

Multidimensional Encoding Strategy of Spiking Neurons

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Neural responses in sensory systems are typically triggered by a multitude of stimulus features. Using information theory, we study the encoding accuracy of a population of stochastically spiking neurons characterized by different tuning widths for the different features. The optimal encoding strategy for representing one feature most accurately consists of narrow tuning in the dimension to be encoded, to increase the single-neuron Fisher information, and broad tuning in all other dimensions, to increase the number of active neurons. Extremely narrow tuning without sufficient receptive field overlap will severely worsen the coding. This implies the existence of an optimal tuning width for the feature to be encoded. Empirically, only a subset of all stimulus features will normally be accessible. In this case, relative encoding errors can be calculated that yield a criterion for the function of a neural population based on the measured tuning curves.

1 Introduction

The question of an optimal tuning width for the representation of a stimulus by a neural population is still controversial. On the one hand, narrowly tuned cells are frequently encountered, emphasizing the importance of single neurons for perception and motor control (Lettvin, Maturana, McCulloch, & Pitts, 1959; Barlow, 1972). On the other hand, theoretical arguments suggest that in most cases, broadly tuned units and distributed information processing are better suited for accurate representations (Hinton, McClelland, & Rumelhart, 1986; Georgopoulos, Schwartz, & Kettner, 1986; Baldi & Heiligenberg, 1988; Snippe & Koenderink, 1992; Seung & Sompolinsky, 1993; Salinas & Abbott, 1994; Snippe, 1996; Eurich & Schwegler, 1997; Zhang, Ginzburg, McNaughton, & Sejnowski, 1998; Zhang & Sejnowski, 1999). A useful measure of the information content of a set of spike trains emitted by a population of neurons is the Fisher information matrix (Deco & Obradovic, 1997; Brunel & Nadal, 1998), which yields a lower bound on the mean squared error for unbiased estimators of the encoded quantity (Cramér-Rao inequality). In a recent approach using Fisher information, Zhang and Sejnowski (1999) derived an expression for the encoding accuracy of a population of spiking neurons as a function of the tuning width,

σ , for radially symmetric receptive fields in a D -dimensional space. The calculation shows that the encoding accuracy increases with σ if $D \geq 3$.

This result can be complemented by the following consideration. Neurons generally respond to many stimulus features. The main function of a neural population, however, may be the processing of only a subset of these features. In the following, we derive an optimal coding strategy of a population of neurons whose tuning widths differ in the different dimensions. We also study the case of extremely small receptive fields where the population approach breaks down, and demonstrate the existence of an optimal tuning width if only one of the stimulus features is to be encoded accurately. Furthermore, we consider the situation that only a part of all encoded stimulus properties is accessible to an observer. General formulas will be illustrated by the example of a population of neurons with gaussian tuning functions and Poissonian spike statistics. Since part of this article is a continuation of Zhang and Sejnowski (1999), we adopt much of their formalism.

2 Model

Consider a stimulus characterized by a position $\mathbf{x} = (x_1, \dots, x_D)$ in a D -dimensional stimulus space, where x_i ($i = 1, \dots, D$) is measured relative to the total range of values in the i th dimension such that it is dimensionless. Furthermore, consider a population of N identical stochastically spiking neurons that fire $\mathbf{n} = (n^{(1)}, \dots, n^{(k)}, \dots, n^{(N)})$ spikes in a time interval τ following the presentation of the stimulus. The joint probability distribution, $P(\mathbf{n}; \mathbf{x})$, is assumed to take the form

$$P(\mathbf{n}; \mathbf{x}) = \prod_{k=1}^N P^{(k)}(n^{(k)}; \mathbf{x}), \quad (2.1)$$

that is, the neurons have independent spike generation mechanisms. Note that the neural firing rates may still be correlated; the neurons may have common input or even share the same tuning function. The tuning function of neuron k , $f^{(k)}(\mathbf{x})$, gives the mean firing rate of neuron k in response to the stimulus at position \mathbf{x} . Unlike Zhang and Sejnowski (1999), we assume here a form of the tuning function that is not necessarily radially symmetric,

$$f^{(k)}(\mathbf{x}) = F\phi\left(\sum_{i=1}^D \frac{(x_i - c_i^{(k)})^2}{\sigma_i^2}\right) =: F\phi(\xi^{(k)2}), \quad (2.2)$$

