Generic noise-enhanced coding in neuronal arrays

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(Received 19 September 2000; revised manuscript received 29 May 2001; published 29 August 2001)

We demonstrate that, in a parallel array of model neurons, the optimizing influence of internal noise on the global information is far greater than that reported for a single neuron. In particular, stochastic resonance (SR) effects, that optimize information transmission, occur independent of stimulus level or the setting of the neural threshold. We further show that adjusting the threshold to maximize information transmission does not remove SR effects. Consequently, and in contrast to a single neuron, in neuronal arrays noise appears to be an essential element of an optimal coding strategy.

The proposal that stochastic resonance may play an important role in the coding of weak sensory stimuli has attracted a great deal of interest [1–4]. Indeed, stochastic resonance (SR), an effect wherein the response of a nonlinear system (such as a nerve fibre) to a *weak* signal can be improved by noise [5], is now well established as an important paradigm that suggests neuronal noise could have a beneficial role in biological sensory systems.

Although it is now well established that SR can lead to the enhanced transmission of weak subthreshold signals, in single neuronal elements it is equally well known that, for suprathreshold stimulus levels, SR effects disappear. This result has been established in both computational models [4,6] and in real neurophysiological studies [3]. Furthermore, these studies also demonstrate that maximal information transmission is achieved using suprathreshold signal levels i.e., when SR is not observed. For a given stimulus level, the information is maximized by lowering the threshold level to make the signal suprathreshold—not by adding noise and using SR. Indeed, SR has been described as a method for overcoming the incorrect setting of the threshold level [6]. A neural coding strategy based on SR, therefore, seems to be largely sub-optimal in terms of information flow and only provides a positive functional role for neuronal noise if the signals are subthreshold. One is therefore led to interpret the role of the noise as a compromise—it enhances weak signal encoding at the expense of a reduction in the information encoded about suprathreshold signals.

In this Rapid Communication, we demonstrate that this compromise may not be necessary. We show that in a population of neurons noise can have a significantly greater optimizing influence, being of *generic* benefit to signal encoding. In particular, the noise is found to enhance signal information independent of the size of the stimulus, i.e., noise enhances information transmission for both subthreshold and suprathreshold signals. Additionally, noise-optimization is found to occur even under the assumption that neurons have dc-adaptive capabilities. Indeed, maximum noise-enhanced information transmission is observed to occur precisely when neurons adapt to the dc signal component level. Consequently, noise appears to play a central role in an optimal coding strategy and does not suffer from the shortcomings of SR in a single neuron where maximizing information trans-

mission (by lowering the threshold) removes the beneficial role of the noise. We also observe that the noise levels at which the information is maximized are observed to be in the correct neurophysiological range; they yield signal-to-noise ratios (SNRs) of approximately 0 dB for an individual neuron. This is in keeping with known SNRs obtained experimentally [7]. Given that perception is based on the accumulated information obtained from many nerve fibres, these results suggest that the high levels of noise observed in biological sensory systems may have purposely evolved and are an essential component of an optimal coding strategy.

The model we consider is a summing network of N FitzHugh-Nagumo (FHN) equations [2], driven by signal and independent noise. The network has the form (for the ith neuron)

$$\epsilon \dot{v}_i = -v_i\left(v_i^2 - \frac{1}{4}\right) - w_i + A - b + S(t) + \xi_i(t),$$

$$\dot{w}_i = v_i - w_i,$$

where the $v_i(t)$ are fast variables (membrane voltages) and $w_i(t)$ are slow (recovery) variables [9]. All neurons are subjected to the same aperiodic Gaussian signal $S(t)$ (prefiltered to give an autocorrelation time of 5 s), and have a common bias b. The individual responses are summed to produce a single output but otherwise they are uncoupled. The neuronal noise $\xi_i(t)$ will be taken to be Gaussian, with zero average and correlation given by

