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Suprathreshold stochastic resonance in neural processing tuned by correlation

Simon Durrant
Department of Informatics, Sussex University, Brighton BN1 9QH, United Kingdom, and Neuroscience and Aphasia Research Unit, University of Manchester, Manchester M13 9PL, United Kingdom

Yanmei Kang
Department of Applied Mathematics Xi'an Jiaotong University Xi'an 710049 People's Republic of China

Nigel Stocks
School of Engineering, University of Warwick, Coventry CV4 7AL, United Kingdom

Jianfeng Feng
Department of Computer Science and Mathematics, University of Warwick, Coventry CV4 7AL, United Kingdom

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Suprathreshold stochastic resonance (SSR) is examined in the context of integrate-and-fire neurons, with an emphasis on the role of correlation in the neuronal firing. We employed a model based on a network of spiking neurons which received synaptic inputs modeled by Poisson processes stimulated by a stepped input signal. The smoothed ensemble firing rate provided an output signal, and the mutual information between this signal and the input was calculated for networks with different noise levels and different numbers of neurons. It was found that an SSR effect was present in this context. We then examined a more biophysically plausible scenario where the noise was not controlled directly, but instead was tuned by the correlation between the inputs. The SSR effect remained present in this scenario with nonzero noise providing improved information transmission, and it was found that negative correlation between the inputs was optimal. Finally, an examination of SSR in the context of this model revealed its connection with more traditional stochastic resonance and showed a trade-off between supratheshold and subthreshold components. We discuss these results in the context of existing empirical evidence concerning correlations in neuronal firing.

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I. INTRODUCTION

One of the more striking facts about neural processing is that neurons *in vitro* fire with considerable regularity in response to a constant stimulus, while neurons *in vivo* exhibit much greater irregularity in response to the same stimulus [1]. This irregularity has often been characterized as noise without this necessarily implying a lack of functional utility [2]. A number of possible sources for neuronal noise *in vivo* have been proposed, including intrinsic channel noise [3] and Johnson electrical noise [4], and one of the most important sources, especially in view of the clear difference between the *in vivo* and *in vitro* cases, is network noise. This argues that noise can arise from the pattern of spiking inputs arriving at synapses to a given neuron, which itself may arise due to the presynaptic neurons themselves having irregular firing patterns, or by their having a particular pattern of connectivity. The presence of this irregularity has led to neural spike trains being treated as stochastic processes, and in particular Poisson processes.

Given the prominence of neuronal noise *in vivo*, it is natural to question what the functional role of such noise might be, especially in neural coding where the map from stimuli to neural response is explored. Two frequently used coding schemes are rate coding, which concerns the average number of spikes per unit time and contains information about the stimuli in the firing rate of the neuron, and temporal coding, which focuses on the precise timing of single spikes or the high-frequency firing-rate fluctuations which may carry information [5]. For many years, there has been a debate on the significance of temporal coding vs rate coding within the neuroscience community. Some suggestions, such as coincidence detection, posit the existence of a precise temporal code in neural spike trains [6,7], arguing that the variability in neural spike trains is directly useful in capturing features of the presynaptic input. Others reject these claims [8–10] and argue for a rate code in which it is the number of spikes occurring in a given short time period that is the principal carrier of information, regardless of the precise timing of the spikes within that period. Although the debate about temporal and rate coding continues [2,11,12], both temporal and rate coding allow for the possibility that neuronal noise is beneficial in neural information processing.

One well-documented example of the benefits of noisy coding is stochastic resonance (SR) [13,14], in which an appropriate amount of noise can help to reveal the temporal structure in a predominantly subthreshold signal. Neurophysiological experiments have suggested that the mechanism could be used by sensory systems [15] and motor systems [16] in enhancing the perception and transfer of information. In neural systems this has also been demonstrated in the context of both temporal coding [17], including specifically coincidence detection [18], and rate coding [19]. However, in general, traditional SR suffers from the problem that neural systems are adaptive in a number of ways, including a limited ability to independently vary firing thresholds and tune the intrinsic noise level, and so an effect which relies on thresholds set above a signal dc level and noise adjusted close to an optimal level is inevitably limited in scope.

In the last decade, an important new form of SR has been discovered which does not require subthreshold signals, but instead operates in a quite different way in the context of a population of simple processing elements [20,21]. Termed suprathreshold stochastic resonance (SSR), this suggests another possible functional role of noise in neural processing and one that is likely to be much wider in scope than traditional SR. This has been demonstrated in simple, discrete time, models of threshold units, the specific context of the bifurcation point of neurons modeled by the Fitzhugh-Nagumo equations [21–25], a population of Poisson neurons [26], and for the more common models of integrate-and-fire neurons and Hodgkin-Huxley neurons [27,28]. These previous investigations mainly concentrate on tuning the noise level, but it is not clear how this relates to the noisy environment in which neurons operate. It is desirable to seek a more biophysically plausible way to realize the phenomenon, and to that end in this paper we present a demonstration for integrate-and-fire neurons when presented with inputs modeled by Poisson processes (the most common paradigm), adopting a rate coding perspective. In particular, we demonstrate that improved information processing shown in SSR may be achieved in neural systems by tuning the correlations in neuronal firing in a way that conforms to known biophysical properties.

II. MODEL AND INPUTS

A. Integrate-and-fire model

We first describe a simplified neuron model that is widely used in the computational neuroscience community as it demonstrates similar dynamics to biological neurons at the level of individual spike trains: the leaky integrate-and-fire model [29–31]. It receives inputs modeled by Poisson processes (that can be nonhomogenous in the general case) which represent the effect on the membrane potential (the principal state variable) of inputs from other neurons; this version, commonly called Stein's model [32,33], has been used previously to examine traditional SR [19].