where $\xi_i^{(k)2} := (x_i - c_i^{(k)})^2 / \sigma_i^2$ for $i = 1, \dots, D$, and $\xi^{(k)2} := \xi_1^{(k)2} + \dots + \xi_D^{(k)2}$. $F > 0$ denotes the maximal firing rate of the neurons, which requires that $\max_z \phi(z) = 1$. The firing rates depend on the stimulus only by the local values of the tuning functions, such that $P^{(k)}(n^{(k)}; \mathbf{x})$ can be written in the form $P^{(k)}(n^{(k)}; \mathbf{x}) = S(n^{(k)}, f^{(k)}(\mathbf{x}), \tau)$. The function $S: \mathbb{N}^0 \times [0; F] \times]0; \infty[\rightarrow]0; 1[$

is required to be logarithmically differentiable with respect to its second argument but is otherwise arbitrary. For a population of tuning functions with centers $\mathbf{c}^{(1)}, \dots, \mathbf{c}^{(N)}$, a density $\eta(\mathbf{x})$ is introduced according to $\eta(\mathbf{x}) := \sum_{k=1}^N \delta(\mathbf{x} - \mathbf{c}^{(k)})$.

The Fisher information matrix, (J_{ij}) , is defined as

$$J_{ij}(\mathbf{x}) := E \left[\left(\frac{\partial}{\partial x_i} \ln P(\mathbf{n}; \mathbf{x}) \right) \left(\frac{\partial}{\partial x_j} \ln P(\mathbf{n}; \mathbf{x}) \right) \right] \tag{2.3}$$

(Deco & Obradovic, 1997), where $E[\dots]$ denotes the expectation value over the probability distribution $P(\mathbf{n}; \mathbf{x})$. The Cramér-Rao inequality gives a lower bound on the expected estimation error in the i th dimension, $\epsilon_{i,\min}$ ($i = 1, \dots, D$), provided that the estimator is unbiased. In the case of a diagonal Fisher information matrix, it is given by $\epsilon_{i,\min}^2 = 1/J_{ii}(\mathbf{x})$.

3 Information Content of Neural Responses

3.1 Population Fisher Information. For a single-model neuron k described in the previous section, the Fisher information (see equation 2.3) reduces to

$$J_{ij}^{(k)}(\mathbf{x}) = \frac{1}{\sigma_i \sigma_j} A_\phi \left(\xi^{(k)2}, F, \tau \right) \xi_i^{(k)} \xi_j^{(k)}. \tag{3.1}$$

The function A_ϕ , which is independent of k , abbreviates the expression

$$A_\phi(z, F, \tau) := 4F^2 \phi'(z)^2 \sum_{n=0}^{\infty} S(n, F\phi(z), \tau) T^2[n, F\phi(z), \tau], \tag{3.2}$$

where $T[n, z, \tau] := \frac{\partial}{\partial z} \ln S(n, z, \tau)$ and $\phi'(z) := \frac{d}{dz} \phi(z)$.

The independence assumption (see equation 2.1) implies that the population Fisher information, $J_{ij}(\mathbf{x})$, is the sum of the contributions of the individual neurons, $J_{ij}(\mathbf{x}) = \sum_{k=1}^N J_{ij}^{(k)}(\mathbf{x})$. For a constant distribution of tuning curves, $\eta(\mathbf{x}) \equiv \eta \equiv \text{const.}$, the population Fisher information becomes independent of \mathbf{x} , and the off-diagonal elements vanish (Zhang & Sejnowski, 1999). In this case, the diagonal elements $J_i := J_{ii}$ are given by

$$J_i = \eta D K_\phi(F, \tau, D) \frac{\prod_{k=1}^D \sigma_k}{\sigma_i^2}, \tag{3.3}$$

where K_ϕ is defined to be

$$K_\phi(F, \tau, D) := \frac{1}{D} \int_{-\infty}^{\infty} d\xi_1 \dots \int_{-\infty}^{\infty} d\xi_D A_\phi(\xi^2, F, \tau) \xi_1^2. \tag{3.4}$$

For identical tuning widths in all dimensions, $\sigma_i \equiv \sigma$ ($i = 1, \dots, D$), the total Fisher information, $J := (\sum_{i=1}^D J_i^{-1})^{-1}$, is given by $J = \eta K_\phi(F, \tau, D) \sigma^{D-2}$, that is, equation 2.3 from Zhang and Sejnowski (1999) is recovered.

