Optimal quantization for energy-efficient information transfer in a population of neuron-like devices

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ABSTRACT

Suprathreshold Stochastic Resonance (SSR) is a recently discovered form of stochastic resonance that occurs in populations of neuron-like devices. A key feature of SSR is that all devices in the population possess identical threshold nonlinearities. It has previously been shown that information transmission through such a system is optimized by nonzero internal noise. It is also clear that it is desirable for the brain to transfer information in an energy efficient manner. In this paper we discuss the energy efficient maximization of information transmission for the case of variable thresholds and constraints imposed on the energy available to the system, as well as minimization of energy for the case of a fixed information rate. We aim to demonstrate that under certain conditions, the SSR configuration of all devices having identical thresholds is optimal. The novel feature of this work is that optimization is performed by finding the optimal threshold settings for the population of devices, which is equivalent to solving a noisy optimal quantization problem.

Keywords: stochastic resonance, suprathreshold stochastic resonance, noise, neural coding, population codes, energy efficient coding, neurons, optimal quantization

1. INTRODUCTION

In recent years there has been much interest in applying the techniques of electronic engineering and signal processing to the field of computational neuroscience.[1,2] The motivation for this is obvious; the brain uses electrical signals (as well as chemical signals) to propagate information, and must employ some sort of coding and decoding mechanism as part of this information transmission. The field of signal processing has many mature techniques for dealing with propagation and coding, and these techniques can be employed to gain new insights into the ways the brain operates and processes information. Of particular interest is the fact that the brain manages to perform so well in very noisy conditions, with a signal to noise ratio orders of magnitude lower than those usually encountered in electronic communication systems.[3] Many studies have shown that through a mechanism known as Stochastic Resonance (SR), neurons are capable of optimal performance in the presence of noise, so that it appears that the brain has evolved to be optimally adapted to operating in such noisy conditions, or alternatively, has evolved to generate noise, to enable its neurons to perform optimally.[4,5] SR is now widely known as the class of phenomena where a certain non-zero level of noise in nonlinear systems provides the optimal output of that system,[6–8] and has been shown to occur in many other systems besides neurons. Also of interest, is the fact that many recent studies in the field of biophysics have shown that energy is an important constraint in neuronal operation, and have investigated the role of this constraint in neural information processing .[9–15]

In this paper, we present an investigation of the optimal noisy encoding of a random input signal in a population of simple neuron models, subject to energy constraints. This work builds on a recently discovered form of SR known as Suprathreshold Stochastic Resonance (SSR).[16–18] SSR occurs in an array of threshold devices, such as neurons, or comparators in an electronic circuit. Each element in the array simply receives the same input signal, and outputs a spike if the output is greater than that elements threshold value. The overall output is the sum of the individual outputs. If *iid*

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additive noise is present at the input to each element, then the overall output becomes a randomly quantized version of the input signal, which for the right level of noise is highly correlated with the input signal. The original work calculated the mutual information between the input and output in such a system for *iid* Gaussian signal and noise, and showed that stochastic resonance occurred regardless of the magnitude of the input signal when all threshold values were set to the input signal's mean value. This is in contrast with a single threshold device, for which SR can only occur for subthreshold signals.

More recently, the same phenomena has been shown to occur in a population of FitzHugh-Nagumo neuron models,[19] and verified using other signal and noise probability densities[20] and using the cross-correlation measure[21] and Fisher information.[22] An analytical approximation to the mutual information as the population size approaches infinity has also been used to find the asymptotic optimal noise intensity.[23] Of most relevance to our current investigation is work that imposed an energy constraint on the system and calculated the optimal input signal distribution given that constraint.[15] Also closely related is work using a similar model that defined an energy efficiency measure.[14]

In our own previous work,[24] we have found the optimal thresholds (those which maximize the mutual information) for a certain value of population size, N. By contrast, here we look at three energy constrained problems. In two of these problems we fix the input distribution and population size, and aim to firstly find the threshold settings that maximize the mutual information subject to a maximum average output energy constraint, and secondly to find the threshold settings that minimize the average output energy, given a minimum mutual information constraint. The third problem is the more biologically relevant problem of minimizing the population size, N, (and therefore the energy expenditure) given a minimum mutual information constraint and fixed thresholds.

