



Encoding efficiency of suprathreshold stochastic resonance on stimulus-specific information



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ABSTRACT

In this paper, we evaluate the encoding efficiency of suprathreshold stochastic resonance (SSR) based on a local information-theoretic measure of stimulus-specific information (SSI), which is the average specific information of responses associated with a particular stimulus. The theoretical and numerical analyses of SSIs reveal that noise can improve neuronal coding efficiency for a large population of neurons, which leads to produce increased information-rich responses. The SSI measure, in contrast to the global measure of average mutual information, can characterize the noise benefits in finer detail for describing the enhancement of neuronal encoding efficiency of a particular stimulus, which may be of general utility in the design and implementation of a SSR coding scheme.

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It is now a well-known fact that noise can sometimes improve, without degrading, the responses of certain nonlinear systems. This viewpoint is primarily motivated by the phenomenon of stochastic resonance (SR) [1–3], where a suitable amount of noise brings an optimized system response characterized by various measures, such as spectral amplification [4], correlation coefficient [5], signal-to-noise ratio [6,7], and mutual information [8]. In its original form, SR often applies to a noise-enhanced subthreshold signal [1–5]. However, in a parallel summing network, a new form of SR termed suprathreshold stochastic resonance (SSR) results in the maximum input-output mutual information at a non-zero level of noise intensity, even if the input signal is predominantly above the threshold [8]. The information content in each individual subsystem is monotonically decreased by the addition of noise, but the summed outputs from all subsystems yield a net gain in information [8–17].

The case of SSR is now well established as an important paradigm that suggests neuronal noise can possibly have a beneficial role in sensory systems [9–11]. This paradigm is based on the facts that there are large numbers of interconnected neurons in the nervous system of animals and humans with variations in structure, function and size, and noise permeates every level of

the nervous system, from the perception of sensory signals to the generation of motor responses [18,19]. The foregoing nervous system features indicate that the potential exploitation of SSR in a neuronal population stands as an interesting question in neuroscience, relevant for instance to sensory neurons [13,20], cochlear implants [10,11,14], motion detection [15], and stochastic pooling sensor networks [21–23]. These research results show that SSR does appear to serve as an efficient coding strategy of information transformation—providing a possible explanation of the role of noise in human sensory processes [8,10,11,13,16].

Mutual information is often used to calculate the information gain or the reduction of uncertainty of the neuronal responses [24]. However, it cannot address which particular stimuli or responses are significant in information transmission [25,26]. Therefore, based on the specific information [25], Butts proposes a new measure of stimulus-specific information (SSI) defined as the average reduction in the uncertainty of one observation given a particular stimulus [26]. This information bearing measure of SSI can be calculated without prior knowledge about the coding scheme, and is also robust to nonlinearities in the system [26]. Recent studies of SSI give rise to a number of interesting results: The effect of variability on SSI illustrates that the best encoded stimulus with the maximum SSI can change systematically from the high-slope region of tuning curve for low noise to the peak of the tuning curve for high noise [27]. The neuronal encoding of sound frequency in the auditory cortex shows that the maximum SSI is always at the

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best frequency and never in the tuning curve tails [28]. In finite neural populations, the shape of the marginal SSI can converge toward that of the Fisher information as the population size increases, and predict the best encoded stimulus precisely [29]. In this paper, we are particularly interested in the noise benefits in enhancing the encoding efficiency of the stimulus in a population of neurons. The obtained theoretical and numerical results show that the SSIs not only straightforwardly explicate how much information a neuronal population provides about a particular stimulus, but also illustrate how effectively each stimulus is enhanced by the optimal noise level to transmit more information via the mechanism of SSR. The SSI measure is particularly useful in making an analytical observation of the positive role of noise, and offers an interesting insight into the application of SSR to neuronal coding schemes.

1. Information measures

Consider a neural system with an ensemble of stimuli X and whose behavior can be classified in a set of responses Y , the mutual information between the ensemble of stimuli X and the set of responses Y is given by

$$I(X, Y) = H(X) - H(X|Y), \quad (1)$$

where the information entropy of the stimulus ensemble [24]

$$H(X) = - \sum_{x \in X} P_x(x) \log_2 P_x(x), \quad (2)$$

and the average conditional entropy [24]

$$H(X|Y) = \sum_{y \in Y} P_y(y) H(X|y) = \sum_{y \in Y} P_y(y) \left[- \sum_{x \in X} P(x|y) \log_2 P(x|y) \right]. \quad (3)$$

The conditional entropy associated with a particular response y is defined as $H(X|y)$ [24], and lowercase characters x and y represent an individual observation within ensembles.

