Attention Modulation of Neural Tuning Through Peak and Base Rate

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This study investigates the influence of attention modulation on neural tuning functions. It has been shown in experiments that attention modulation alters neural tuning curves. Attention has been considered at least to serve to resolve limiting capacities and to increase the sensitivity to attended stimulus, while the exact functions of attention are still under debate. Inspired by recent experimental results on attention modulation, we investigate the influence of changes in the height and base rate of the tuning curve on the encoding accuracy, using the Fisher information. Under an assumption of stimulus-conditional independence of neural responses, we derive explicit conditions that determine when the height and base rate should be increased or decreased to improve encoding accuracy. Notably, a decrease in the tuning height and base rate can improve the encoding accuracy in some cases. Our theoretical results can predict the effective size of attention modulation on the neural population with respect to encoding accuracy. We discuss how our method can be used quantitatively to evaluate different aspects of attention function.

1 Introduction

One of the central issues in neuroscience is to understand how an ensemble of neural population encodes the external world. Many theoretical studies have addressed the accuracy of neural population coding with respect to tuning functions (Paradiso, 1988; Lehky & Sejnowski, 1988; Seung & Sompolinsky, 1993; Salinas & Abbott, 1994; Brunel & Nadal, 1998; Zohary, 1992; Sanger, 1998; Zemel, Dayan, & Pouget, 1998; Brown, Frank, Tang, Quirk, & Wilson, 1998; Oram, Földiak, Perrett, & Sengpiel, 1998). The approaches taken by these studies often use Fisher information in terms of tuning functions (Paradiso, 1988; Seung & Sompolinsky, 1993; Snippe, 1996; Pouget, Zhang, Deneve, & Latham, 1998; Zhang & Sejnowski, 1999; Deneve, Latham, & Pouget, 1999; Abbott & Dayan, 1999). This is because the inverse of the Fisher information gives the Cramér-Rao lower bound for decoding errors. In particular, the effect of the tuning width as a parameter of the tuning function is investigated (Seung & Sompolinsky, 1993; Brunel & Nadal, 1998;
Pouget, Deneve, Ducom, & Latham, 1999; Zhang & Sejnowski, 1999). Using this theoretical framework, this study investigates the influence of attention modulation on encoding accuracy through the heights and the base rates of neural tuning functions. Our investigation is inspired by recent experimental findings (McAdams & Maunsell, 1999a; Treue & Martinez-Trujillo, 1999).

Experimental studies have shown that attention alters the properties of tuning functions (Moran & Desimone, 1985; Motter, 1993; Treue & Maunsell, 1996; Luck, Chelazzi, Hillyard, & Desimone, 1997; Reynolds, Chelazzi, & Desimone, 1999). Some experimental studies have suggested that attention induces systematic narrowing of tuning widths (Spitzer, Desimone, & Moran, 1988; Haenny & Schiller, 1988), whereas other studies have failed to show evidence of narrowing tuning widths (Vogels & Orban, 1990). Recently McAdams and Maunsell (1999a) investigated this question of whether attention modulation leads to a narrowing of neural tuning widths. Interestingly, they have shown for neurons in V4 that attention modulation does not change the tuning width but rather increases the height measured from the base rate of the tuning function, while attention modulation also increases the base rate. Treue and Martinez-Trujillo (1999) observed similar phenomena for the neurons in MT. It is then important to ask how attention modulation via the height and base rate instead of the width of the tuning function affects the encoding accuracy of a neural population.

This article answers this question by assuming the Poisson spike distribution with stimulus-conditional independence. The study shows, using Fisher information as a measure, that encoding accuracy is improved by an increase in both the height and base rate of neurons when the centers of the tuning function are close to the given stimulus. At the same time, we show that the accuracy can be improved not by an increase but by a decrease in the height and base rate when the centers are not so close to the given stimulus. A mathematical analysis provides us with explicit conditions that determine when the height and base rate should be increased or decreased together to improve encoding accuracy. With this analysis, we show the optimal size of an attention region, in which both the tuning heights and base rates of a neural population are increased, and outside of which both are decreased, in order to optimize the overall accuracy.