$$\langle \xi_i(t)\xi_j(s)\rangle = \delta_{ij}2D\delta(t-s). \tag{2}$$

The tonic activation signal, A, is chosen such that, when $b=0$, the neurons are biased at their Hopf bifurcation point. From a linear stability analysis we determine this occurs when $A = -(1/12\sqrt{3})(5-2\epsilon)\sqrt{(1-4\epsilon)}$, taking $\epsilon = 0.005$ yields $A = -0.2377$. However, a spike is only deemed to be transmitted if the oscillations (spikes) grow beyond a fixed level [fixed at $v(t)=0$], otherwise the transmitted response was taken to be zero. Using this criteria, and in the absence of noise and signal, firing events only occur provided b exceeds -0.0016. For this reason the effective dc-signal-level to threshold distance is given by b_{th} where $b_{th} = b + 0.0016$.
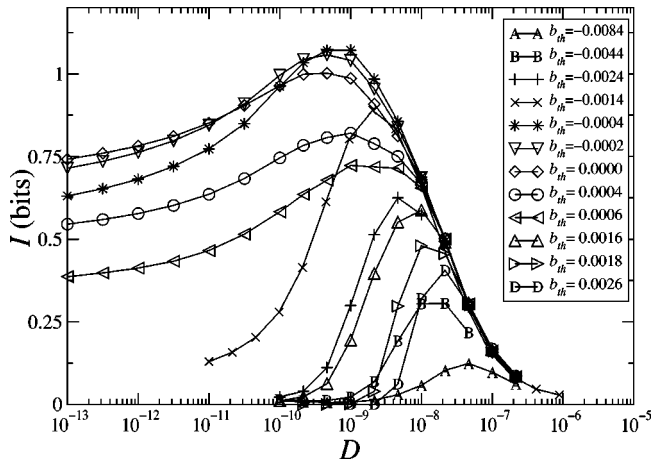
FIG. 1. Transinformation I vs noise intensity D for various threshold settings b_{th}, average signal variance $S^2 = 1.5 \times 10^{-7}$ and $N = 64$. The data points are from the simulation and the solid lines are guides to the eye.

FIG. 2. Dependence of transinformation on b for $D = 0$, $S^2 = 1.5 \times 10^{-7}$, and $N = 1$. The maximum coincides with the value of b for which $b_{th} = 0$. However, finite noise modifies the position of the maximum slightly; see results in Fig. 1.

The integration of the relevant equations of motion was done with the Heun algorithm [10]. The output of the different neurons were added together to give the summed response $\tilde{r}(t) = \Sigma_{i=1}^{N} v_i(t)$ and the firing rate, $r(t)$, was obtained by passing the summed response through a filter,

$$\dot{r}(t) = -\frac{1}{t_p} r(t) + \tilde{r}(t). \quad (3)$$

This method of obtaining the rate was adopted, in preference to applying a Hanning window to $\tilde{r}(t)$, as it gives a causal response and is approximately what would be expected to occur at the membrane of a summing neuron. The quantity t_p can, therefore, be taken as the relaxation time of the membrane of the summing neuron.

The global information transmission through the network is characterized by the transinformation (*trans*mitted *information*) I, which, for a continuous channel, is defined as

$$I = H(r) - H(r|s)$$

$$= -\int_{-\infty}^{\infty} P_r(r) \log_2 P_r(r) dr$$

$$-\left(-\int_{-\infty}^{\infty} P_s(s) ds \int_{-\infty}^{\infty} P(r|s) \log_2 P(r|s) dr \right), \quad (4)$$

where $H(r)$ is the information content (or entropy) of $r(t)$ and $H(r|s)$ can be interpreted as the amount of encoded information lost in the transmission of the signal. $P_r(r)$ and $P_s(s)$ are the probability density functions (pdfs) of $r(t)$ and $s(t)$ respectively and $P(r|s)$ is the conditional pdf.