Mathematical formulations of these problems are presented in Section 4, along with the solutions we have found. However, first in Section 2 we describe our model and the formulae used to calculate mutual information and average output energy. In Section 3 we give a brief indication of how we numerically calculate these quantities under the assumption of given signal and noise probability density functions. Finally, we draw some conclusions from our results in Section 5.

2. THE MODEL

The array of neuron-like elements we use as the basis of our model is shown in Fig. 1.

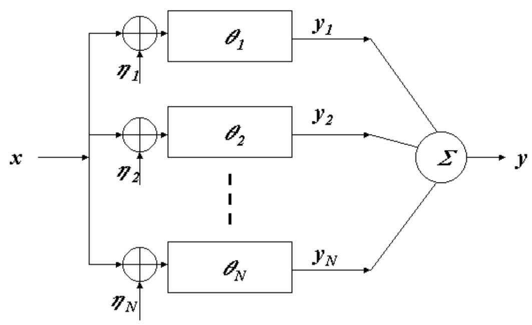

Figure 1. Array of N model neurons. Each neuron receives the same input signal, x, and is subject to independent additive noise, η_n. The output, y_n, from neuron n is unity if the sum of the signal and noise is greater than that neuron's threshold, θ_n, and zero otherwise. The overall output, y, is the sum of the individual neural outputs.

2.1. Mutual information

If the input signal has probability density function $P_x(x)$, then the mutual information between the input and output is given by[16]

$$I(x,y) = -\sum_{n=0}^{N} P_y(n)\log_2 P_y(n) - \left(-\int_{-\infty}^{\infty} P_x(x)\sum_{n=0}^{N} P(n|x)\log_2 P(n|x)dx\right), \tag{1}$$

where

$$P_y(n) = \int_{-\infty}^{\infty} P(n|x)P_x(x)dx.$$

Therefore for given signal and noise distributions, the mutual information depends entirely on the transition probabilities, $P(n|x)$, and the only free variables are the population size, N, and the threshold values of the neurons. Let $\hat{P}_n$ be the probability of neuron n being triggered by signal value x. Then

$$\hat{P}_n = \int_{\theta_n - x}^{\infty} R(\eta)d\eta = 1 - F_R(\theta_n - x), \tag{2}$$

where F_R is the cumulative distribution function of the noise and $n = 1, .., N$.

Given a noise density and threshold value, $\hat{P}_n$ can be calculated exactly for any value of x from (2). Assuming $\hat{P}_n$ has been calculated for desired values of x, a convenient way of numerically calculating the probabilities $P(n|x)$ for an array of size N is as follows. Let $T_{n,k}$ denote the probability that n of the neurons $1, \ldots, k$ are "on," given x. Then let $T_{0,1} = 1 - \hat{P}_1$ and $T_{1,1} = \hat{P}_1$ and we have the recursive formula

$$T_{n,k+1} = \hat{P}_{k+1}T_{n-1,k} + (1 - \hat{P}_{k+1})T_{n,k}, \tag{3}$$

where $k = 1, .., N-1$, $n = 0, .., k+1$, $T_{-1,k} = T_{k+1,k} = 0$ and we have $P(n|x)$ given by $T_{n,N}$.[20] For the particular case when the thresholds all have the same value, and all noise densities are *iid*, then each $\hat{P}_n$ has the same value $\hat{P}$ and, as noted by Stocks[16] we have the binomial distribution

$$P(n|x) = \binom{N}{n}(\hat{P})^n(1-\hat{P})^{N-n} \quad (0 \leq n \leq N). \tag{4}$$

Thus, for any arbitrary threshold settings and signal and noise probability distributions, $P(n|x)$ can be easily calculated numerically from (2) and (3).