The main state equation for the integrate-and-fire neuron is

$$dV(t) = -\frac{1}{\gamma}V(t)dt + dI(t), \tag{1}$$

where $V(t)$ is the membrane potential and is a function of time, γ is the membrane time constant which controls the speed of decay of the membrane potential, and $I(t)$ is the external input to the neuron. A spike is recorded when $V(t)$ crosses the threshold V_{thresh}, at which point the neuron is reset to the resting potential V_{rest}. This gives us a set of s firing times τ_i which make up a spike train that is characterized by the neural response function $\rho(t)$:

$$\begin{gathered}\tau_i = \inf\{t > \tau_{i-1} : V(t) \geqslant V_{\text{thresh}} | V(\tau_{i-1}) = V_{\text{rest}}\},\\ \tau_0 = 0,\\ \rho(t) = \sum_{i=1}^{s} \delta(t - \tau_i),\end{gathered} \tag{2}$$

For all experiments presented in this paper, $\gamma = 20$ ms, $V(t)$ has a resting potential $V_{\text{rest}} = -70$ mV and a firing threshold $V_{\text{thresh}} = -50$ mV. These values were chosen to be in a biophysically plausible range.

Our model consists of N integrate-and-fire neurons, each of which receives a continuous noisy input $I_n(t)$ and generates a spike train output $\rho_n(t)$, with $1 \leqslant n \leqslant N$. The spike train of the nth neuron is converted into a continuous firing rate by convolution with a Gaussian filter:

$$\begin{gathered}y_n(t) = \int_{-\infty}^{\infty} d\tau\ \omega(\tau)\rho_n(t-\tau),\\ \omega(\tau) = \frac{1}{\sqrt{2\pi}\sigma_\omega}\exp\left(-\frac{\tau^2}{2\sigma_\omega^2}\right).\end{gathered} \tag{3}$$

The Gaussian filter is noncausal (centered upon the current time and therefore using spikes from the future as well as the past in its estimate), which provides an unbiased estimate of the firing rate at any given point in time, and has a width equal to the membrane time constant ($\sigma_\omega = 20$ ms). This method avoids problems of edge effects associated with more straightforward binning and counting methods [34]. The output of the complete system of neurons, $y(t)$, is simply the mean firing rate averaged across the population:

$$y(t) = \frac{1}{N}\sum_{n=1}^{N} y_n(t). \tag{4}$$

This model is used in all of the experiments presented here.

B. Input stimulus

The inputs ξ_k are independent, uniformly distributed integer random variables, between limits [10,40] which were chosen to reflect typical firing rates. χ is the indicator function and $T_W = 250$ ms is the length of time the signal remains at one value, giving the time-dependent stimulus $x(t)$:

$$x(t) = \sum_k \xi_k \chi(t \in \{(k-1)T_W, kT_W\}). \tag{5}$$

The input therefore consists of a simple stepped signal taking four values in turn (10, 20, 30, 40) and which changes every 250 ms. These inputs are used in all of our experiments here except the final ones on adaptive correlation control (where they are replaced by a similar step function but covering a wider range of values). How the stimulus $x(t)$ is mapped onto the inputs $I(t)$ which the neurons actually receive is specified in individual experiments.

C. Performance measurement

In keeping with previous work on SSR [21–23], our performance measurement is given by the mutual information of the system, which characterizes the information processing capability of the system. This is a probability-based approach which essentially measures the extent to which the inputs and outputs can be predicted from each other. It is given by

$$\begin{gathered}\text{MI} = H_y - H_{\text{noise}},\\ H_y = -\int_{-\infty}^{\infty} dy\ P_y(y)\log_2 P_y(y),\end{gathered}$$

$$H_{\text{noise}} = -\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} dx\, dy\; P_x(x)P_y(y|x)\log_2 P_y(y|x). \quad (6)$$

Here H_y is the entropy of the output, and H_{noise} gives the noise entropy, which essentially represents how much of the output entropy is due to noise rather than the input signal x. The difference between them is the mutual information MI, which characterizes how well the output y can be predicted given knowledge of the input signal x. The mutual information is evaluated numerically throughout; the source code used to achieve this and all other aspects of our simulations presented here can be downloaded from [35]. It is calculated from the probability distributions of the respective input and output variables, which are estimated with a histogram technique with the same measurement resolution used in all instances. This ensures that the distributions are accurately estimated and that the measurement resolution plays no direct role in the estimation of mutual information.

In general, noisier inputs will lead to lower mutual information, all other things being equal, but if the information processing capability of the system is actually enhanced by the presence of a certain level of noise, then we would expect to see the mutual information increase in these circumstances; hence, mutual information is a very appropriate way to test for SSR. In our model, if the population of neurons have an input that is completely predictable on the basis of the firing rate output (assuming that the output system has enough capability to represent all of the input information), even if the output itself is not smooth (as may be the case for a neural population subject to intrinsic noise, depending on the specific form of the noise) or in the same range as the input, then the mutual information will match the entropy of the input. An example of the input signal and performance measurement used in our model is shown in Fig. 1. The stepped input to the model takes just four discrete values and is the limiting information factor in all of our simulations here (except the last ones on adaptive correlation control), so the maximum mutual information attainable with this input is two bits.

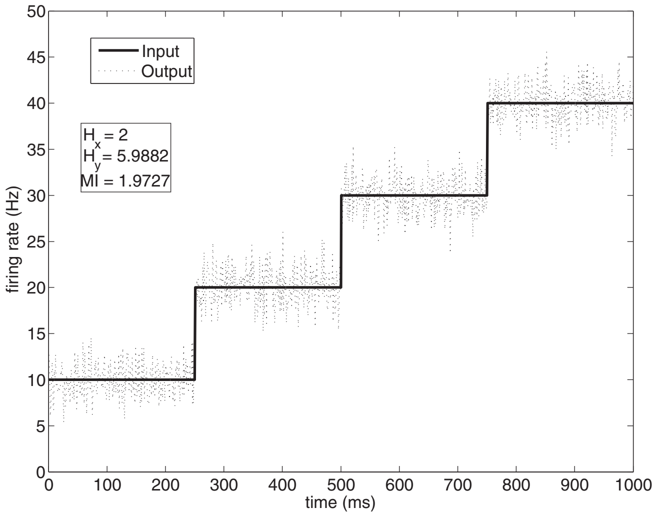

FIG. 1. Entropy and mutual information with a noise-free stepped input and a noisy output. The input signal has an entropy of 2 bits, which limits the amount of information that can be transmitted to that level, while the output signal has a much higher entropy of just under 6 bits. The mutual information nearly matches the input entropy, reflecting the fact that in spite of the noisy output, the input can still be strongly predicted on the basis of a given output value.