Figure 1 shows the noise dependence of the global transinformation for various values of the effective threshold level b_{th}. Clearly, all the curves display an SR type effect (noise-induced maximum) but attain different maximum values which we denote by $I_{max}(b_{th})$. The ability of the array to transmit the signal is seen to be strongly dependent on the
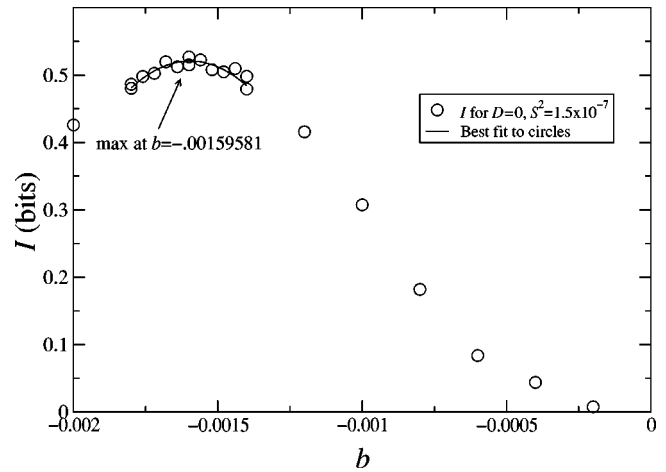
value of b_{th}. For sufficiently large b_{th} ($|b_{th}| > 0.0014$) the signal is entirely subthreshold (or entirely above the threshold for sufficiently large negative b_{th}). As b_{th} is decreased $I_{max}(b_{th})$ increases, goes through a maximum, and then decreases (see Fig. 2). The optimal threshold setting ($b_{th} \sim 0$) coincides with all thresholds set equal to the dc level of the signal. In this situation the signal is strongly suprathreshold in the sense that the deterministic (signal induced) threshold crossings are maximized.

These results demonstrate that, in addition to the subthreshold signal enhancements previously reported [2], noise can also enhance the transmission of suprathreshold signals. Indeed, noise is observed to be of benefit independent of the threshold setting. It is also interesting to note that the array attains its highest transinformation when the threshold is set to be suprathreshold with respect to the signal. Consequently, not only does noise not impair the encoding of suprathreshold signals as previously thought, but it can actually enhance them preferentially. Furthermore, maximizing the transinformation by adjusting the threshold does not remove the beneficial role of the noise; this is not the case in a single neuron. It has been proposed [7] that neurons maximize information by adjusting their threshold. If this is the case, then these results indicate that, although noise degrades the information transmitted by a single element, it still plays a central role in maximizing *global* information transmission.

Figure 1 also indicates an additional benefit of having suprathreshold signals is also observed: they give rise to a much broader peak. This is because in the limit $D \to 0$ I tends to a finite nonzero value, whereas for subthreshold signals $I \to 0$ as $D \to 0$. Consequently, suprathreshold signal encoding is more robust against changes in noise variance or signal strength and requires little ''tuning'' of the noise intensity [2] to maintain the transinformation at a near optimal level.

The fact that SR type effects are also observed for suprathreshold signal levels is a manifestation of the suprathreshold SR (SSR) effect recently reported in a nondynamical array of simple threshold devices [8]. Here we report an
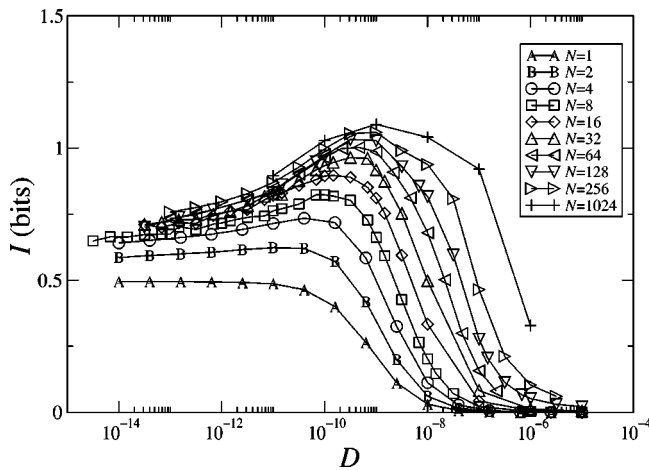
FIG. 3. Dependence of transinformation on noise intensity for various N, average signal variance $S^2 = 1.5 \times 10^{-7}$ and $b_{th} = 0$. The data points are from the simulation and the lines are guides to the eye. Note, in the limit $D \to 0$ (not shown) all transinformation curves collapse onto the $N=1$ curve.
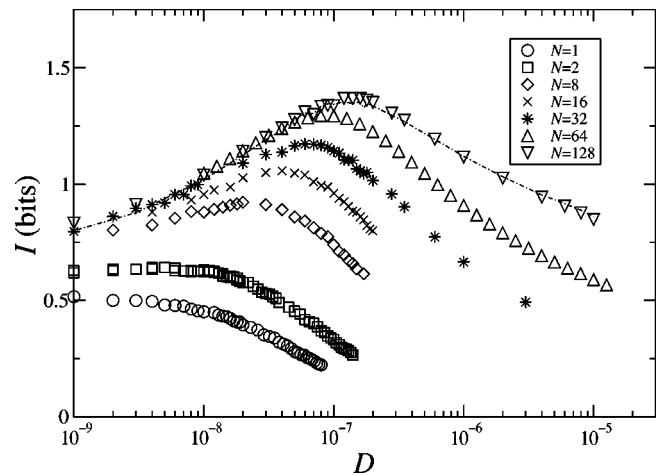