2.2. Average output energy

The simplest approach is to assume that the energy expended is the same constant amount every time a neuron emits a spike. Therefore, to minimize the average output energy consumption requires minimization of the mean output value, that is, E$[y]$, which is

$$\mathrm{E}[y] = \sum_{n=0}^{N} nP_y(n) = \sum_{n=0}^{N} n\int_{-\infty}^{\infty} P(n|x)P_x(x)dx = \int_{-\infty}^{\infty} P_x(x)\left(\sum_{n=0}^{N} nP(n|x)\right)dx. \tag{5}$$

For the SSR case, we have $P(n|x)$ given by the binomial formula as in Equation (4). Therefore $\sum_{n=0}^{N} nP(n|x)$ is the mean value of a binomial distribution and is given by $N\hat{P}$. For even $R(\eta)$, E$[\hat{P}] = 0.5$ and therefore E$[y] = N/2$.

For arbitrary thresholds however, the threshold settings control the output state probabilities. Therefore by ensuring some thresholds are set high enough, higher output values can be made less probable in order to reduce the average output energy expended.

2.3. Energy efficiency

Previous work has made use of an efficiency measure in a related study.[14] This was defined as the ratio of mutual information to metabolic energy required in a neural coding. Hence we use a similar metric, the ratio of mutual information to average output energy, which we denote as

$$\xi = \frac{I(x,y)}{\mathrm{E}[y]}. \tag{6}$$

This quantity is a measure of bits per unit energy. Clearly this efficiency measure is increased if either the mutual information increases, or average output energy decreases. Thus, it is only useful if some constraint is placed on either mutual information or energy, since the efficiency can be made near infinite by ensuring that the population output is almost always zero. Hence, maximizing the energy efficiency requires either maximizing the mutual information subject to a maximum output energy constraint, or minimizing the average output energy subject to a minimum mutual information constraint. We will consider both of these methods below.

3. NUMERICAL CALCULATIONS

Recall that we assume knowledge of the noise and signal densities and that therefore using (3) we can always calculate $P(n|x)$ for given values of x and y. Hence, it is possible to numerically calculate the mutual information or average output energy for arbitrary threshold values and a given value of noise variance. Both of these measures require us to perform numerical integrations over x. We could use sophisticated numerical integration schemes, but for simplicity and numerical speed we have decided to simply approximate the signal density function by a discrete version, with resolution $\Delta x \ll 1/N$. Hence, if in the case of the continuous density function $P(x)$ we have $a \leq x \leq b$, then discretization with resolution Δx gives discrete values $x = a + i\Delta x, i = 0, 1, .., (b-a)/\Delta x$. For an input distribution with finite support such as the uniform distribution, where $x \in [a, b]$, we only need to define the resolution. However for a distribution which has infinite support, such as a Gaussian, we need to restrict the upper and lower bounds of x. We will set these to be a multiple, w, of the standard deviation, σ_x, that is $x \in [-w\sigma_x, w\sigma_x]$, and then discretize to a resolution of Δx.

Note from Equation (2) that the probability of the n-th neuron emitting a spike is one minus the cumulative distribution function of the noise at $\theta_n - x$. Hence, since we are discretizing x, $\hat{P}_n$ is also effectively discretized. Performing the discretization of x transforms Equation (1) into

$$I)x, y) = -\sum_{n=0}^{N} P_y(n) \log_2 P_y(n) - \left(-\Delta x \sum_x P(x) \sum_{n=0}^{N} P(n|x) \log_2 P(n|x) \right),$$

where

$$P_y(n) = \Delta x \sum_x P(n|x)P(x).$$

Discretizing the average output energy of (5) gives

$$\mathrm{E}[y] = \Delta x \sum_x P_x(x) \sum_{n=0}^{N} nP(n|x).$$

4. OPTIMAL QUANTIZATION

As discussed, we aim to maximize the mutual information subject to an average output energy constraint. Both $I(x, y)$ and $\mathrm{E}[y]$ are functions of the transition probabilities, $P(n|x)$. It is possible to formulate such an optimization as a variational problem, where the aim is to find the optimal $N + 1$ functions, $P(n|x)$. However, from Section 2, we know that given a noise density, then the $N + 1$ functions $P(n|x)$ can be calculated for any given set of thresholds for any value of x. Therefore, the set of $P(n|x)$ depends entirely on the set of thresholds, θ_n. Hence, to solve our constrained problem, we can instead focus on finding the optimal threshold settings. With such an approach, we have a nonlinear program with N real valued variables and the problems we are aiming to solve can now be written as the optimization problems described in the following subsections.

