

Which are the best-encoded stimuli in a sensory neuron's tuning curve?

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We analyze the relationship between a neuron's tuning curve and how well the neuron encodes different stimuli. Using data derived from experimental measurements, we identify the stimuli about which a neuron conveys the most information. For low noise, the best-encoded stimuli are located near the maximal slope region of the tuning curve where the neuron is most sensitive. As noise increases, the maximum shifts toward the tuning curve peak where the response is relatively insensitive to noise. Our results demonstrate quantitatively how the level of noise in a system can dramatically affect the encoding properties of sensory neurons.

INTRODUCTION

Tuning curves have been used to characterize neurons in a wide variety of systems ranging from wind direction sensors in the cricket cercal system (Miller *et al.*, 1991) to orientation columns in the visual cortex (Watkins and Berkley, 1974) to place cells in the hippocampus (O'Keefe and Nadel, 1978). A tuning curve describes a neuron's firing rate as a function of a single or multiple stimulus parameters. For example, a tuning curve of a neuron in the primary visual cortex may give its firing rate as a function of the orientation, spatial phase, frequency, or contrast of a presented grating.

A common assumption in the interpretation of tuning curves is that the maximum firing rate designates the most important stimulus to the neuron. For example, orientation columns in the visual cortex are often identified by the stimulus that evokes the peak activity in each area, in a sense reducing each neuron's tuning curve to a single point at its peak. Such a reduction has strong intuitive appeal because such stimuli drive the neuron the strongest, and the corresponding responses are the most distinguishable from the background firing of the neuron or other noise in the system.

In contrast, many studies have noted that regions of the tuning curve with a large slope are most sensitive to the stimulus, because in these regions small changes in the stimulus result in the largest changes in firing rate. This implies that stimuli on the sides of the tuning curve, around the maximum slope, are best encoded by the neuron (Salinas and Abbott, 1994; Seung and Sompolinsky, 1993). From this perspective, the peak of the tuning curve (at the maximum firing rate) is a particularly insensitive region of the neuron's response because the slope at the peak is zero.

To address this apparent contradiction, we calculate the significance of different stimuli by using a recently derived measure of the information associated with particular stimuli, the stimulus-specific information (SSI) (Butts, 2003). The SSI identifies the stimuli that are best encoded by neural responses without relying on assumptions about coding scheme or decoding mechanism.

Below, we calculate the SSI first for a single isolated neuron and then for a population of four neurons with tuning curve and noise model taken from an experimental characterization of the cricket cercal system (Miller *et al.*, 1991, Theunissen and Miller, 1991). We show that there is a transition between "maximum slope" and "maximum firing rate" encoding of information as the intrinsic variability of the neuronal response increases. This transition reflects a tradeoff: firing rates are most sensitive to small changes in stimulus in the large slope regions of the tuning curve, but the information conveyed by high firing rates is most resistant to noise and more easily distinguishable from background noise. Thus, we show how the level of noise in a system can dramatically change the features of the tuning curve that are best encoded by a sensory neuron.

RESULTS

Defining the information associated with particular stimuli

To determine which stimuli are best encoded by a neuron, we use a newly derived measure of the information associated with specific stimuli, the *stimulus-specific information* (SSI) (Butts 2003). This measure represents the average information conveyed by a response when a particular stimulus is present, where the information of a response is defined by the specific information (DeWeese and Meister, 1998):

$$i_{sp}(r) = H[\sigma] - H[\sigma|r], \quad (1)$$

This is the difference between the entropy of the stimulus ensemble $H[\sigma] = -\sum_{\sigma} p(\sigma) \log_2 p(\sigma)$ and that of the stimulus distribution conditional on a particular measurement $H[\sigma|r] = -\sum_{\sigma} p(\sigma|r) \log_2 p(\sigma|r)$. Since the entropy of a stimulus distribution is a measure of how uncertain the stimulus is, the specific information $i_{sp}(r)$ gives the reduction in uncertainty about the stimulus gained by a particular response r .

The SSI of a particular stimulus is then the average of these reductions in uncertainty over the responses associated with that stimulus:

$$i_{\text{ssi}}(\theta) = \int_{\theta} p(r|\theta) i_{\text{sp}}(r), \quad (2)$$

These quantities can be calculated analytically for a given tuning curve and model of variability (see Methods for details).