The analysis treats only the case of stimulus-conditional independent neural responses, which is simplest to begin with. One very important case is correlated firing, which can decrease the total Fisher information (Yoon & Sompolinsky, 1999). For some correlational structures, some of the important results derived in this study still hold qualitatively in the correlated case with attention, provided both the central limit theorem and the law of large numbers are valid. Further discussion is provided later, although a detailed analysis in such cases will have to be performed in the future. Finally, a brief discussion is given in relation to a competitive attention model (Desimone & Duncan, 1995).
2 Analysis

2.1 Formulation. Let us first consider the situation where a population of $M$ neurons ($m = 1, \ldots, M$) encodes a stimulus with respect to its one-dimensional feature, denoted by $x$. For example, $x$ can be an orientation selectivity scaled by $[-90^\circ, 90^\circ]$. Given $x$, we suppose that the $m$th neuron emits $n_m$ spikes with probability $p(n_m; \psi_m(x))$, where $\psi_m$ stands for the tuning function of the $m$th neuron. For example, if $p(n_m; \psi_m(x))$ is the Poisson distribution, $\psi_m(x)$ is the parameter indicating the mean firing rate given the stimuli $x$. The entire Fisher information $I$, defined below, provides a good measure for decoding the accuracy of $x$. This is because the inverse of $I$ sets the Cramér-Rao lower bound on the mean squared decoding error $\varepsilon = \hat{x} - x$, where $\hat{x}$ is an estimated $x$, decoded from the activities of all the neurons. This is written as

$$E[\varepsilon^2] \geq \frac{1}{I},$$

where $E$ denotes expectation. The bound can be achieved by using the maximum likelihood method, asymptotically in general, exactly when the probability distribution is of exponential family and the expectation parameters are used (Lehmann, 1983). It has been suggested that biologically plausible neural models may almost achieve this bound (Pouget et al., 1998; Deneve et al., 1999). For simplicity, we assume that the joint probability of spikes of a neural population is uncorrelated given a stimulus $x$, that is, the stimulus-conditional independence assumption; this assumption is similar to many previous studies (Paradiso, 1988; Seung & Sompolinsky, 1993; Pouget et al., 1998; Zhang & Sejnowski, 1999). In this case, we can write

$$I(x) = \sum_{m=1}^{M} I_m(x),$$

(2.1)

where $I_m(x)$ is the Fisher information of the $m$th neuron given $x$ and is defined by

$$I_m(x) \equiv E_m \left[ \left( \frac{d}{dx} \log p(n_m; \psi_m(x)) \right)^2 \right],$$

(2.2)

where $E_m$ denotes expectation with respect to probability $p(n_m; \psi_m(x))$.

In this study, we suppose that the spike probability distribution $p(n_m; \psi_m(x))$ is Poisson:

$$p(n_m; \psi_m(x)) = \frac{(\psi_m(x) \Delta t)^n}{n!} e^{-\psi_m(x) \Delta t},$$

(2.3)

where $\Delta t$ indicates a unit of time period used to count the number of spikes. To simplify the derivations, we consider the time period as one unit in the following ($\Delta t = 1$).
2.2 Tuning Function. We set the tuning function \( \psi_m(x) \) of the \( m \)th neuron as

\[
\psi_m(x) = \psi(x; a_m, b_m, c_m, \sigma_m) = a_m \phi_m(x; c_m, \sigma_m) + b_m,
\]

where \( b_m \) stands for the background noise, or the spontaneous firing rate, which we call the base rate in this article, and \( c_m \) and \( \sigma_m \) are the center and the tuning width of the tuning function, respectively; \( \phi_m(x) = \phi_m(x; c_m, \sigma_m) \) determines the shape of the tuning function normalized by \( \phi_m(x) = 1 \) at \( x = c_m \), which is usually radial symmetric, and monotonically decreases with respect to \(|x - c_m|\), satisfying \( \phi_m(x) \to 0 \) \((|x - c_m| \to \infty)\). A typical example is given as \( \phi_m(x) = \exp(-\frac{(x-c_m)^2}{\sigma_m^2}) \). To be more concrete, this form will be used in the following analysis, although a specific form of \( \phi(x) \) plays a minor role in our analysis. The height \( a_m \) of the tuning function is measured from the base rate \( b_m \). Figure 1 (top) shows an example of the tuning function.