The mutual information can be used to quantify the information provided by an entire response ensemble about an entire stimulus ensemble, but it is often of interest to know which particular stimuli are effectively encoded by the system, and which particular responses communicate information about the stimuli [25–29]. Then, DeWeese and Meister [25] propose the specific information measure

$$I_{sp}(y) = H(X) - H(X|y), \quad (4)$$

which is an appropriate representation of the degree to which a given response y contributes to the overall mutual information in Eq. (1) [25,26]. However, due to the asymmetry of stimulus and response with respect to causality, the specific information of a particular stimulus $I_{sp}(x) = H(Y) - H(Y|x)$ fails to select the effective encoded stimuli [26,27]. The largest value of $I_{sp}(x)$ corresponds to those stimuli that have few responses associated with them, without regard to whether these responses are informative or not [26]. Therefore, Butts defines a new information theoretic measure of SSI as

$$I_{ssi}(x) = \sum_{y \in Y} P(y|x) I_{sp}(y), \quad (5)$$

which explicitly represents the average specific information of the response ensemble Y that occurs when a particular stimulus x is present [26]. It is also noted that the average SSI over the entire ensemble of stimulus yields the mutual information, as follows

$$I(X, Y) = \sum_{x \in X} P_x(x) I_{ssi}(x). \quad (6)$$

In Eq. (6), it is interesting to note that the term $P_x(x) I_{ssi}(x)$ represents the average informative contribution of each stimulus to the mutual information. Therefore, we can define the encoding efficiency of each stimulus as

$$E_{ssi}(x) = P_x(x) I_{ssi}(x), \quad (7)$$

which can be considered as a useful metric to characterize the positive role of noise in the enhancement of the encoding efficiency of neuronal information transmission.

2. Binary threshold SSR model

Consider a typical SSR model consisting of N binary threshold neurons, and each neuron is subject to the same continuous stimulus signal $x(t)$ but independent noise components $\eta_i(t)$ [8]. The output y_i is given by the neuronal response function

$$y_i = \begin{cases} 1 & \text{if } x + \eta_i \geq \theta, \\ 0 & \text{otherwise,} \end{cases} \quad (8)$$

where θ is the threshold level of the neuronal population. The overall response is $y = \sum_{i=1}^N y_i$ with probability mass function $P_y(n)$ as y being equal to n for $n = 0, 1, \dots, N$ [8,9]. Furthermore, we assume that the noise distribution is f_η and the cumulative distribution function is F_η , then the transition probability

$$P(1|x) = P(x + \eta > \theta|x) = 1 - F_\eta(\theta - x) \quad (9)$$

is the conditional probability of neuron responses being in state 1. Consequently, the conditional probability of neuron responses being in state 0 can be written as $P(0|x) = 1 - P(1|x)$ [8,9]. Noting that, for any given stimulus value x , each device acts independently under the influence of its own noise η_i , thus the probability that n neurons are triggered accords with the binomial distribution

$$P(n|x) = C_n^N P^n(1|x) P^{N-n}(0|x) \quad (10)$$

with the binomial coefficient C_n^N [8]. Therefore, the probability mass function $P_y(n)$ can be calculated as

$$P_y(n) = \int P(n|x) P_x(x) dx = C_n^N B(n), \quad (11)$$

$$B(n) = \int P^n(1|x) P^{N-n}(0|x) P_x(x) dx. \quad (12)$$

Using Bayes' theorem, the conditional probability for a particular stimulus x knowing the response $y = n$ is given by

$$P(x|n) = \frac{P(n|x) P_x(x)}{P_y(n)}. \quad (13)$$

Then, the specific information $I_{sp}(n)$ in Eq. (4) can be written as

$$I_{sp}(n) = H(X) - H(X|n) = - \int P_x(x) \log P_x(x) dx + \int P(x|n) \log_2 P(x|n) dx, \quad (14)$$

with the differential entropy of stimulus signal $H(X)$ and the conditional entropy $H(X|n)$. Based on Eqs. (10) and (14), the SSI of a particular stimulus value x can be expressed as

$$I_{ssi}(x) = \sum_{n=0}^N P(n|x) I_{sp}(n). \quad (15)$$

Next, we specifically consider the generalized Gaussian stimulus signal $x(t)$ with its distribution

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