FIG. 4. Same as Fig. 3 except $S^2 = 1.5 \times 10^{-5}$. The dotted-dashed line is an evaluation of I using the result $I = -\frac{1}{2}\log_2(1 - C^2)$.

observation of this effect in a dynamical neuronal model. The SSR effect occurs because noise introduces a degree of independence between the information carried by individual neurons. Although, in the absence of noise, the timing precision of the spikes are at their most precise [7,11], thus maximizing the information transmitted by individual neuronal element, similar neurons produce identical spike trains. Consequently, no additional information is gained by making simultaneous measurements of similar neurons. In fact, the global (total) information is simply equal to that carried by a single element. However, the introduction of neuronal noise randomizes the times at which each neuron "samples" the signal and, although this lowers the amount of information carried by individual elements, there is a net gain to the global information transmitted.

For suprathreshold signal strengths, noise always lowers the information carried by individual neurons. This implies that SSR effects can only be observed when considering the global information transmitted by two or more elements. This can be seen in Figs. 3 and 4 which show the noise dependence of the transmitted information on the number of elements for two different signal strengths. Clearly, both figures show similar qualitative behavior, indicating that SSR effects do not diminish with increasing stimulus strength. Additionally, the information is seen to increase with increasing numbers of neurons, as one would expect, but no maximum is observed for $N=1$. This clearly demonstrates that it is the global information that is enhanced by the noise and not that carried by individual elements (all of which, individually, follow the $N=1$ curve). For $N>1$, the maximum information transmission is observed at nonzero levels of noise, indicating that maximization of the global information is not necessarily achieved by maximising the transinformation of individual elements.

We have compared our results with those expected from linear Gaussian channel theory [12]. For Gaussian probability density functions the transinformation is given by $I = -\frac{1}{2}\log_2(1 - C^2)$ where C is the cross-correlation coefficient

between signal and response [12]. The dotted-dashed line in Fig. 4 shows numerical results for $N=128$; C was obtained from the simulations. The maximum is seen to be well described by the Gaussian channel approximation but small discrepancies appear at lower noise values. This result validates those obtained directly from the definition of transinformation using numerically obtained pdfs and also indicates that the system is acting, at least at moderate to large noise intensities, as a Gaussian channel. Such a result could be anticipated because of noise-induced linearization (an effect that occurs in most nonlinear systems [13]), and has been observed previously in neuronal arrays [2].