2.3 Fisher Information of a Single Neuron. Let us first evaluate the Fisher information of a single neuron. The subscript \( m \) is dropped in this section when no confusion occurs. Since the inverse of the Fisher information \( I = I_m \) sets the lower bound of the encoding error, a larger value of \( I \) implies a smaller encoding error, that is, an increased sensitivity. For attention modulation, then, it is natural to expect that \( I(x) \) will be increased by attention for stimulus \( x \), so that stimulus \( x \) is encoded more accurately.

The Fisher information is computed as

\[
I = E_p \left[ \left( \frac{\partial}{\partial x} \log p(n; \psi(x)) \right)^2 \right] \\
= \frac{1}{\psi(x)} \left( \frac{\partial \psi(x)}{\partial x} \right)^2 \\
= \frac{4(x - c)^2 \phi^2(x)}{\sigma^4} \frac{a^2}{\psi(x)} + b.
\]

Figure 1 (middle) shows \( I(x) \), given the tuning function in Figure 1 (top). Note that the maximum of \( I(x) \) is not at the center of the tuning function. This is because the first derivative of the tuning function with respect to \( x \) becomes zero at the center.

Given the form of \( I(x) \) in equation 2.5, it is clear that an increase in the base rate \( b \) leads to a decrease in \( I(x) \). By checking \( \frac{\partial I}{\partial a} \), it is easy to see that an increase in the height \( a \) leads to an increase in \( I \) for any \( x \). Hence, if possible, the optimal strategy to alter the tuning function with respect to \( a \) and \( b \) is to increase \( a \) and decrease \( b \) at the same time, so that \( I(x) \) is increased for any
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Figure 1: (Top) An example of tuning function: \( \psi_m(x) = a \phi_m(x; c_m, \sigma_m) + b_m \) where \( \phi(x) = \exp(-\frac{(x-c)^2}{2\sigma^2}) \) and \( a = 30, b = 3, \sigma = 30, c = 0 \). (Middle) Fisher information \( I(x) \) given the above tuning function. (Bottom) Distance \( l^* \) is indicated as a vertical line measured from \( c = EX_c \), where \( (\delta a, \delta b) = (\pm 4, 2) \) is used. With these parameters, \( l^* = 32.92 \). The form of tuning function and Fisher information is also superimposed with scaling to illustrate their relationship with \( l^* \) in this example.

In contrast to this optimal strategy, the experimental results (McAdams & Maunsell, 1999a; Treue and Martínez-Trujillo, 1999) indicate that by attention modulation, the height and base rate, \( (a, b) \), increase or decrease together. This may be caused by physiological constraints on the neurons. In the rest of the article, therefore, we will be concerned only with the two cases: \( a \) and \( b \) increase or decrease together.
Let us inspect the variational change of $I$, denoted by $\delta I$, with respect to a small change of the height and the base rate, denoted by $\delta a$ and $\delta b$ as

$$\delta I = \frac{\partial I}{\partial a} \delta a + \frac{\partial I}{\partial b} \delta b,$$

from which we obtain

$$\delta I = \frac{4a^2(x-c)^2\phi^2(x)}{\sigma^4\psi^2(x)} \left\{ \left( \phi(x) + \frac{2b}{a} \right) \delta a - \delta b \right\}.$$