D. Suprathreshold stochastic resonance

It is useful when first testing for an SSR effect in our model of integrate-and-fire neurons to adopt a similar approach to that used in the basic SSR model [21–23] and control the input signal and noise level directly. In this case, therefore, the inputs $dI_n(t)$ to each neuron of the model were directly characterized by independent signal and noise terms. The signal is simply the value of the stimulus $x(t)$ as previously described, with the same value for all units at a given time point, and the noise is a random Gaussian variable with zero mean and variance σ_x^2, which is independent for each neuron, hence the inputs can be described as

$$dI_n(t) = x(t)dt + \sigma_x dB_n(t), \quad (7)$$

where $B_n(t)(n = 1,2,\ldots,N)$ are mutually independent standard Brownian motions. The results for different numbers of neurons in the model, in terms of mutual information as a function of the noise parameter σ_x, are shown in Fig. 2. These results have a strong similarity to the results of the basic model and of previous SSR models using integrate-and-fire neurons [27,36] and clearly show that our model of integrate-and-fire neurons is capable of demonstrating SSR behavior. Networks with more than one neuron improved performance in the presence of noise, with greater improvement for a greater number of neurons, while a model containing just a single neuron showed no improvement.

III. POISSON INPUTS AND DIFFUSION APPROXIMATION

The experiment in the previous section demonstrates the existence of SSR in a network of integrate-and-fire neurons but does so by directly specifying the inputs, including an

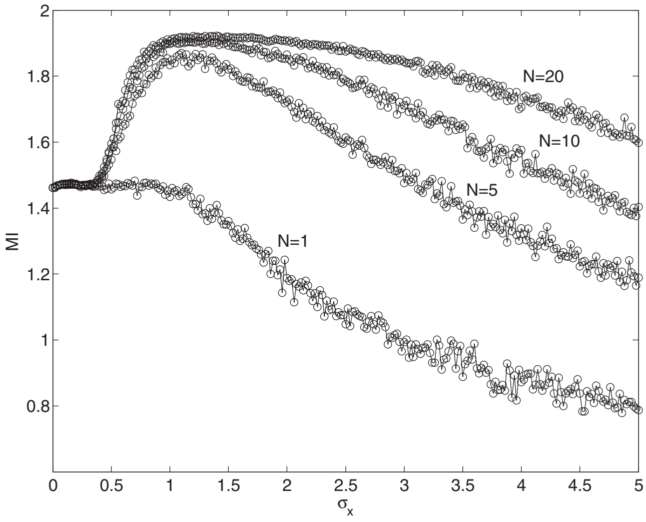

FIG. 2. Mutual information shown as a function of the noise strength. Networks containing more than one neuron benefit from some noise, as predicted by SSR theory.

independent additive noise component, to each neuron. In reality, neurons are subject to spiking inputs from other neurons. Given this, the inputs $I_n(t)$ are most commonly modeled as Poisson processes where the noise level scales with the signal; in other words, we have a system with signal-dependent noise rather than independent additive noise.

The state equation of the nth neuron in our model is given by Eq. (1) but with $dI_n(t)$ now specified in terms of excitatory and inhibitory postsynaptic potentials due to presynaptic action potentials:

$$\begin{aligned} dV_n(t) &= -\frac{1}{\gamma}V_n(t)dt + dI_n(t), \\ dI_n(t) &= \sum_{i=1}^{p} a_i d\mathrm{Exc}_{n,i}(t) - \sum_{j=1}^{q} b_j d\mathrm{Inh}_{n,j}(t). \end{aligned} \tag{8}$$

$\mathrm{Exc}_{n,i}(t)$ are nonhomogeneous Poisson processes that represent the p excitatory postsynaptic potentials (EPSPs) with rate $\lambda_{E,i}(t)$ and a magnitude of a_i; the q inhibitory postsynaptic potentials (IPSPs) $\mathrm{Inh}_{n,j}(t)$ are also nonhomogeneous Poisson processes with a rate $\lambda_{I,j}(t)$ and a magnitude of b_j. For the sake of clarity, in the following the subscript i (j) is dropped from $\lambda_{E,i}(t)$ and a_i ($\lambda_{I,j}(t)$ and b_i) and we adopt the simplifying assumption that the input processes share the same magnitude a (b) and rate λ_E (λ_I). Invoking a diffusion approximation [37,38] and thereby separating out the mean and variance terms, we can write these inputs as

$$\begin{aligned} \mathrm{Exc}_{n,i}(t) &= \lambda_E(t) + \sqrt{\lambda_E(t)}B_{n,i}^{E}(t), \\ \mathrm{Inh}_{n,j}(t) &= \lambda_I(t) + \sqrt{\lambda_I(t)}B_{n,j}^{I}(t), \end{aligned} \tag{9}$$

which gives the total synaptic input to the nth neuron as

$$\begin{aligned} dI_n(t) = {} & a\sum_{i=1}^{p}\lambda_E(t)dt - b\sum_{j=1}^{q}\lambda_I(t)dt \\ & + a\sum_{i=1}^{p}\sqrt{\lambda_E(t)}dB_{n,i}^{E}(t) \\ & - b\sum_{j=1}^{q}\sqrt{\lambda_I(t)}dB_{n,j}^{I}(t), \end{aligned} \tag{10}$$