Equation 3.3 shows that the Fisher information in the i th dimension is determined by a trade-off between the product of the tuning widths in the remaining dimensions $k \neq i$, $\prod_{k \neq i} \sigma_k$, and the tuning width in dimension i , σ_i . In order to assess the consequences of equation 3.3 for neural encoding strategies, we provide an intuitive interpretation of the ratio of tuning widths by introducing effective receptive fields.

3.2 Effective Receptive Fields and Encoding Subpopulation. The tuning functions $f^{(k)}(\mathbf{x})$ encountered empirically typically have a single maximum. For such curves, large values of the single-neuron Fisher information (see equation 3.1) are generally restricted to a region around the center of the tuning function, $\mathbf{c}^{(k)}$. The fraction $p(\beta)$ of Fisher information that falls into a region $\sqrt{\xi^{(k)2}} \leq \beta$ around $\mathbf{c}^{(k)}$ is given by

$$p(\beta) := \frac{\int_{E_D} d^D \mathbf{x} \sum_{i=1}^D J_{ii}(\mathbf{x})}{\int_{\mathbb{R}^D} d^D \mathbf{x} \sum_{i=1}^D J_{ii}(\mathbf{x})}, \quad (3.5)$$

where the index (k) was dropped because the tuning curves are assumed to have identical forms. A straightforward calculation shows that $p(\beta)$ is given by

$$p(\beta) = \frac{\int_0^\beta d\xi \xi^{D+1} A_\phi(\xi^2, F, \tau)}{\int_0^\infty d\xi \xi^{D+1} A_\phi(\xi^2, F, \tau)}. \quad (3.6)$$

Equation 3.6 allows the definition of an effective receptive field, $\text{RF}_{\text{eff}}^{(k)}$, inside of which neuron k conveys a major fraction p_0 of Fisher information,

$$\text{RF}_{\text{eff}}^{(k)} := \left\{ \mathbf{x} \mid \sqrt{\xi^{(k)2}} \leq \beta_0 \right\}, \quad (3.7)$$

where β_0 is chosen such that $p(\beta_0) = p_0$.

The Fisher information a neuron k carries is small unless $\mathbf{x} \in \text{RF}_{\text{eff}}^{(k)}$. This has the consequence that a fixed stimulus \mathbf{x} is actually encoded by only a subpopulation of neurons. If the distribution of tuning functions does not vary in the proximity of the stimulus position \mathbf{x} , $\eta(\mathbf{x}') \equiv \eta = \text{const}$ for $|x_i - x'_i| < \beta_0 \sigma_i$ ($i = 1, \dots, D$), the point \mathbf{x} in stimulus space is covered by

$$N_{\text{code}} := \eta \frac{2\pi^{D/2}(\beta_0)^D}{D\Gamma(D/2)} \prod_{j=1}^D \sigma_j \quad (3.8)$$

receptive fields. With the help of equation 3.8, the population Fisher information (see equation 3.3) can be rewritten as

$$J_i = \frac{D^2 \Gamma(D/2)}{2\pi^{D/2} (\beta_0)^D} K_\phi(F, \tau, D) \frac{N_{\text{code}}}{\sigma_i^2}. \quad (3.9)$$

Equation 3.9 can be interpreted as follows: We assume that the population of neurons encodes stimulus dimension i accurately, while all other dimension are of secondary importance. The minimal encoding error for dimension i , J_i^{-1} , is determined by the shape of the tuning curve that enters through β_0 , $K_\phi(F, \tau, D)$, and N_{code} ; by the tuning width in dimension i , σ_i ; and by the active subpopulation, N_{code} . There is a trade-off between σ_i and N_{code} . On the one hand, the encoding error can be decreased by decreasing σ_i , which enhances the Fisher information carried by each single neuron. Decreasing σ_i , on the other hand, will also shrink the active subpopulation via equation 3.8. This impairs the encoding accuracy, because the stimulus position is evaluated by fewer independent estimators. If equation 3.9 is valid due to a sufficient receptive field overlap, N_{code} can be increased by increasing the tuning widths, σ_j , in all other dimensions $j \neq i$. This effect is illustrated in Figure 1.