Since the thresholds are real valued, the most practical technique for solving such optimization problems is a random search method, for example a genetic algorithm or simulated annealing.[25] Previously, a method known as deterministic annealing has been applied to rate-distortion analysis in a similar context,[26] however here, with no knowledge of the convexity of the solution space in our problem, we rely on simulated annealing.

The original work on SSR presented its results as a plot of mutual information against the ratio of noise standard deviation to signal standard deviation, denoted as σ. The mutual information had a maximum value for a nonzero value of σ (i.e. for the presence of an optimal amount of noise), which is the key characteristic of SR. Throughout the following subsections, the results shown assume a zero mean Gaussian signal, with variance σ_x^2 and *iid* zero mean Gaussian noise with variance σ_η^2. Thus, we can present our results in the same fashion as the previous SSR work, by plotting mutual information, average output energy, energy efficiency, or optimal threshold values against $\sigma = \sigma_\eta/\sigma_x$.

4.1. All thresholds equal

As a useful point of reference, we first present results for the mutual information and average output energy for the case of all thresholds equal and no energy constraint. We know that if all thresholds are zero, then the system is in the SSR configuration, and the average output energy is $N/2$. Clearly, if we increase all the thresholds above zero, then both the mutual information and average output energy will decrease. Examining the behavior of the energy efficiency of (6) as the average output energy increases will provide a useful benchmark for our later constrained results.

It is clear from Figs. 2, 3 and 4 that as expected the mutual information and energy both decrease as the thresholds increase. It is also clear that the energy efficiency increases with decreasing energy. Thus, if we wish to maximize the energy efficiency, this illustrates the requirement for placing a minimal mutual information or minimal average output energy constraint for nontrivial results.

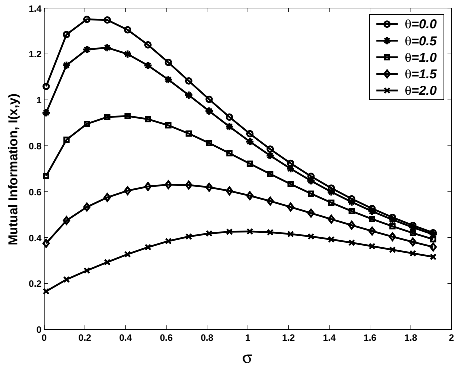

Figure 2. Plot of mutual information, $I(x, y)$, against σ for increasing values of θ, when all neurons have the same value of θ and $N = 5$.

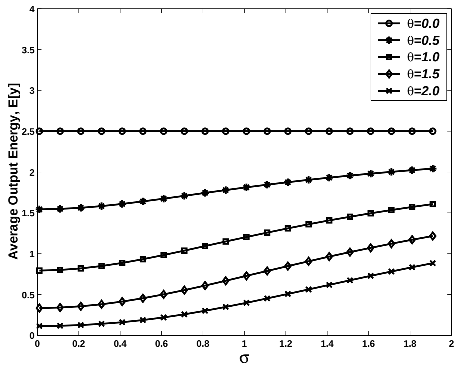

Figure 3. Plot of average output energy expended, $\mathrm{E}[y]$, against σ for increasing values of θ, when all neurons have the same value of θ and $N = 5$.

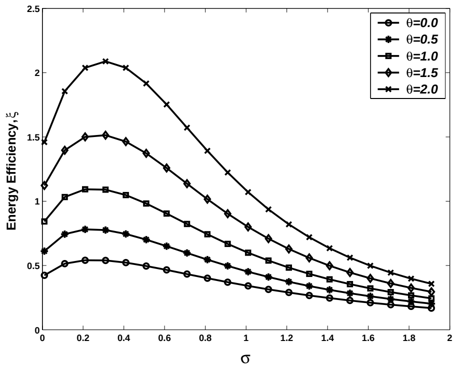

Figure 4. Plot of information efficiency, ξ, against σ for increasing values of θ, when all neurons have the same value of θ and $N = 5$.