When does $\delta I$ increase? Let us denote a specific value of an attended stimulus with $x^*$ for clarity. Attention modulation gives changes in $a$ and $b$, that is, $\delta a$ and $\delta b$, which are, for example, positive in a neighborhood of $x^*$ and negative outside it. That is, these changes may depend on the relative position ($c$) of the neuron and the attended stimuli $x^*$, that is, $\| x^* - c \|$. Here, we search for the condition that $I(x)$ is enhanced by attended stimulus $x^*$. In order to see if the attention to the stimulus $x^*$ enhances the estimation of $x$, we analyze the case when the sensory stimulus $x$ is close to it ($x \approx x^*$), that is, when attention is approximately correct. Provided $\phi(x) = \exp\left(-\frac{(x-c)^2}{\sigma^2}\right)$, an inspection of equation 2.7 leads to the following condition:

$$\begin{cases}
  \text{when } l^* > \| x^* - c \|, & \delta I(x^*) > 0 \text{ for } \delta a, \delta b > 0 \\
  \text{when } l^* < \| x^* - c \|, & \delta I(x^*) > 0, \text{ for } \delta a, \delta b < 0,
\end{cases}$$

where $l^*$ is defined by

$$l^* = \begin{cases}
  \sigma \sqrt{-\log \left( \frac{\delta b}{\delta a} - \frac{2b}{a} \right)} \left( \frac{\delta b}{\delta a} - \frac{2b}{a} > 0 \right) \\
  \infty \left( \frac{\delta b}{\delta a} - \frac{2b}{a} \leq 0 \right),
\end{cases}$$

where $\delta b/\delta a < 1$ is presumed based on an experimental finding (McAdams & Maunsell, 1999a), which implies $\frac{\delta b}{\delta a} - \frac{2b}{a} < 1$.

Note that a decrease in the height and base rate at the same time can increase the Fisher information when an attended stimulus $x^*$, and hence $x$, which is supposed to be in a small neighborhood of $x^*$, is relatively far from the center of the tuning function (i.e., $l^* < \| x^* - c \|$), provided $l^* \neq \infty$. This result is illuminating. We tend to interpret a decrease in the neural firing, or a decrease in the height and base rate of the neural tuning curve, as an indication that the neuron is modulated to not contribute to further information processing. In contrast, this result suggests that the decrease in the height and base rate of a neuron under some conditions indeed helps the neuron encode the attended stimulus more accurately. In Figure 1 (bottom), as an example, $l^*$ is plotted with respect to the tuning function, and the Fisher
information in Figure 1 (top) and (middle), respectively, with a specific value of \( \delta_a \) and \( \delta_b \). In this example, the peak of the Fisher information is located inside \( l^* \).

The above analysis is done by inspecting the variational change of \( I(x) \). This indicates that the Fisher information \( I(x) \) increases by a decrease in the height and base rate for neurons whose center \( c \) of the tuning function satisfies \( l^* < \|x^* - c\| \). Since the magnitude of \( I(x) \) decreases as \( \|x^* - c\| \) becomes larger after attaining the maximum of \( I(x) \), one may wonder if the region,

\[
R^- = \{c \mid l^* < \|x^* - c\|\},
\]

is significant. For example, if \( I(x^*) \approx 0 \) for neurons in the region \( x^* \in R^- \), the increase in \( I(x^*) \) by \( \delta_a, \delta_b < 0 \) does not seem so important. In fact, however, \( R^- \) is not trivial, at least in some cases. To demonstrate this, let us define

\[
\begin{align*}
&\{x_{\text{max}} = \text{arg max}_x I(x, c)\} \\
&l_{\text{max}} = \|x_{\text{max}} - c\|
\end{align*}
\]

where the distance \( l_{\text{max}} \) is given by solving

\[
\frac{\partial I(x,c)}{\partial x} = 0,
\]

or

\[
l_{\text{max}} = \sigma \sqrt{\frac{a\phi(x_{\text{max}}) + b}{a\phi(x_{\text{max}}) + 2b}},
\]

The relationship between \( l^* \) and \( l_{\text{max}} \) (i.e., whether \( l^* > l_{\text{max}} \) or \( l_{\text{max}} > l^* \)) can vary, depending on parameters. In other words, there are some cases when, even for \( x_{\text{max}} \) that gives the maximum Fisher information, not an increase but a decrease in the height and base rate yields the increase in the Fisher information.