3.3 Narrow Tuning. In order to study the effects of narrow tuning in dimension i , $\sigma_i \rightarrow 0$, we consider a constant distribution of stimuli, $\rho(\mathbf{x}) = \text{const.}$, in the region of stimulus space containing the receptive fields of the neural population. A straightforward calculation shows that in this case, the stimulus-averaged Fisher information,

$$\langle J_i \rangle := \int_{-\infty}^{\infty} dx_1 \dots \int_{-\infty}^{\infty} dx_D \rho(\mathbf{x}) J_i(\mathbf{x}), \quad (3.10)$$

is given by $\langle J_i \rangle = J_i$, that is, the average Fisher information for arbitrary distributions of tuning functions $\eta(\mathbf{x})$ is equal to the Fisher information (see equation 3.3) for the uniformly distributed population. Even if σ_i becomes so small that gaps appear between the receptive fields, the mean Fisher information still increases with decreasing σ_i . This property is due to those few stimuli that can be localized extremely accurately by the firing of the narrowly tuned cells. The majority of stimuli, however, fall into the gaps and are not well represented any more. A neural system with these properties is obviously a bad encoder, which shows that $\langle J_i \rangle$ is not a suitable measure for the system performance. Consider instead the stimulus-averaged squared minimal encoding error for unbiased estimators,

$$\langle \epsilon_{i,\min}^2 \rangle := \int_{-\infty}^{\infty} dx_1 \dots \int_{-\infty}^{\infty} dx_D \rho(\mathbf{x}) \left[J(\mathbf{x})^{-1} \right]_{ii}. \quad (3.11)$$

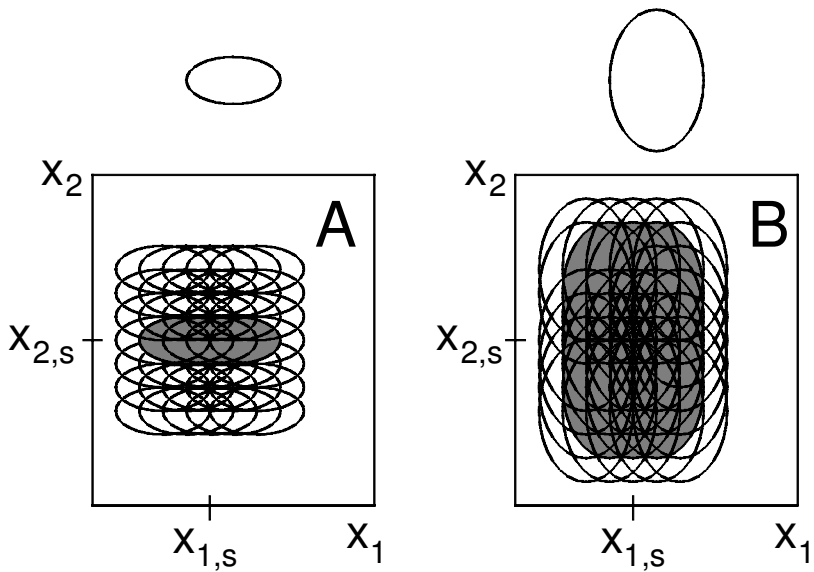


Figure 1: Population response to the presentation of a stimulus characterized by parameters $x_{1,s}$ and $x_{2,s}$. Feature x_1 is to be encoded accurately. Effective receptive field shapes are indicated for both populations. If neurons are narrowly tuned in x_2 (A), the active population (shaded) is small (here: $N_{\text{code}} = 3$). Broadly tuned receptive fields for x_2 (B) yield a much larger population (here: $N_{\text{code}} = 15$), thus increasing the encoding accuracy.

For uniformly distributed tuning curves and a sufficient receptive field overlap, equation 3.11 can be simplified using equation 3.9, which yields $\langle \epsilon_{i,\text{min}}^2 \rangle = 1/J_i$ as expected.