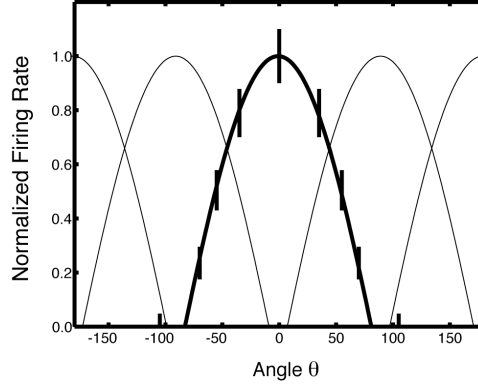


Figure 1: The tuning curves and variability for wind-direction sensitive neurons of the cricket cercal system.

Stimulus-specific information for a single neuron

We first compute the SSI for a single neuron with parameters corresponding to those measured in the cricket cercal system (Miller *et al.*, 1991). The cricket has four wind-sensitive neurons whose tuning curves have approximately identical, truncated cosine shape but with peaks offset by 90 degrees (Figure 1, thin lines; vertical bars give the standard deviations of the firing rates for a given stimulus; for parameters, see Methods). Cosine-shaped tuning curves have been widely used to describe the sensory responses in a wide variety of systems (for a summary of such systems see Salinas and Abbott, 1994). In the cricket wind-detection system, both the tuning curves and the noise responses of the neurons have been particularly well characterized. We therefore use these neurons as a model system in which to relate tuning curve data to a quantitative measure of encoding efficacy.

Consistent with theoretical studies of this neuron (Theunissen and Miller, 1991; Salinas and Abbott, 1994), we find that the maximum SSI does not occur at the peak of the tuning curve θ_0 . Rather, the best-encoded stimuli occur at ± 67 degrees (Figure 2A, labeled θ_i and θ_i'), close to the maximum slope of the tuning curve (which in this case is located at the firing threshold).

This result suggests that the regions of high slope are the most significant to the neuron. However, two points are of note: (1) the peak SSI is close to, but not directly at, the point of maximum slope, and (2) there is a smaller peak in the SSI at the maximum value θ_0 for which the slope of the tuning curve is zero.

To gain a better understanding of this result, we show the information associated with the underlying neural responses ($i_{\text{sp}}(r)$, eq. 1) in Figure 2B. The SSI of a stimulus θ is obtained from $i_{\text{sp}}(r)$ by averaging over the probable responses (characterized by the conditional distribution $p(r|\theta)$) (see eq. 2). Figure 2B (*dotted lines*) shows $p(r|\theta)$ for θ_0 and θ_i .

The specific information is largest when the conditional entropy of the stimulus ensemble is smallest, meaning that responses with high specific information are those triggered by relatively few stimuli. Since the number of stimuli associated with a given response is roughly proportional to the reciprocal of the tuning curve slope, responses in high slope regions of the tuning curve will generally have higher specific informations.

However, the specific information does not peak where the slope is maximal, which in this case is at zero firing rate (Figure 1). Rather, $i_{\text{sp}}(r)$ drops precipitously at low firing rates. This reflects that low firing rates can be generated equally well (due to noise) by any stimulus in the flat “non-tuned” portion of the tuning curve. Thus, low firing rates correspond to a wide range of possible stimuli and, correspondingly, to low specific information. Because these low firing rates are adjacent to the maximum slope portion of the tuning curve, the stimulus with the maximum SSI (θ_i) is associated with slightly higher firing rates (see $p(r|\theta_i)$ as a dotted line in Figure 2B).

In addition to assuming large values near the maximum slope of the tuning curve, the specific information also is large for very high firing rates. This is because very few stimuli are associated with firing rates much greater than unity, since the only way these responses can occur is when noise carries the firing rate to these high values. (Note that the normalization of the firing rates is such that unity corresponds to the maximal firing rate in the absence of noise (see Figure 1)). As a result, extremely high firing rates are nearly as informative as firing rates near regions of maximal slope, leading to the local maximum of the SSI at θ_0 seen in Figure 2A.