where $\lambda_E(t)$ is the excitatory Poisson process parameter, $\lambda_I(t)$ is the inhibitory Poisson process parameter, $B_{n,i}^{E}(t)$ are standard Brownian motions for the EPSPs, $B_{n,j}^{I}(t)$ are standard Brownian motions for the IPSPs, and all other variables are as previously specified. Noting that the standard deviation of a sum or difference of N (not generally independent) Gaussian processes η with mean individual variance σ_η^2 and mean correlation coefficient $c = \frac{2}{N(N-1)\sigma_\eta^2}\sum_{i<j=1}^{N}(\langle\eta_i\eta_j\rangle - \langle\eta_i\rangle\langle\eta_j\rangle)$ is given by $\sqrt{N[\sigma_\eta^2 + c(N-1)\sigma_\eta^2]}$, and that the sum of a set of Brownian motions is also a Brownian motion, we can further simplify this to

$$dI_n(t) = [ap\lambda_E(t) - bq\lambda_I(t)]\,dt + \left(\sqrt{a^2\lambda_E(t)p[1+(p-1)c_E] + b^2\lambda_I(t)q[1+(q-1)c_I]}\right)dB_n(t), \tag{11}$$

in which the first term represents the signal, the second term describes the noise fluctuations, and c_E and c_I are the mean correlation coefficients for the excitatory and inhibitory synaptic inputs, respectively. In general, c_E and c_I can take positive or negative values, with an upper bound of 1 (fully positively correlated) and a lower bound of $c_E \geqslant -1/(p-1)$ and $c_I \geqslant -1/(q-1)$. $B_n(t)$ are by definition independent of each other, since any mutual dependence between the inputs is incorporated into the correlation coefficients and the Gaussian form ensures no higher order dependencies exist.

It is important to note that in the above diffusion approximation we treat the sum of N Gaussian random variables as a Gaussian random variable, but this is not inherently true in the general case. There are, however, an important set of scenarios for which this assumption does hold true. These include the case of independent Gaussian random variables (not relevant in our scenario), the case where the joint distribution of the correlated variables is still Gaussian (a more widely applicable case, including in our scenario) and a much wider case based on consideration of the following facts. Suppose X_1 and X_2 are two uncorrelated standard normal random variables, and if we define a new random variable Y_1 as $Y_1 = \rho X_1 + \sqrt{(1-\rho^2)}X_2$, then Y_1 is also a Gaussian random variable. Obviously, Y_1 is not generally independent of X_2, having a correlation coefficient ρ, but their sum $Z = Y_1 + X_2$ is still a Gaussian random variable. In many cases, the sum of potentially correlated Gaussian random variables is thus still Gaussian, and this kind of treatment has been commonly used in theoretical neuroscience and our scenario is also founded on this premise.

For SSR, it is necessary that the mean input value is greater than or equal to the neural firing threshold in our model. To achieve this in the context of integrate-and-fire neurons receiving excitatory and inhibitory Poisson inputs we control the ratio of excitatory and inhibitory inputs [39] by specifying a single firing rate parameter $\lambda(t)$, which is defined as the sum of the parameters $\lambda_E(t)$ that characterize the individual EPSPs, and a time-averaged constant ratio of excitatory to inhibitory inputs r such that $r\lambda(t)$ is the sum of the parameters for the IPSPs:

$$\begin{aligned} \lambda(t) &= \sum_{i=1}^{p}\lambda_E(t), \\ r\lambda(t) &= \sum_{j=1}^{q}\lambda_I(t). \end{aligned} \tag{12}$$

This framework is more commonly used in the context of balanced inputs, that is, where excitatory and inhibitory inputs exactly match [40,41], and where this ratio is preserved at all times (even under changing stimulus conditions) by an implied mechanism that scales excitatory and inhibitory inputs simultaneously. Here we have relaxed these two assumptions, and instead adopted a balance that, averaged over time and spatial fluctuations in the model, favors excitatory inputs just to the extent required to reach firing threshold on average, in which circumstances we have $E\{\frac{dV(t)}{dt}\} = 0$ and $E\{V(t)\} = V_{\text{thresh}}$, noting that these refer purely to the requirements for the inputs and give the actual expected values in the absence of a reset mechanism after firing. This has the additional benefit of being biophysically more plausible than the exactly-balanced-at-all-times scenario because it does not require a mechanism for the instantaneous shift of the excitatory-inhibitory ratio under different stimulus conditions in order to maintain the balance.

We first rewrite the signal and noise in terms of separate mean and standard deviation:

$$\begin{aligned} dI_n(t) &= \mu(t)dt + \sigma(t)dB_n(t),\\ \mu(t) &= ap\lambda_E(t) - bq\lambda_I(t), \qquad (13)\\ \sigma(t) &= \sqrt{a^2\lambda_E(t)p[1+(p-1)c_E] + b^2\lambda_I(t)q[1+(q-1)c_I]}. \end{aligned}$$

Our requirement of inputs on average matching the firing threshold as previously stated means

$$\begin{aligned} 0 &= E\left\{-\frac{1}{\gamma}V_{\text{thresh}} + \sum_n I_n(t)\right\}\\ \Rightarrow \frac{V_{\text{thresh}}}{\gamma} &= E\{\mu(t)\}, \end{aligned} \qquad (14)$$

because $\mu(t)$ is the expected signal value and the expected noise value is zero by definition. Expressing this in terms of our firing rate parameter λ and ratio r gives us the general result

$$\begin{aligned} \mu(t) &= \lambda(t)(a - br)\\ \sigma(t) &= \sqrt{a^2\lambda(t)[1+(p-1)c_E] + b^2\lambda(t)r[1+(q-1)c_I]}\\ r &= E\left\{\frac{a}{b} - \frac{V_{\text{thresh}}}{b\lambda(t)\gamma}\right\}. \end{aligned} \qquad (15)$$