4.2. Maximizing mutual information with a maximum average output energy constraint

For this problem we to wish to fix N and find the thresholds settings which maximize the mutual information, for a range of σ, while imposing a maximum average output energy expenditure constraint. We have obtained the solution to this problem in the absence of the energy constraint in previous work,[24] the result of which is shown in Fig. 5 for $N = 5$. It turns out that the output energy of the optimal unconstrained solution is the same as for the case of SSR, that is $\mathrm{E}[y] = N/2$. Hence, we restrict out attention to the case of $\mathrm{E}[y] < N/2$. Thus, this problem can be expressed as

$$
\begin{aligned}
\text{Find:} \quad & \max_{\{\theta_n\}} \quad I(P(n|x)), \\
\text{where} \quad & P(n|x) \text{ is a function of} \\
\hat{P}_n \quad & = \int_{\theta_n - x}^{\infty} R(\eta) d\eta = F_R(x - \theta_n) \quad (n = 1, .., N), \\
\text{subject to:} \quad & \mathrm{E}[y] \leq A < N/2 \\
\text{and} \quad & \theta_n \in \mathbf{R}.
\end{aligned} \tag{7}
$$

The results of numerical solutions of (7) for $N = 5$ and various values of A are shown in Figs. 6, 7 and 8. Note that the energy constraint is always met with equality. As the maximum output energy decreases, the mutual information also decreases, but only by a small fraction of a bit per sample, in each case shown. The energy efficiency increases as the maximum output energy decreases. From this result, it is clear that energy efficiency can be substantially increased with only a small decrease in mutual information.

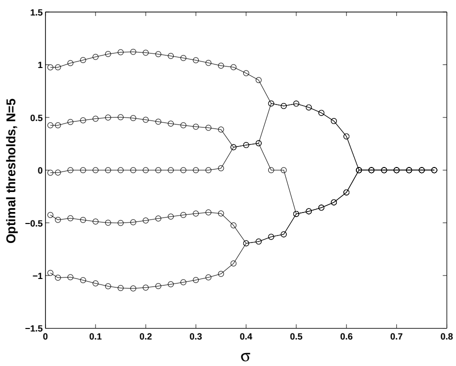

Figure 5. Plot of optimal thresholds against σ in the absence of an energy constraint for $N = 5$.

Fig. 8 shows that unlike SSR, where above a certain value of σ the optimal solution is for all thresholds equal to the signal mean, the optimal thresholds remain widely spaced. However this is only the optimal solution found with our current algorithm. Further improvement of the algorithm is likely to yield a less scattered result for the optimal thresholds, as in Fig. 5. If it turns out that above a certain value of σ, the optimal solution is for all thresholds equal to the same value, then the optimal coding for our model is that which employs the use of SSR.

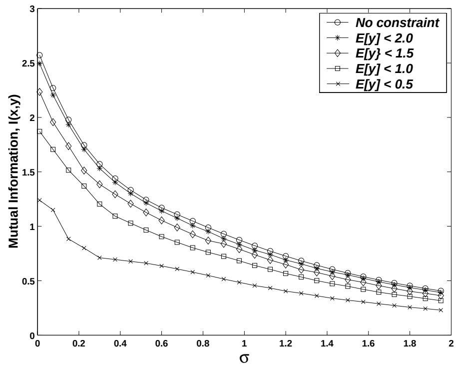

Figure 6. Plot of mutual information, $I(x, y)$, against σ for various energy constraints, optimized thresholds, and $N = 5$.

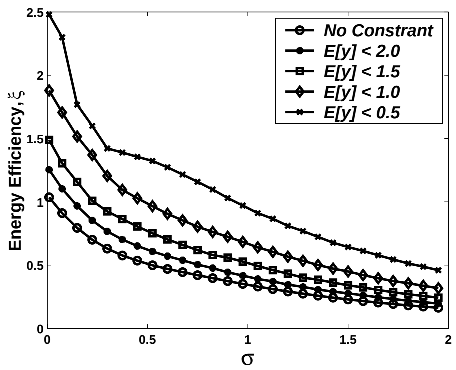

Figure 7. Plot of information efficiency, ξ, against σ for various energy constraints, optimized thresholds, and $N = 5$.