For narrowly tuned cells, however, the condition $\eta(\mathbf{x}) \equiv \eta = \text{const.}$ breaks down, and equation 3.9 is no longer valid. The following argument shows that in contrast to the high-overlap approximation $1/J_i$, $\langle \epsilon_{i,\text{min}}^2 \rangle$ will diverge for $\sigma_i \rightarrow 0$. Let $\lambda_k(\mathbf{x}) \geq 0$ be the k th eigenvalue of the real-valued, symmetrical Fisher information matrix, and $U(\mathbf{x})$ the orthogonal transformation that diagonalizes $J(\mathbf{x})$, that is, $U(\mathbf{x})J(\mathbf{x})U(\mathbf{x})^T = \text{diag}[\lambda_1(\mathbf{x}), \dots, \lambda_D(\mathbf{x})]$. If $\lambda_{\text{max}}(\mathbf{x}) := \max_j \{\lambda_j(\mathbf{x})\}$, one has

$$\begin{aligned} \langle \epsilon_{i,\text{min}}^2 \rangle &= \left\langle \sum_{j=1}^D [U(\mathbf{x})_{ij}]^2 \frac{1}{\lambda_j(\mathbf{x})} \right\rangle \\ &\geq \left\langle \frac{1}{\lambda_{\text{max}}(\mathbf{x})} \sum_{j=1}^D [U(\mathbf{x})_{ij}]^2 \right\rangle = \left\langle \frac{1}{\lambda_{\text{max}}(\mathbf{x})} \right\rangle \end{aligned} \tag{3.12}$$

independent of i . For $\sigma_i \rightarrow 0$, regions of stimulus space emerge that are not covered by any receptive fields. These gaps are characterized by very small eigenvalues of $J(\mathbf{x})$, that is, $\lambda_{\max}(\mathbf{x}) \rightarrow 0$. Thus, the minimal encoding error $\langle \epsilon_{i,\min}^2 \rangle$ diverges in the presence of unrepresented areas in stimulus space. This implies that the total error $\langle \epsilon_{\min}^2 \rangle := \sum_{i=1}^D \langle \epsilon_{i,\min}^2 \rangle$ will also become infinite if any of the tuning widths approaches zero.

Equation 3.3 shows that the accuracy also decreases for large σ_i . Consequently, there must be an optimal tuning width between the two regimes of broad and small tuning. In the next section, we calculate this optimal tuning width in a specific example.

Example: Poissonian Spiking and Gaussian Tuning Functions. For Poissonian spike generation and gaussian tuning functions, the single-neuron Fisher information, equation 3.1, becomes

$$f_{ij}^{(k)}(\mathbf{x}) = \frac{1}{\sigma_i \sigma_j} F \tau \exp\left(-\xi^{(k)2}/2\right) \xi_i^{(k)} \xi_j^{(k)}. \tag{3.13}$$

The population Fisher information, equation 3.3, reduces to

$$J_i = (2\pi)^{D/2} \eta F \tau \frac{\prod_{k=1}^D \sigma_k}{\sigma_i^2}. \tag{3.14}$$

The definition of the effective receptive field is obtained from $p(\beta)$ in equation 3.6, for which we have

$$p(\beta) = \begin{cases} 1 - e^{-\beta^2/2} \sum_{k=0}^{D/2} \frac{\beta^{2k}}{2^k k!}, & D \text{ even} \\ \frac{1}{2^{D/2} \Gamma(1+D/2)} \left[-e^{-\beta^2/2} \sum_{k=0}^{(D-1)/2} \frac{D!! \beta^{D-2k}}{(D-2k)!!} + D!! \sqrt{\frac{\pi}{2}} \operatorname{Erf}\left(\frac{\beta}{\sqrt{2}}\right) \right], & D \text{ odd,} \end{cases} \tag{3.15}$$

where $\operatorname{Erf}(x) := \frac{2}{\sqrt{\pi}} \int_0^x dt \exp(-t^2)$ is the gaussian error function.

For a specific distribution of tuning curves in the stimulus space, the optimal tuning width mentioned in the previous paragraph can be calculated explicitly. Consider a population of neurons with tuning curves aligned on a regular grid with fixed spacing Δ , such that $\mathbf{c}^{(k)} = \sum_{l=1}^D \Delta k_l \mathbf{e}_l$, where $k_l \in \mathbf{Z}$, and \mathbf{e}_l is the l th unit vector. For simplicity, we restrict the calculation to the case $D = 2$ and study the stimulus-averaged minimal encoding error $\langle \epsilon_{1,\min}^2 \rangle$

defined in equation 3.11 as a function of the tuning widths $\hat{\sigma}_1 := \sigma_1/\Delta$ and $\hat{\sigma}_2 := \sigma_2/\Delta$. As a consequence of the grid regularity, it can be written in the form