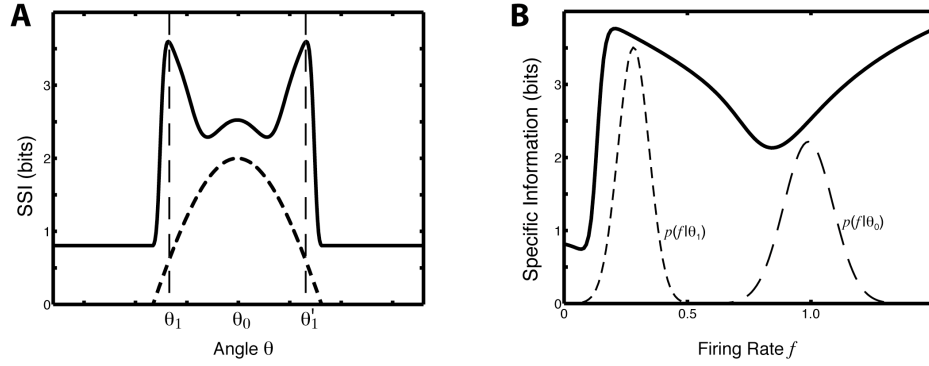


Figure 2: The stimulus-specific information (A) and specific information (B) for low noise.

The Effect of Higher Noise

Figure 3A shows the SSI for a neuron with the same tuning curve as in the example of Figure 2A but with three times the noise level. The stimulus with the highest SSI in this case occurs at the maximum firing rate θ_0 . This reflects the growth of the central peak seen in the low noise case (Figure 2A) with increasing noise, and can be understood by again considering the underlying specific information of responses (Figure 3B).

The specific information has changed in two important ways as a result of noise. First, the non-tuned stimuli have a farther-reaching effect on low firing rates, since non-tuned stimuli can now evoke a much larger range of firing rates. As a result, the specific information reaches a minimum at a firing rate of 0.26 (Figure 3B) instead of 0.08 (Figure 2B).

More crucially, high firing rates now have the largest specific informations, due to their relative lack of sensitivity to noise. Whereas a given intermediate firing rate can result from stimuli with lower average firing rates (that noise can raise) or stimuli with larger average firing rates (that noise can lower), very high firing rates (those at or above the peak average firing rate) can result only from lower firing rates that noise has raised. Furthermore, as noise increases, more firing rates above one are possible, and these rates all preferentially encode the stimulus at the peak of the tuning curve. Thus, the SSI of the stimulus at the peak of the tuning curve in this case reflects an average over the most informative responses. As a result, this stimulus is the best encoded.

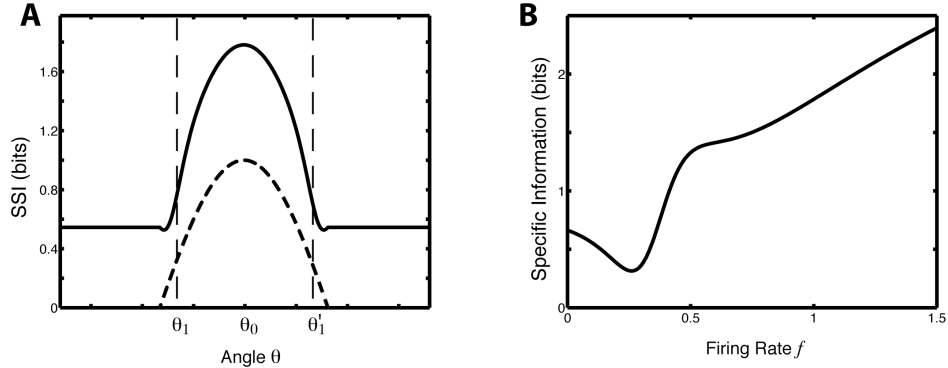


Figure 3: The stimulus-specific information (A) and specific information (B) for high noise.

Stimulus-specific information for a four-neuron population

Sensory systems commonly mitigate the effects of noise by having several neurons responsible for encoding the same stimulus feature. In the context of a population, the information that an individual neuron contributes might not be the same as the information that this neuron would convey in isolation, because information may be encoded redundantly or synergistically between neurons (Brenner *et al.*, 2000). To address the population coding issue, we first compute the SSI corresponding to the population responses $\{r_1, r_2, r_3, r_4\}$ for the four-neuron population of Figure 1. We then calculate the contribution of a single neuron to this population SSI.

The SSI for the four-neuron population with noise level as measured by Miller *et al.* (1991) is shown in Figure 4 (dotted line). Figure 4B shows the population SSI with three times this noise level, and Figure 4C for five times this noise level. To analyze the information contributed by an individual neuron in this context, we compute the reduction in the SSI when a single neuron is removed from the population. That is, we define the single-neuron information in the context of a population as the difference between the four-neuron population SSI and the SSI of the population of the remaining three neurons after the single neuron is removed (solid line, Figure 4A-C).