It is only when \( \frac{ab}{2a} - \frac{2b}{T} > 0 \) that a decrease in the height and base rate may induce an improvement in the encoding accuracy for \( x^* \) for which \( l^* < \|x^* - c\| \). The condition \( \frac{ab}{2a} - \frac{2b}{T} > 0 \), or equivalently \( \frac{ab}{2a} > \frac{2b}{T} \), hence, may be useful in investigating the property of each neuron in experimental data.

**Examples.** The distance \( l^* \) is a useful measure in determining whether to increase or decrease \( a \) and \( b \) for neuron \( c \) to attain \( \delta I(x^*) > 0 \) for an attended stimulus \( x^* \), given the tuning function parameters of a neuron. Figure 2 shows different examples of the tuning functions with respect to \( l^* \). Figure 2A shows a tuning function and its \( l^* \), using the same parameters in Figure 1 (top). Figure 2B shows the tuning function that has the same parameters as the function in Figure 2A except for the smaller width \( \sigma \). Figures 2C and 2D show two cases where \( l^* = \infty \) so that \( I(x) \) always increases by \( \delta a, \delta b > 0 \) for any \( x \). Figure 2E indicates an example where \( \frac{ab}{2a} \sim 1 \). The plot in Figure 2F is inspired by the observations of McAdams and Maunsell (1999a). This tuning function has a high base rate and a low height in the
normal (unattended) condition and can have a relatively larger height increase in the attended condition. These two characteristics together or either of them can easily lead to $l^* = \infty$ because $\frac{1}{2} \frac{\delta b}{\delta a} < \frac{\delta b}{\delta a}$.

2.4 Population Coding. Let us now consider a population of $M$ neurons ($m = 1, \ldots, M$), where the heights, base rates, and widths of all neurons are the same—$a_m = a, b_m = b, \sigma_m = \sigma$—in a normal or unattended condition. We search for the condition when, in this neural population, attention modulation leads to an improvement in the encoding accuracy for the attended stimulus $x^*$, where the sensory stimulus is assumed to be close to the attended stimulus ($x \approx x^*$). In other words, the Fisher information $I(x^*) = \sum_{m=1}^{M} I(x^*, c_m)$ (by equation 2.1) should increase. The analysis in the previous section leads us to conclude that the optimal attention modulation is, for each neuron $m$,

$$
\begin{cases}
\text{when } \|x^* - c_m\| < l^*, & \delta a_m, \delta b_m > 0 \\
\text{when } \|x^* - c_m\| > l^*, & \delta a_m, \delta b_m < 0.
\end{cases}
$$

Now let us assume $\delta a_m = \pm \delta a$ and $\delta b_m = \pm \delta b$ ($\delta a, \delta b > 0$) for simplicity. Then,

$$(\delta a_m, \delta b_m) = \begin{cases}
(\delta a, \delta b), & \text{when } c_m \in R^+(x^*) \\
(-\delta a, -\delta b), & \text{when } c_m \in R^-(x^*),
\end{cases}$$

where

$$R^+(x^*) = \left\{ c \mid \|x^* - c\| < l^*, l^* = \sigma \sqrt{-\log \left( \frac{\delta b}{\delta a} - \frac{2b}{a} \right)} \right\}.$$  

Thus, to increase the Fisher information, the attention modulatory effect should be positive (i.e., $\delta a, \delta b > 0$) on the neurons whose center $c_m$ is within the region $R^+(x^*)$, that is, $c_m \in R^+(x^*)$, whereas it should be negative in $R^-(x^*)$. In this manner, the distance $l^*$ is also useful in determining an effective attention region for $x^*$. Figure 3 (top) shows an example of the neural population that uses the same parameters in Figure 1 with different centers. Provided the attended stimulus $x^* = 0$, then we obtain $R^+(x^*) = \{ c \mid \|c\| < l^* \}$, where $l^* = \sigma \sqrt{-\log(v - \frac{2b}{a})} = 32.92$ and $v = v_m = \frac{6b}{\delta a} = \frac{1}{2}$ (see Figure 3, bottom).