$$\langle \epsilon_{1,\min}^2 \rangle = \Delta^2 \frac{4\hat{\sigma}_1^3 \hat{\sigma}_2}{F\tau} \int_0^{\frac{1}{2\hat{\sigma}_1}} d\xi_1 \int_0^{\frac{1}{2\hat{\sigma}_2}} d\xi_2 \times \left[E_2(\xi_1, \hat{\sigma}_1) E_0(\xi_2, \hat{\sigma}_2) - \frac{E_1(\xi_1, \hat{\sigma}_1)^2 E_1(\xi_2, \hat{\sigma}_2)^2}{E_2(\xi_2, \hat{\sigma}_2) E_0(\xi_1, \hat{\sigma}_1)} \right]^{-1}, \quad (3.16)$$

where $E_l(\xi, \hat{\sigma}) := \sum_{k \in \mathbb{Z}} \exp[-(\xi - k/\hat{\sigma})^2/2]/(\xi - k/\hat{\sigma})^l$. For large tuning width in either direction, $\hat{\sigma} \gg 1$, the sum in $E_l(\xi, \hat{\sigma})$ may be approximated by an integral that is independent of ξ , and one finds $\lim_{\hat{\sigma} \rightarrow \infty} E_1(\xi, \hat{\sigma}) \rightarrow 0$ and $\lim_{\hat{\sigma} \rightarrow \infty} E_l(\xi, \hat{\sigma}) \rightarrow \sqrt{2\pi} \hat{\sigma}$ for $l = 0, 2$. Thus, the broad-tuning limit $\hat{\sigma}_1 \gg 1$ and $\hat{\sigma}_2 \gg 1$ yields $\langle \epsilon_{1,\min}^2 \rangle = \Delta^2 \hat{\sigma}_1 / (2\pi F\tau \hat{\sigma}_2) = 1/J_i$; one recovers the broad-tuning Fisher information J_i from (3.14) with $D = 2$ and $1/\eta = \Delta^2$.

The encoding error (see equation 3.16) is plotted in Figure 2 as a function of $\hat{\sigma}_1$ for different values of $\hat{\sigma}_2$. The agreement with the broad-tuning approximation for large tuning widths is clearly visible. If one of the tuning widths is small, however, the minimal encoding error ($\langle \epsilon_{1,\min}^2 \rangle$) no longer equals the inverse of equation 3.14. The deviations can be observed in Figure 2 for small $\hat{\sigma}_1$ (right part of the plotted functions) and small $\hat{\sigma}_2$ (upper curve).

Thus, Figure 2 reflects two main results of this article. First, the broader the tuning is for feature 2, the smaller the encoding error of feature 1. This illustrates our proposed encoding strategy. Second, the encoding error for feature 1 has a unique minimum as a function of $\hat{\sigma}_1$. From the arguments of the previous paragraph, one expects the optimal tuning width σ_1^{opt} to be approximately equal to the smallest possible tuning width for which no gaps appear between the receptive fields of neighboring neurons. Indeed, the numerical calculation yields an optimal tuning curve width of $2\sigma_1^{\text{opt}} \approx 0.8\Delta$, which corresponds to the array of tuning curves shown in the inset of Figure 2.

For very small tuning widths $\hat{\sigma}_i$, one practically leaves the validity range of our Fisher information analysis. If the stimulus falls into a gap between receptive fields such that the cells do not fire within a reasonable time interval τ , there is no possibility of making an unbiased estimation of the stimulus features. Thus, the Fisher information measure cannot be applied for $\hat{\sigma}_i \rightarrow 0$. At the calculated optimal tuning width in our example, however, there is still a sufficient receptive field overlap to allow unbiased estimates (cf. the inset of Figure 2). Therefore, we argue that σ_1^{opt} is well within the range where Fisher information is a valid measure of encoding accuracy.