For low noise levels (Figure 4A), there are eight peaks of the population SSI (*dotted line*), near the points of maximal slope of all four neurons (analogous to the single neuron in Figure 2), with each neuron contributing two of these peaks (*solid line*). Note that the single-neuron SSI is approximately zero at the peak of its tuning curve, since this information is redundant with information encoded by the slope of the neighboring curves.

For higher levels of noise (Figure 4B), the peak of the population SSI shifts to the points of intersection of the tuning curves. At these points, the effect of noise is reduced by the cooperative encoding of the neighboring neurons, and as a result these points have the largest population-SSI (dotted line). Even at five times the noise level (Figure 4C), the peak of the population SSI does not transition to locations of the individual tuning curve peaks.

The maximum single-neuron SSI in the context of the population (Figure 4B, solid line), unlike the single-neuron SSI in isolation, does not transition to the peak of the tuning curve for three times the low noise level. For higher noise, however, the transition does occur (Figure 4C, solid line). The difference between the results for an isolated neuron and in the context of a population can be attributed to the fact that the noise is independent between the four neurons, and as a result the population is able to average over the noise, reducing the effective noise level.

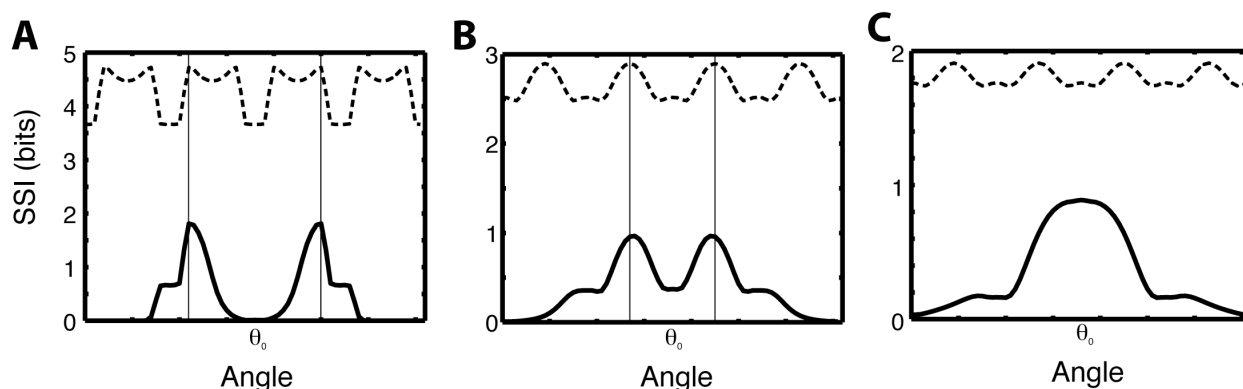


Figure 4: Population- and single neuron SSI in the context of a 4-neuron population.

DISCUSSION

Previous studies have identified either the maximum firing rate or the maximum slope portion of a tuning curve as the most significant stimulus for the system. We have shown that the best-encoded stimulus, in the sense of having the maximum stimulus-specific information (SSI), changes systematically from a point near the maximum slope of the tuning curve for low noise to the peak of the tuning curve for high noise. In particular, our analysis suggests that in the limit of zero noise, the maximum slope portion of a tuning curve conveys the maximal information because it is most sensitive to changes in the stimulus. In the limit of very high noise, stimuli associated with the peak of the tuning curve are the best encoded because, relative to lower firing rates, fewer stimuli can cause the highest firing rates.

The transition from maximum slope to maximum firing rate encoding occurs both for an isolated neuron (Figures 2 and 3) and for a neuron in the context of a population (Figure 4). However, the transition in the context of a population occurs at a higher noise level because the population can partially average out noise. This is consistent with results found with the Fisher information, which apply in the limit of large numbers of independent neurons, and which give the maximum information at the point of maximum slope (Dayan and Abbott, 2001; Seung and Sompolinsky, 1993). In practice, it is unclear how many neurons are pooled together in transmitting information to higher processing levels. Further, correlations may effectively limit the number of neurons that can usefully contribute to the decoding of a stimulus (Zohary *et al.*, 1994).

Although we have chosen the SSI because of its rigorous interpretation in terms of information transmission, other metrics such as the trans-information (Theunissen and Miller, 1991) or any of several stimulus reconstruction errors (Salinas and Abbott, 1994) could provide alternative metrics of how well a stimulus is encoded. In fact, the previous information-theoretical analysis of this system with the trans-information gives similar results to those presented here in the case of low noise. However, these authors did not consider the effect of different noise levels, which is the primary focus of this study. Methods studying the significant stimuli in the cricket cercal system have been applied to temporal coding of these neurons (Dimitrov and Miller, 2003). Although our paper focuses on tuning curves based on firing rates, the SSI can be extended to the characterization of neuronal responses based on spike times rather than firing rates (Butts, 2003). It will be interesting to see if these two measures reveal similar features in this case.

