tasks, like discrimination at threshold, where the performance of a subject may be limited by basic constraints on neuronal encoding accuracy.

3.4 Spike-Train Decoding

The decoding methods we have considered estimate or discriminate static stimulus values on the basis of spike-count firing rates. Spike-count firing rates do not provide sufficient information for reconstructing a stimulus that varies during the course of a trial. Instead, we can estimate such a stimulus from the sequence of firing times t_i for $i = 1, 2, \dots, n$ of the spikes that it evokes. One method for doing this is similar to the Wiener kernel approach used to estimate the firing rate from the stimulus in chapter 2, and to approximate a firing rate using a sliding window function in chapter 1. For simplicity, we restrict our discussion to the decoding of a single neuron. We assume, as we did in chapter 2, that the time average of the stimulus being estimated is 0.

In spike-train decoding, we attempt to construct an estimate of the stimulus at time t from the sequence of spikes evoked up to that time. There are paradoxical aspects of this procedure. The firing of an action potential at time t_i is only affected by the stimulus $s(t)$ prior to that time, $t < t_i$, and yet, in spike decoding, we attempt to extract information from this