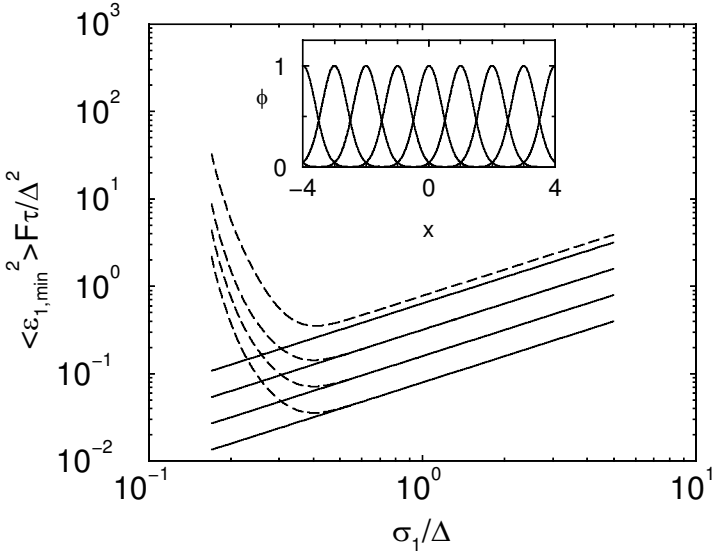


Figure 2: Numerical results for the stimulus-averaged squared minimal encoding error from equation 3.16. Dashed line: $\langle \epsilon_{1,\min}^2 \rangle / (\Delta^2 F^{-1} \tau^{-1})$ as a function of $\hat{\sigma}_1$ for $D = 2$ and different values of $\hat{\sigma}_2$ (from top to bottom): $\hat{\sigma}_2 = 0.25, 0.5, 1, 2$. Solid line: analytical broad-tuning result, that is, $\langle \epsilon_{1,\min}^2 \rangle / (\Delta^2 F^{-1} \tau^{-1}) = (1/J_1) / (\Delta^2 F^{-1} \tau^{-1})$ from equation 3.14. The inset shows gaussian tuning curves of optimal width, $\sigma^{\text{opt}} \approx 0.4\Delta$.

3.4 The Problem of Hidden Dimensions. A situation that is frequently encountered empirically is that of incomplete knowledge of the neural behavior. Usually an observer will study a neural population with respect to a number of well-defined stimulus dimensions and be unable to find all relevant dimensions or unable to find a suitable parameterization for certain stimulus properties. We assume that only $d \leq D$ of the D total dimensions are known. The Fisher information (see equation 3.3) can be written as $J_i = X(\prod_{j=1}^d \sigma_j) / \sigma_i^2$, where $X := \eta DK_\phi(F, \tau, D)(\prod_{j=d+1}^D \sigma_j)$ is an experimentally unknown constant. If the neurons' tuning curves have been measured in more than one dimension, X can be eliminated by considering the tuning widths as a relative measure of information content,

$$\frac{\epsilon_{i,\min}^2}{\sum_{j=1}^d \epsilon_{j,\min}^2} = \frac{\sigma_i^2}{\sum_{j=1}^d \sigma_j^2}, \quad (3.17)$$

where i is one of the known dimensions $1, \dots, d$. Equation 3.17 is independent of the unknown (or experimentally ignored) stimulus dimensions $d + 1, \dots, D$, which are to be held fixed during the measurement of the d tuning widths. On the basis of the accessible tuning widths only, it gives a relative quantitative measure on how accurately the individual stimulus dimensions are encoded by the neural population.

Equation 3.17 states that if σ_i^2 is small compared to the sum of the squares of all measured tuning widths, the population activity allows an accurate reconstruction of the corresponding stimulus feature: the population contains much information about x_i . A large ratio, on the other hand, indicates that the population response is unspecific with respect to feature x_i . As an example, consider the different pathways of signal processing that have been suggested for the visual system (Livingstone & Hubel, 1988). The model states that information about form, color, movement, and depth is in part processed separately in the visual cortex. Based on the physiological properties of visual cortical neurons, equation 3.17 yields a quantitative assessment of the specificity of their encoding with respect to the above-mentioned properties—our method provides a test criterion for the validity of the pathway model.

4 Conclusion

We have calculated the Fisher information for a population of stochastically spiking neurons encoding a multitude of stimulus features. If a single feature is to be encoded accurately, narrow tuning for this dimension and a broad tuning in all other dimensions is found to be the optimal encoding strategy. The narrow tuning increases the information content of individual neurons for the feature to be encoded, while the broad tuning in other dimensions increases the population of neurons that actively take part in the representation. However, extremely narrow tuning functions impair performance because the tuning functions must always have sufficient overlap. For an accurate representation of a single feature, there is an optimal tuning width no matter how many stimulus dimensions are encoded in addition. Our results are suitable for applications to sensory or motor systems. Equation 3.17 provides a criterion that can be used to derive quantitative statements on the functional significance of neuron classes based on the measurement of tuning curves.

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