Though the noise level measured in the experiments of Miller *et al.* (1991) fits into the low noise regime both for isolated neurons (Figure 2) and in the context of a population (Figure 4A), experiments performed with different wind profiles might lead to higher noise levels. As a result, the cricket cercal system may itself operate at a

variety of different noise levels, depending on the experimental context. If this is the case, it suggests that neurons may use different encoding and/or decoding strategies for different levels of noise. For example, retinal ganglion cells are known to change the shape of their tuning curves as a function of contrast (Atick and Redlich, 1992).

In conclusion, tuning curves are widely used to characterize the responses of sensory neurons. Although tuning curves describe which stimuli cause a neuron to fire the most, they do not reveal which stimuli are the best encoded by the system. This is because tuning curves themselves provide no means by which to interpret the noise associated with responses. The analysis method presented here, by combining average firing rate and response variability data into a single metric, allows tuning curves to be interpreted in terms of which stimuli a neuron conveys the most information about. As we have shown, such analyses can reveal effects of noise level on sensory encoding that are not obvious from the examination of tuning curves alone.

Methods

The firing rate of each neuron was fit from the measurements of Miller et al. (1991) as $r(q) = [r_{\text{tun}}(q) + h]_+$ where $[\]_+$ denotes thresholding of negative values to zero, the tuning curve function $r_{\text{tun}}(q) = (\cos(q - q_0) - 0.14)/0.86$, and h corresponds to Gaussian noise of zero mean and standard deviation $s = A*(0.048 + 0.052*r_{\text{tun}}(q))$. Here, q_0 is the wind direction value that elicits the maximum average firing rate and differs by 90 degrees for each of the four neurons. The Miller et al. (1991) measurements, which we refer to as the low noise case, correspond to $A=1$. For the high noise case, we assume the noise is scaled by a factor of three, $A=3$. In the four-neuron population model, $A=5$.

The SSI was computed numerically from the joint probability distribution $p(r, q) = p(r|q)p(q)$ where $p(r|q)$ was obtained from the tuning curve model and $p(q)$ was assumed to correspond to a uniform distribution. r and q were discretized into bins of size 0.01 and 1 degree, respectively, for the single-neuron results and into bins of size 0.06 and 5 degrees, respectively, for the population results. Tests with finer discretizations produced no detectable change in results.

References

- Atick JJ, Redlich AN (1992) What does the retina know about natural scenes. *Neural Comput.* 4:196-210.
- Brenner N, Strong SP, Koberle R, Bialek W, de Ruyter van Steveninck RR (2000) Synergy in a neural code. *Neural Comp.* 12: 1531-52.
- Butts (2003) How much information is associated with a particular stimulus? *Network: Comput. Neural Syst.* 14: 177-187.
- Dayan P, Abbott LF (2001) *Theoretical Neuroscience* (Cambridge, MA, MIT Press), pp. 108-113.
- Dimitrov AG, Miller JP, Gedeon T, Aldworth Z, Parker AE (2003) Analysis of neural coding through quantization with an information-based distortion measure. *Network: Comput. Neural Syst.* 14: 151-176.
- Miller JP, Jacobs GA, Theunissen FE (1991) Representation of sensory information in the cricket cercal sensory system. I. Response properties of the primary interneurons. *J. Neurophysiol.* 66: 1680-9.
- O'Keefe J, Nadel L (1978) *The Hippocampus as a Cognitive Map* (Clarendon, Oxford).
- Salinas and Abbott (1994). Vector reconstruction from firing rates. *J. Comput. Neurosci.* 1: 89-107.
- Seung HS, Sompolinsky H (1993) Simple models for reading neuronal population codes. *Proc. Natl. Acad. Sci.* 90: 10749-53.
- Theunissen FE, Miller JP (1991) Representation of sensory information in the cricket cercal sensory system. II. Information theoretic calculation of system accuracy and optimal tuning-curve widths of four primary interneurons. *J. Neurophysiol.* 66: 1690-703.
- Watkins DW, Berkley MA (1974) The orientation selectivity of single neurons in cat striate cortex. *Exp. Brain Res.* 19: 433-46.
- Zohary E, Shadlen MN, Newsome WT (1994) Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature* 370: 140-3.