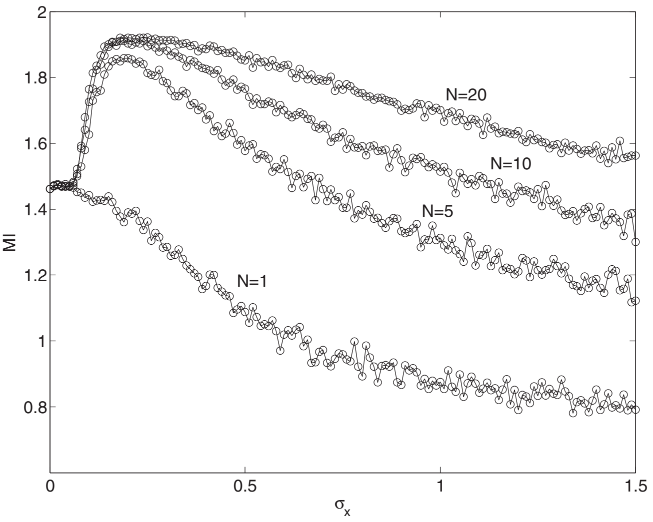

FIG. 3. Mutual information shown as a function of the noise strength. Once again, networks containing more than one neuron benefit from some noise.

Here the symbol {} denotes taking the average value of $\lambda(t)$ over time. For our demonstration of SSR in a model of integrate-and-fire neurons receiving Poisson inputs, and to facilitate comparison with [19], we set $a = b = 1$, $p = q = 50$, and $c_E = c_I = 0$ (uncorrelated inputs); it should, however, be noted that in general the central behavior of the model is similar across a very wide parameter space. We also need to be able to separately control the noise level in order to determine whether or not any nonzero level of noise gives improved performance. For this experiment we use a noise coefficient σ_x prepended to the synaptic input expression given in Eq. (15). It should be noted that only in the special case of $\sigma_x = 1$ are the inputs strictly Poisson processes; nevertheless varying the parameter from this value can be seen as a reflection of the wide variety of Fano factors both above and below that of a Poisson process reported in the literature for neural spike trains under different conditions [42]. These facts allow us to simplify Eq. (15) for this particular experiment to

$$\begin{aligned} \mu(t) &= \lambda(t)(1 - r),\\ \sigma(t) &= \sqrt{\sigma_x(1 + r)}, \qquad (16)\\ r &= E\left\{1 - \frac{V_{\text{thresh}}}{\lambda(t)\gamma}\right\}. \end{aligned}$$

Setting the input firing rate parameter to the stepped input signal previously defined in Sec. II B, $\lambda(t) = x(t)$, we obtained the results shown in Fig. 3. The SSR effect is once again clearly present, demonstrating that neurons receiving spike train inputs appear to benefit from noise.

IV. CORRELATION CONTROL

In the previous experiment, although neurons received summarized spiking inputs stimulated by a stepped input signal and which allows noise to scale with the inputs, the noise was further scaled explicitly and independently of the signal (via the parameter σ_x). In addition, the inputs were strictly uncorrelated; that is, $c_E = c_I = 0$ in Eq. (15). Both of these are unlikely to be true in the general case, so in this section we present a model which still receives spike train inputs (including in one example strictly Poisson spike trains), but where noise is no longer directly controlled (except insofar as we set different noise parameter values for comparison across different simulations), and inputs can now be correlated. Correlation has previously been studied in the context of SSR [43], where it was found that positive correlations in the background noise decrease information transmission and reduce the benefits of population coding. Here, we study the more biophysically interesting case of the correlations in spiking neuronal inputs, rather than artificially controlling noise correlation directly. We also consider the full range of negative to positive correlations, in contrast to the exclusively positive correlations studied by [43]. In principle, the excitatory and inhibitory input correlations c_E and c_I can be tuned independently of each other and certain combinations will still lead to SSR, but a full exploration of this parameter space is beyond the scope of the current study. Instead, here we adopt a single correlation parameter in this section by defining $c = c_E = c_I$ for the purpose of clarity of demonstration and to allow a comparison with previous work [19,43] which also used a single correlation parameter.

We first fixed the input noise parameter σ_x at a chosen value (shown in the figures) and then measured mutual information as a function of correlation instead by systematically varying the value of c [$c_E$and c_I in Eq. (15)] across a range of values and obtaining the output of the network for each correlation value in turn. We again set $a = b = 1$, $p = q = 50$ to facilitate comparison with our earlier results.

It can be seen in Fig. 4 that for a typical low value (<1) of the input noise parameter ($\sigma_x = 0.4$), negatively correlated inputs give optimal performance. In fact, σ_x must be approximately 0.2 for small numbers of neurons N to have optimal performance from uncorrelated inputs. In the special case of $\sigma_x = 1.0$, which is equivalent to having no additional noise scaling parameter σ_x prepended to the variance of the diffusion approximation in Eq. (15) and therefore gives strictly Poisson inputs, optimal performance comes from negatively correlated inputs. The more general result across a range of σ_x and correlation values can be seen in Fig. 5. The ridge of highest mutual information values shows that as the noise parameter becomes larger, the correlation must become more negative to compensate and retain optimal information transmission. Importantly, this ridge is also higher than the plateau that exists for low values of σ_x and c; this plateau represents the situation where the noise input is too low to drive neurons in receipt of subthreshold input signals to reach their firing threshold. In other words, a significant nonzero amount of noise results in improved information transmission in this network of $N = 30$ neurons, which is in keeping with SSR.