2.5 Experimental Testing. This section briefly describes how our analysis can be used to design experiments for future studies. First, $x$ in our analysis represents any one-dimensional stimulus parameter falling in the receptive field of a neuron, such as the orientation of a grating, the direction of random dots’ motion, or the location of a stimulus. Second, we acknowledge two typical experimental paradigms with attention (Moran
Figure 2: Examples of different tuning functions with respect to distance $l^*$. Vertical solid lines indicate distance $l^*$ in each graph, measured from the center of the tuning function at $x = 0$. The tuning function in the normal condition is plotted with a solid line, and possible tuning function modulated by attention is plotted with a dotted line. The vertical dotted line indicates base rate in the normal condition. When Fisher information always increases by $\delta a, \delta b > 0$ for any $x$ (that is, $l^* = \infty$), distance $l^*$ is put at $x = \pm 90$ for purposes of presentation.
Figure 3: An example of population coding. (Top) The tuning functions of the neural population are plotted, using the same parameters in Figure 1. Centers of neurons are allocated at $c = 0, \pm 15, \pm 30, \pm 45, \pm 60$. The horizontal dotted line indicates base rate $b$. (Bottom) Using the same parameters $(\delta a, \delta b) = (\pm 4, \pm 2)$ in Figure 1, tuning height and base rates have been changed to increase Fisher information $I = \sum_m I(x^*, c_m)$ for attended stimulus $x^* = 0$, according to distance $l^* = \sigma \sqrt{-\log(v - \frac{2}{v})} = 32.92$ where $v = v_m = \frac{\delta a}{\delta b} = \frac{1}{2}$. If $l^* < c_m$, $\delta a = 4$ (and $\delta b = 2$), and $\delta a = -4$ otherwise. The vertical dotted line indicates $l^* = 32.92$.

& Desimone, 1985; Vogels & Orban, 1990; Motter, 1993; Treue & Maunsell, 1996, 1999; Luck et al., 1997; McAdams & Maunsell, 1999a; Reynolds et al., 1999). In these paradigms, subjects are presented with identical stimuli (or sets of stimuli) in a receptive field of a neuron in trials, but attention may shift between two different conditions across trials. In one paradigm, attention shifts to different values of $x$. Typically, attended and unattended
conditions are those when the most preferred and least preferred values \( x \) are attended by subjects, respectively. In the other paradigm, trials that require attention to any \( x \) value are interleaved with trials that may require attention at a different modality or feature, unrelated to \( x \). Here, the former and the latter are attended and unattended conditions, respectively.

Our analysis is formulated to test how the peak and base rate of the tuning curve, plotted in normal condition where no specific \( x \) value is attended by subjects, should be changed to improve the accuracy of \( x \) in the attended condition, where a specific value of \( x \) is attended. It is interesting to check the effective size \( l^* \) of attention by experimentation. Strictly speaking, however, there is no such normal condition in the above experimental paradigms because it is difficult to define the normal condition in experimental manipulations. In the second paradigm, if attention paid to a different modality does not alter the tuning function, the unattended condition can be treated as the normal condition, so our analysis is directly applicable. For example, McAdams & Maunsell (1999a, Fig. 4) provide the values of the peaks and base rates, averaged over the neural population in V4, in attended and unattended conditions in this paradigm. From their data, we obtain \((a, b) = (0.551, 0.295)\) in the unattended condition and \((\delta a, \delta b) = (0.674, 0.333) - (0.551, 0.295) = (0.123, 0.038)\) and then obtain \(\delta a/a > \delta b/b\). According to our analysis, the encoding accuracy of this tuning curve increases for any stimuli \( x \) by increasing the peak and base rate, which matches the experimental result in Figure 4 of McAdams and Maunsell (1999a). We must mention caveats in applying our analysis to their data; attention paid to a different modality is assumed not to alter the tuning curve. Their data are the average of neural population, in which not all neurons have identical parameters, whereas our analysis treated their data as if sampled from the same tuning curve. Our analysis is for the case where attention is approximately correct (\( x \approx x^* \)) and based on two assumptions: the stimulus-conditional independence assumption and the assumption that attention modulation does not modify the correlational structures, which seem to be the case (McAdams & Maunsell, 1999b).