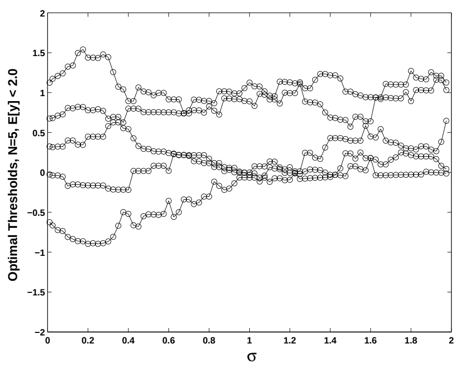

Figure 8. Plot of optimal thresholds against σ for the energy constraint $\mathrm{E}[y] \leq 2.0$ for $N = 5$.

4.3. Energy minimization with a minimal mutual information constraint

For this problem we wish to fix the mutual information and N, and find the threshold settings that minimize the average output energy, for a range of σ. Mathematically, fixing the mutual information is equivalent to the imposition of a minimum mutual information constraint. As discussed, imposition of such a constraint is necessary if we wish to maximize the energy efficiency by minimizing the energy, since otherwise the optimal solution would be to simply ensure no neuron ever fires. As N is fixed, the maximum possible mutual information for a particular value of σ is the optimal solution of (7) obtained in the absence of the energy constraint. Label this value as $\hat{I}(\sigma)$. We wish to find an energy efficient solution that provides some minimum percentage of $\hat{I}(\sigma)$. This problem can be expressed as

$$\begin{aligned}
\text{Find:} \quad & \min_{\{\theta_n\}} \quad \mathrm{E}[y] = \int_{-\infty}^{\infty} P_x(x) \left(\sum_{n=0}^{N} nP(n|x) \right) dx, \\
\text{where} \quad & P(n|x) \text{ is a function of} \\
\hat{P}_n \quad & = \int_{\theta_n - x}^{\infty} R(\eta) d\eta = F_R(x - \theta_n) \quad (n = 1, .., N), \\
\text{subject to:} \quad & I(P(n|x)) \geq B\hat{I}(\sigma), B \in [0, 1] \\
\text{and} \quad & \theta_n \in \mathbf{R}.
\end{aligned} \tag{8}$$

The results of numerical solutions of (8) for $N = 5$ and various values of B are shown in Figs. 9 and 10. Similar results to those of the previous section are apparent. Note that the mutual information constraint is always met with equality. As the minimum mutual information constraint decreases, the average output energy also decreases, and the energy efficiency decreases. Again, especially for lower values of noise, the percentage increase in energy efficiency is larger than the percentage decrease in mutual information.

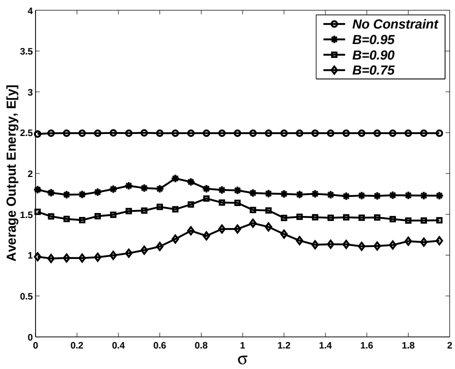

Figure 9. Plot of average output energy, $\mathrm{E}[y]$, against σ for various minimum mutual information constraints, optimized thresholds, and $N = 5$.

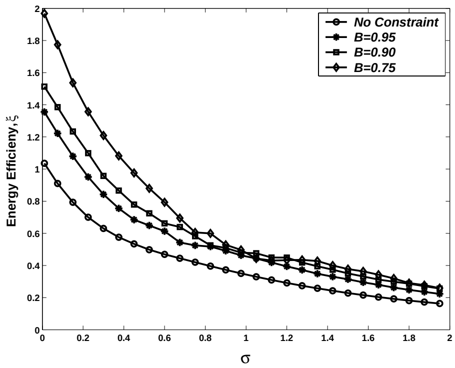

Figure 10. Plot of information efficiency, ξ, against σ for various minimum mutual information constraints, optimized thresholds, and $N = 5$.