It is instructive to examine the mutual information separately for the subthreshold and suprathreshold regions of the input space, as well the total (combined) mutual information. We are able to do this due to the use of a time-averaged ratio of excitatory and inhibitory inputs r in combination with a stepped input signal $x(t)$ [still defined by Eq. (5), but here with limits (5,100) and an increment size of 5], shown in the bottom panel of Fig. 6. This means that the inputs are, averaged over time, enough to cause the network neurons to spike without any additional noise, but this can be divided into subthreshold inputs, which are below average and insufficient to stimulate spiking behavior without additional noise, and suprathreshold inputs which are above average and can stimulate spiking behavior without additional noise. The results for a network of 20 neurons receiving either subthreshold, suprathreshold, or all (subthreshold and suprathreshold) inputs, are shown in the top panel of Fig. 6. It is clearly apparent that as correlation becomes more positive, thereby increasing noise, the suprathreshold signal loses MI, while the subthrehold signal gains MI. This provides an interesting link between SSR and classical SR; we are seeing a classical SR effect for the subthreshold component of the signal which up to a certain level outweighs the detrimental effect on the suprathreshold signal, giving an overall benefit. The bottom of Fig. 6 clearly

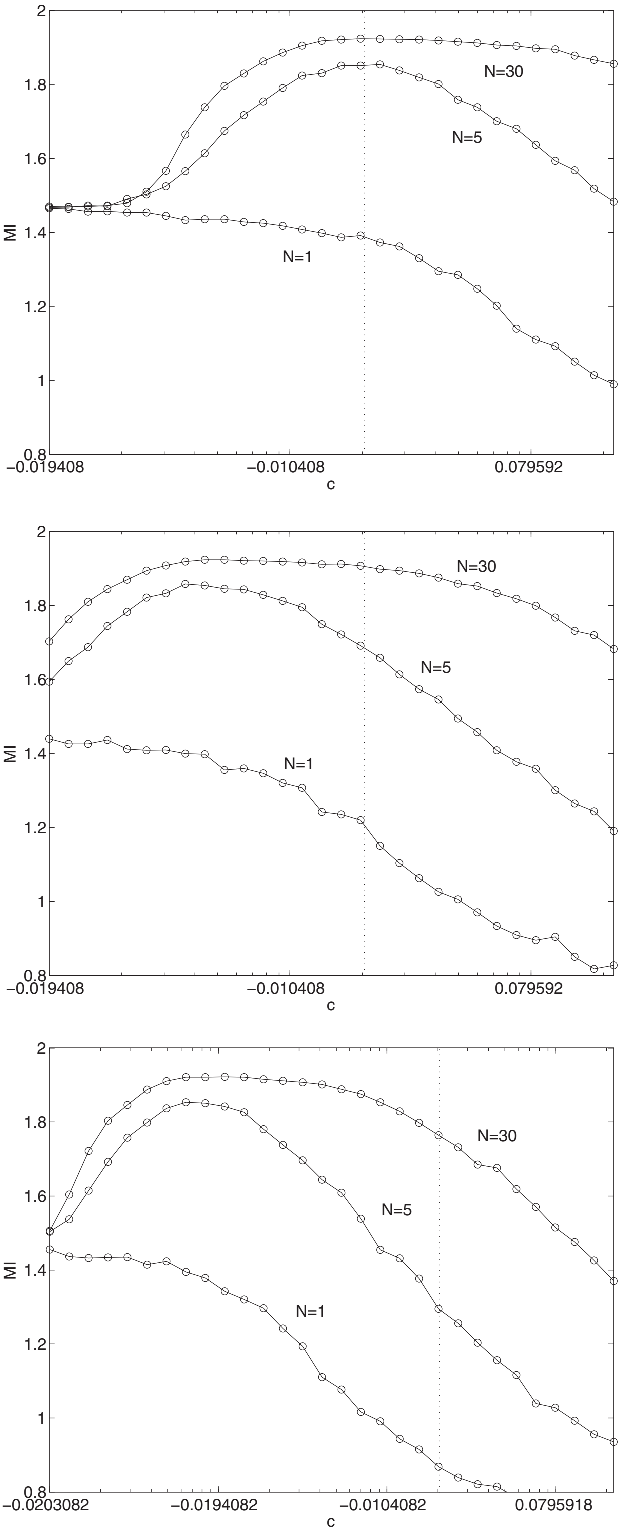

FIG. 4. Mutual information as function of correlation. The vertical dotted line gives the zero correlation position; logarithmic spacing is used for visual clarity. (Top) $\sigma_x = 0.2$; uncorrelated inputs give optimal performance. (Middle) $\sigma_x = 0.4$; negatively correlated inputs give optimal performance at this noise level. (Bottom) $\sigma_x = 1$; negatively correlated inputs give optimal performance in the absence of a special noise parameter.

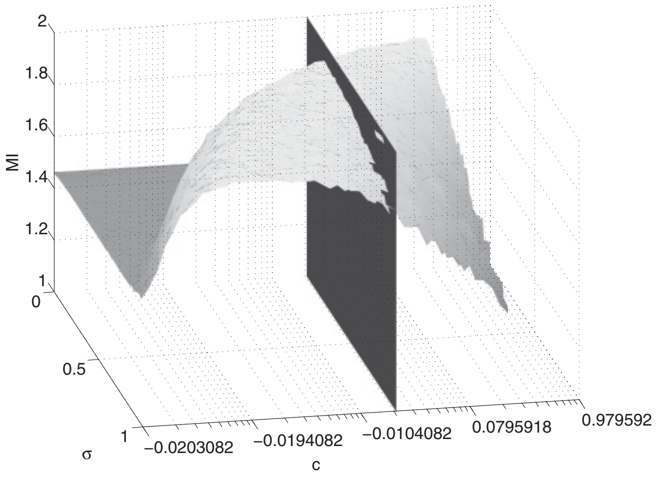

FIG. 5. Mutual information shown as a function of correlation and noise strength, for a network of $N = 30$ neurons. The vertical plane shows the position of zero correlation.

shows the reason why; the subthreshold signal has no response at all because the signal is not strong enough to reach threshold and there is no noise to assist it. This is both traditional SR, because noise would clearly help to sometimes push the input over threshold, and more often when the signal is closer to the threshold, and SSR because varied thresholds in the neurons would allow some to respond to a subthreshold signal because their individual thresholds would also be below the signal dc level. This is the theoretical link between SR and SSR.