The analysis is not directly applicable to the first paradigm. Since the analysis takes a variational approach, however, it can treat a relative change between the two conditions. For example, suppose that the magnitude of changes is the same between two conditions \((\delta a, \delta b) = (\pm \alpha, \pm \beta)\), where \(\alpha, \beta > 0\). Then the analysis implies that the relative change in the peak should always be nonnegative, \(2\alpha\) or 0.

3 Remarks

3.1 Higher-Dimension Inputs. The analysis so far has performed with respect to a one-dimensional stimulus parameter \( x \). It is straightforward to carry out the same analysis for higher-dimensional parameters. Let us
denote the \( n \)-dimensional input vector and a center of tuning function by \( x \) and \( c \), respectively. Let the tuning function be

\[
\psi(x) = a\phi(x; c, \Sigma) + b.
\]

where we assume \( \phi(x) = \exp(-(x-c)^T \Sigma^{-1} (x-c)) \) and \( T \) stands for transpose. Given the Poisson distribution for spikes, we obtain

\[
I(x) = \frac{a^2}{a\phi(x) + b} \left( \frac{\partial \phi(x)}{\partial x} \right) \left( \frac{\partial \phi(x)}{\partial x} \right)^T.
\]

An analysis of this function \( I(x) \) can be performed in the same manner as in the previous section. It should be noted that since \( I \) is a matrix, \( \delta I(x) > 0 \) should be interpreted in the sense of positive-definiteness. Another way is to use \( \sqrt{\det(I)} \), which is the information volume element of the parameter space. It is obvious that with this \( I(x) \), the results will lead to similar ones in a one-dimensional input case. If we make an additive assumption (McAdams & Maunsell, 1999a; Treue & Martinez-Trujillo, 1999) on attention modulation for different stimulus parameters, a variational change in the Fisher information is given as

\[
\delta I = \frac{\partial I}{\partial a} \delta a^* + \frac{\partial I}{\partial b} \delta b^*, \text{ where } \delta a^* = \sum_{i \in S} \delta a_i, \delta b^* = \sum_{i \in S} \delta b_i.
\] (3.1)

In this study, the effects of the height and base rate on the Fisher information are investigated as parameters, while the tuning width is fixed. We note the results of Zhang and Sejnowski (1999). They have shown that sharpening the tuning width does not improve the encoding accuracy if the input dimension is higher than two while the height is fixed and the base rate is zero.

### 3.2 Gaussian Spike Distribution.

The Poisson distribution is assumed for neural spikes in this study. Another popular assumption is gaussian. If the spike \( n \sim N(\psi(x), \sigma_n^2) \) is assumed, where \( \sigma_n^2 \) is independent from the mean firing rate \( \psi(x) \) (and also the stimulus-conditional independence is assumed), interestingly enough the Fisher information does not depend on the base rate. In this case, the conclusions can be different. It is known, however, that the variance of the spikes usually depends on the mean firing rates (Dean, 1981; Tolhurst, Movshon, & Dean, 1983; Britten, Shadlen, Newsome, & Movshon, 1992; Lee, Port, Kruse, & Georgopoulos, 1998; McAdams & Maunsell, 1999b). For example, if we fit the spike distribution with \( n \sim N(\psi(x), k\psi(x)^p) \), where \( k \) is a constant, a parameter \( p \) is measured experimentally as \( 1 < p < 2 \), approximately around 1.5. In this region of \( p \), we can find \( p \) that shows a similar tendency, as in the case of Poisson distribution (Nakahara & Amari, submitted).
4 Discussion