4.4. Energy minimization for fixed thresholds and a minimum mutual information constraint

In a biological context, the above formulations may not be the most relevant. To be useful to an organism, a sensory system must convey a certain amount of information, $\hat{I}$ to the brain. Any less than this and the sensory function is not useful. For example, to avoid becoming prey, a herbivore must be able to distinguish a sound at, say, 100 m whereas 50 m is not sufficient. To develop such a sensory ability, the animal must use more neurons, and therefore use more energy (in the form of generated spike trains, as well as energy to grow them in the first place) to convey the information to the brain. For maximum evolutionary advantage the animal must do this in the most energy efficient manner (otherwise it may have to eat more than is feasible), so the problem that evolution solves in the animal is not to fix N and maximize $I(x, y)$, but fix $I(x, y)$ and minimize N (or, more generally, minimize the energy, which we might assume is a (possibly linear) function of N). This is also slightly different to the problem of maximizing information subject to an energy constraint, although the most efficient way of transmitting $I(x, y)$ bits of information must be equivalent to finding the value of energy E that gives rise to the optimal amount of information $I(x, y)$.

Thus, for this problem we wish to fix the mutual information and threshold settings, and find the population size, N, that minimizes the energy for a range of σ. This problem can be expressed as

$$\begin{aligned}
\text{Find:} \quad & \min_{N} \quad \mathrm{E}[y] = \int_{-\infty}^{\infty} P_x(x) \left(\sum_{n=0}^{N} nP(n|x) \right) dx, \\
\text{where} \quad & P(n|x) \text{ is a function of} \\
\hat{P}_n \quad & = \int_{\theta_n - x}^{\infty} R(\eta) d\eta = F_R(x - \theta_n) \quad (n = 1, .., N), \\
\text{subject to:} \quad & I(P(n|x)) \geq C \\
\text{and} \quad & \theta_n \text{ fixed.}
\end{aligned} \tag{9}$$

For the SSR case where all thresholds are zero, the average output energy is simply $N/2$ and hence increases with N. Therefore the solution to this problem reduces to finding the minimum N that satisfies $I(x, y) \geq C$. The result of solving (9) for Gaussian signal and noise and three values of $I(x, y)$ is shown in Fig. 11. It is clear that the value of σ at which the lowest N which satisfies the constraint occurs is nonzero. This is to be expected, given that this is the same situation as SSR, where for a particular value of N the maximum mutual information occurs for nonzero σ. We are currently extending this problem to cases involving variable thresholds, and energy constraints.

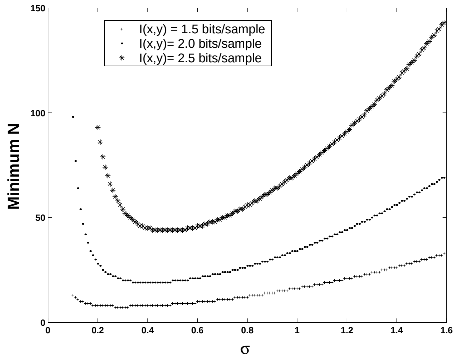

Figure 11. Results of minimizing N for fixed $I(x, y)$, against σ for zero mean *iid* Gaussian signal and noise.

5. CONCLUSIONS AND FURTHER WORK

In this paper we have formulated several energy constrained information transmission optimization problems, and solved them for a model system consisting of a population of noisy neurons. For the problem of finding the threshold settings that maximize the energy efficiency with fixed N, our results clearly indicate that the energy efficiency always increases for decreasing average output energy and always decreases for increasing mutual information. However, a fairly large energy efficieny increase can occur for only a small decrease in mutual information.

We have also seen that the maximum energy efficiency with optimized thresholds is always strictly decreasing for increasing σ, that is, no stochastic resonance effect is seen in these problems. However, since populations of real neurons are not known for having widely distributed thresholds, the energy efficiency results shown in Fig. 4 are the most biologically relevent. This figure shows that the maximum energy efficiency occurs for nonzero noise. This is due to the same mechanism as SSR, where the noise acts to randomly distribute the threshold values.

There is much further work to be completed on these problems. As mentioned, we are currently investigating methods to improve the results of Fig. 8. We also wish to introduce energy constraints and variable thresholds to the problem investigated in Section 4.4. Insight gained from the study of these model problems may be of benefit to the understanding of neural coding in the presence of noise in more realistic neuron models and real neurons.

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