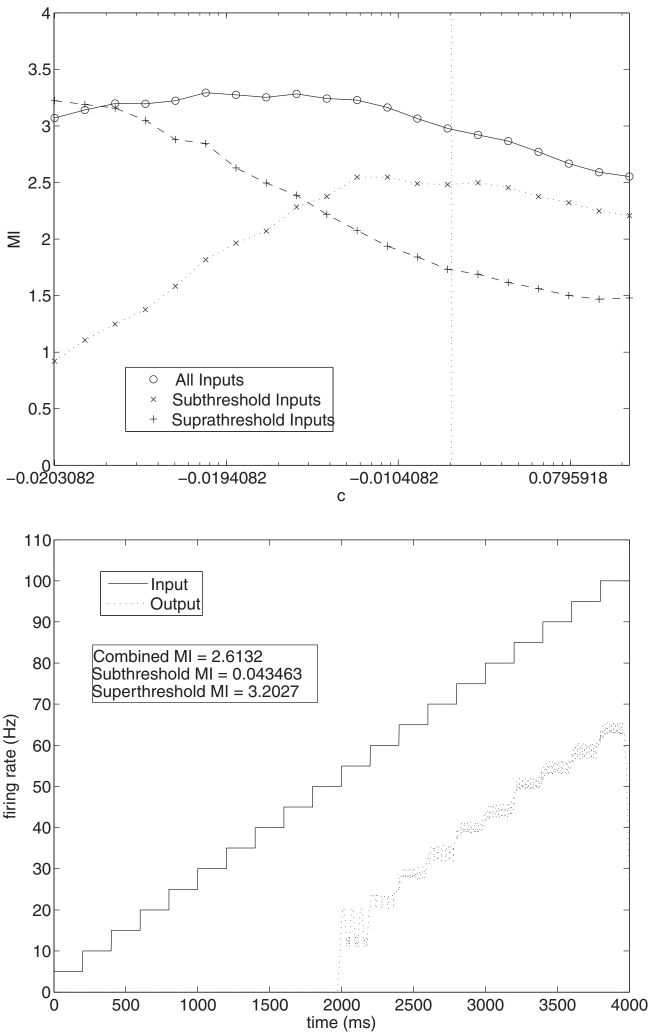

FIG. 6. (Top) Mutual information as a function of correlation for all inputs, subthreshold inputs, and suprathreshold inputs; $N = 20$ here. This shows that increased noise is beneficial for the subthreshold part of the signal and detrimental to the suprathreshold part of the signal. (Bottom) Stimulus and response for a zero-noise case ($\sigma_x = 0$). The flat response in the subthreshold region results in low mutual information in the absence of noise.

The fact that noise is required to boost subthreshold signals, but potentially damaging for suprathreshold signals, suggests that an adaptive correlation control procedure could be highly beneficial in optimizing information transmission. A relatively high correlation (according to a model-specific scale; in this case relatively high essentially means uncorrelated) at low signal levels could generate a high level of noise that would boost the signal into the threshold region, and as the signal level becomes higher, the correlation should become more negative, reducing noise and thus limiting the detrimental effect on the suprathreshold signal region. An example of this is shown in Fig. 7. Whereas in previous simulations the correlation value was held constant across time within a single run, here the correlation value was varied with time in the way shown in the top panel of Fig. 7. This correlation function was created in a simple piecewise fashion, with the correlation decreasing from an upper limit of -0.01, to a lower limit of $-0.020\,408$ which is the minimum possible correlation value $-1/(q-1)$ where $q = 50$ is the number of Poisson input processes. The correlation decreased as a logarithmically spaced step function with 11 steps, each timed to coincide with a change in the input stimulus value. As the stepped inputs increased, the correlation became more negative, reducing the noise level accordingly, until the input stimulus reached the suprathreshold point, at which time the correlation attained its most negative value and remained there for the remainder of the simulation. This is an adaptive correlation control in the sense that the correlation decreases when the signal increases; this was defined arbitrarily in this case, but a mechanism specifically linking these can be conceived in principle. The results of simulating the same network of 20 neurons with the same stepped input signal as that used in the previous example (Fig. 6), but now with adaptive correlation control, is shown in the bottom panel of Fig. 7. It can clearly be seen that overall information transmission is improved by using the adaptive procedure beyond the highest level possible with a fixed correlation value that does not change over time, by controlling noise level in response to prevailing stimulus conditions. This example is certainly not optimal in any sense, but is presented as a proof of concept. It uses the same model, including the same time-averaged ratio of balanced inputs r, as our examples in the previous sections. In practice, the r could not be estimated from the input signal prior to that signal being presented to the model; that is, our mechanism as above is not strictly causal. However, the model is in practice robust to different values of this ratio, and as long as inputs are usually within limits learned from prior experience, as is the case for