This study investigates the effect of the height and base rate as parameters of the neural tuning curve on the encoding accuracy in a framework of population coding. Using the Fisher information as a measure to access the encoding accuracy, we derived explicit conditions that can determine whether the tuning height and base rate should be increased or decreased together to improve the encoding accuracy for an attended stimulus, where the sensory stimulus is close to the attended stimulus. Thus, the analysis indicates how a population of neural activities should be changed by attention modulation to improve encoding accuracy. Notably, encoding accuracy can be improved by decreasing the tuning height and base rate for some neurons (that is, in case of $\|x^* - c\| > l^*$). This result, on the surface, may seem to be against the “biased competition model” of attention (Desimone & Duncan, 1995), or against an idea of attention serving to select neurons for further information processing in a more general term (Posner & Petersen, 1990), for example, the “spotlight” hypothesis (Crick, 1984; Koch & Ullman, 1985; Olshausen, Anderson, & Van Essen, 1993). Our analysis, however, treats the encoding accuracy of population coding by attention, whereas the competition model concerns the decoding in population coding. Hence, our results can be considered complementary to the biased competition model. Our analysis is testable in experiments. Since the analysis is applicable to the tuning curve of each neuron, it may help to reveal different roles in attention modulation among neurons of different tuning parameters. Any discrepancy in $l^*$ between experimental observations and the predictions by the analysis quantitatively indicates roles of attention function other than encoding accuracy.

Let us briefly discuss the limitations and future goals of this study. First, the analysis is developed for the case where there is only one stimulus $x$ in the receptive field of a neuron. It has been experimentally shown that attention modulation is more prominent with two stimuli in the receptive field, either of which subjects pay attention to in different trials (Moran & Desimone, 1985; Treue & Maunsell, 1996; Luck et al., 1997; Reynolds et al., 1999). This fact is considered to indicate biased competition (Desimone & Duncan, 1995; Luck et al., 1997; Reynolds et al., 1999). There does not seem to be a general agreement on a parametric form of a neural tuning curve in the two-stimuli case. Once the form of the tuning curve is determined, it is very interesting to carry out our approach (Zohary, 1992; Anderson & Van Essen, 1994; Luck et al., 1997; Zemel et al., 1998; Reynolds et al., 1999). Second, in the future we need to investigate the interaction of the two tuning curve parameters in this study, the height and base rate, with other parameters such as the width and even the center of tuning functions (Moran & Desimone, 1985; Spitzer et al., 1988; Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Lee, Itti, Koch, & Braun, 1999). Third, our analysis is performed under the stimulus-conditional independence assumption.
When there is correlation over neural activities, the total Fisher information is not a mere addition of the component ones. This discrepancy has been shown to be large when some correlation structures are assumed but to be small under other structures (Zohary, Shadlen, & Newsome, 1994; Abbott & Dayan, 1999; Yoon & Sompolinsky, 1999). In general, when the correlation decreases rapidly as two neurons become far away, we can apply the standard asymptotic technique of statistics. In such a case, our results still hold qualitatively. However, when attention increases correlation in addition to changes in tuning curves, we should be careful in carrying out a quantitative evaluation of $I^\ast$. Whether the nature of $I^\ast$ would change, provided some correlation structures, is an important future study (Nakahara & Amari, submitted). Finally, our analysis is limited to encoding accuracy. We are mostly interested in how attention-modulated neural responses are decoded to reach decision making (Britten et al., 1992; Shadlen, Britten, Newsome, & Movshon, 1996; Thompson, Hanes, Bichot, & Schall, 1996; Zemel et al., 1998; Pouget et al., 1998; Kim & Shadlen, 1999; Wu, Nakahara, Murata, & Amari, 2000). In this aspect, it is necessary to consider what happens with neural activities when only some dimensional feature values are relevant (Lehky & Sejnowski, 1988, 1999; Zohary, 1992).

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References


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