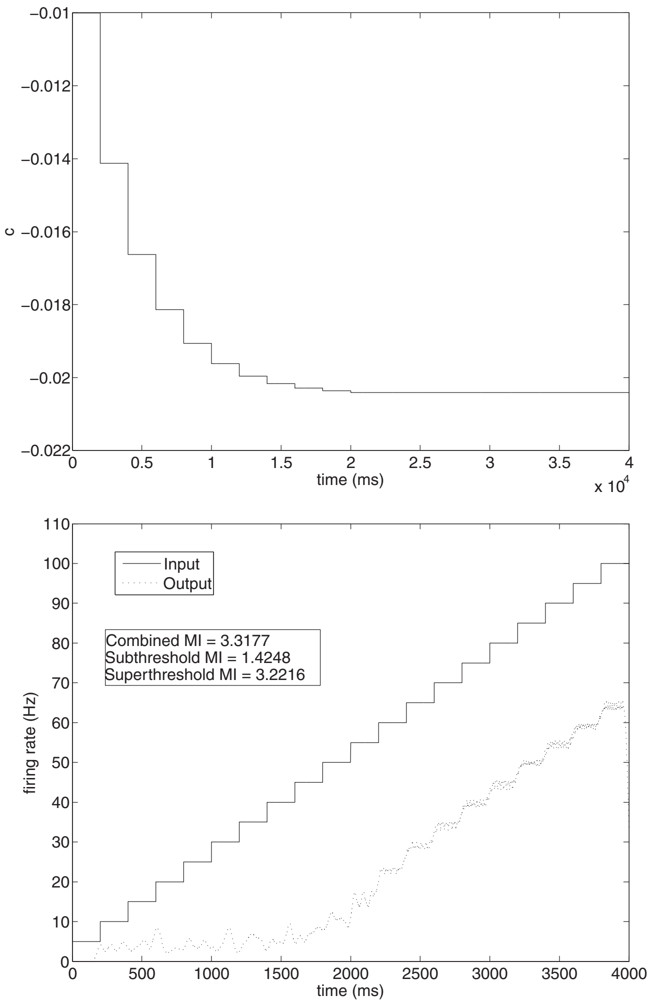

FIG. 7. (Top) Adaptive correlation control. The correlation decreases as a function of input, using a piecewise step function as shown. (Bottom) Stimulus and response with adaptive correlation control. The subthreshold region now has some response, though not optimal, and the suprathreshold region remains largely free of the detrimental effect of noise.

typical firing rates of particular types of neurons [44], then a value for this ratio can be obtained in advance. However, the question of the optimal adaptive technique that could be used remains open to research, as does the question of how, if at all, the brain implements such a feature.

V. DISCUSSION

Suprathreshold stochastic resonance is an important new phenomenon that offers a functional explanation of noise in information processing systems. We have developed a framework for SSR in the context of integrate-and-fire neural models, both with independent noise and with Poisson process spiking inputs modeled by a diffusion approximation. Our results demonstrate that within a model of spiking neurons receiving other spiking inputs driven by a simple stimulus, SSR is present and optimal information transmission can be achieved with a nonzero level of noise. Moreover, we have shown that this noise level can be tuned by correlations in the presynaptic neural firing, with more negatively correlated firing resulting in decreased noise (and vice versa). In our simulations, a model receiving Poisson inputs with a fixed level of correlation achieved optimal information transmission when the presynaptic firing was negatively correlated. We also demonstrated, however, that there is a theoretical link between SSR and traditional SR in our model, and that information transmission could be improved still further by the use of an adaptive correlation measure, which boosts noise when the input signal is in a subthreshold regime and reduces it when the signal is suprathreshold.

Our results are in broad agreement with previous theoretical studies on correlation in neural systems, which have demonstrated that even small positive correlation results in reduced information transmission [43], to the extent that population coding is redundant beyond units of at most a few hundred neurons [45,46], while negative correlation results in increased information transmission in the context of traditional SR [19]. The benefits of negative correlation exist not only for presynaptic firing, but also extend to neurons within the model itself, which may occur due to mutual inhibitory connections [47].

Given these clearly established theoretical benefits of negatively correlated firing, it seems odd at first glance that empirical findings suggest the presence of weak positive correlations in neural firing *in vivo* [46,48,49]. However, there are several possible explanations for this which are compatible with the results of theoretical modeling. First, the concept of redundancy reduction has been proposed for the visual system [50,51] (but see also [52]), which suggests an increasingly sparse representation as we move from retinal ganglion neurons through the lateral geniculate nucleus into the primary visual cortex and beyond, something which is corroborated by results from sparse coding and independent components analysis models [53–56]. As a sparse representation is inherently likely to exhibit reduced correlation, this suggests that the weak positive correlation observed in retinal ganglion neurons may be reduced in cortical areas. Second, existing correlation measures have looked primarily at neighboring neurons in sensory areas such as the retina. These are typically organized in a way that neighboring neurons will have similar receptive fields [57], so mutual input to these neurons is an extrinsic driving force toward positively correlated firing [8]. Just as spike timing variability increases along the visual pathway from retina to cortex [58], so it may also be expected that the influence of mutual input on the positive correlation of neighboring neurons decreases, particularly in higher cognitive areas which have less of a sensory topological organization. Third, SSR is based on increasing the diversity of the output response [21,25]. This should be more strongly present in neural areas with a greater biophysical diversity of neuronal properties than retinal ganglion or even thalamic neurons. Recent evidence suggests that this is indeed the case [59], with more intrinsically diverse neurons exhibiting reduced correlation and increased information transfer.

These additional factors suggest that, rather than looking at a single correlation measure in sensory areas, it may be more beneficial to look at correlation in the same areas under different conditions [60]. In particular, our model predicts that as a signal gets stronger, the correlation should decrease in order to control the noise and continue to optimize information transfer. This has received little empirical investigation to date, but was addressed in two recent multielectrode studies looking at the olfactory bulb of the sheep [61] and the anterior superior temporal sulcus of the macaque monkey [42]. Both of these studies found that stimulus onset (as opposed to background, rest or habituation) was accompanied by a temporarily decreased correlation between neurons. Modeling this response, the author of [42] found that this transiently decreased correlation at stimulus onset increased the transmission of information about this stimulus beyond what could be achieved with a purely static correlation measure. We believe that SSR, and its connection to traditional SR demonstrated in our model, provides the theoretical underpinning of these findings. This also emphasizes the importance of adopting the right measure of correlation, in particular, using an appropriate baseline condition and treating correlation as a nonstationary variable. It is too early to say for certain that SSR exists in real neural systems, but our demonstration and explanation outlined here suggest that this is very likely to be the case, and the evidence to date is encouraging.

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