It is of some interest to interpret the results in the context of existing neurophysiological data. First, an estimate of the output signal-to-noise ratio (SNR) of individual elements (which at the maximum in the transinformation is found to be approximately -3 dB) indicates that maximum global information is always achieved when the SNR ~ 0 dB. This is in keeping with known experimentally measured SNRs of sensory neurons [7] and, hence, appears to be in the correct range physiologically. Second, it is known that linear decoding strategies are usually sufficient to reconstruct signals from spike train data; little improvement is obtained by using nonlinear methods [7]. Our observation that the transinformation (near the maximum) is well described by linear Gaussian channel theory is consistent with the linear decoding strategy and again suggests, indirectly, that neuronal noise may well be at the appropriate level to maximize transinformation. Third, our results indicate that noise-optimization of the transinformation is maximized when the thresholds adapt to the dc signal component. dc-adaptation in biological sensory systems is known to occur, the most well known example being light or dark adaptation of the human eye [14]. It is, therefore, possible that dc adaptation occurs not only to increase the dynamic range of the signals to be encoded but also to maximize the global information transmission via SSR.

Finally, we note that these results have implications for the design of coding strategies for use in implantable co-

chlear [15] and visual [16] prostheses. Such prostheses work by the artificial electrical stimulation of populations of nerve fibres—similar in form to the model we consider here. Our results suggest that a combination of noise and suprathreshold stimuli should lead to improved information transmission. This strategy is in-keeping with recent results [17] which demonstrate that the coding of formant information in cochlear implants can be improved by the use of noise and suprathreshold stimuli.

Two main conclusions can be drawn: first that, in principle, neuronal noise can generically enhance the global information transmitted by a population of sensory neurons. The benefit of neuronal noise is not restricted to subthreshold stimuli as previously thought. Second, this conclusion re-

mains valid even under the assumption that neurons have dc-adaptive capabilities. That single neurons could in principle lower their thresholds to remove SR effects and maximize information transmission, had led to the suggestion that SR, and hence neuronal noise, may be useful if there was insufficient adaptability in sensory systems [4]. This may indeed be true. However, we see that the restriction of limited adaptability is not required if the global information of a population of neurons is considered. Neuronal noise can have a positive beneficial role regardless of stimulus intensity or the adaptive capabilities of neurons.

[1] A. Longtin, A. R. Bulsara, and F. Moss, Phys. Rev. Lett. **67**, 656 (1991); J. K. Douglass *et al.*, Nature (London) **365**, 337 (1993); J. J. Collins, T. T. Imhoff, and P. Grigg, J. Neurophysiol. **76**, 642 (1996); K. Wiesenfeld and F. Moss, Nature (London) **373**, 33 (1995); F. Y. Chiou Tan, *et al.*, Int. J. Bifurcation Chaos Appl. Sci. Eng. **6**, 1389 (1996); P. Cordo *et al.*, Nature (London) **383**, 769 (1996); S. M. Bezrukov and I. Vodyanoy, *ibid.* **385**, 319 (1997); P. C. Gaily *et al.*, Phys. Rev. Lett. **79**, 4701 (1997).

[2] J. J. Collins, C. C. Chow, and T. T. Imhoff, Nature (London) **376**, 236 (1995); D. R. Chialvo, A. Longtin, and J. Müller-Gerking, Phys. Rev. E **55**, 1798 (1997); A. Neiman, L. Schimansky Geier, and F. Moss, *ibid.* **56**, R9 (1997).

[3] J. E. Levin and J. P. Miller, Nature (London) **380**, 165 (1996).

[4] A. R. Bulsara and A. Zador, Phys. Rev. E **54**, R2185 (1996).

[5] L. Gammaitoni, P. Hänggi, P. Jung, and F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998); *Proceedings of the International Workshop on Fluctuations in Physics and Biology: Stochastic Resonance, Signal Processing and Related Phenomena*, edited by A. Bulsara *et al.* [Nuovo Cimento D **17D**, 653 (1995)].

[6] D. DeWeese and W. Bialek, Nuovo Cimento D **17D**, 733 (1995).

[7] F. Rieke *et al.*, *Spikes: Exploring the Neural Code* (MIT Press, Cambridge, MA, 1997).

[8] N. G. Stocks, Phys. Rev. Lett. **84**, 2310 (2000).

[9] C. Heneghan, Phys. Rev. E **54**, R2228 (1996).

[10] R. Mannella, in *Supercomputation in Nonlinear and Disordered Systems: Algorithms, Applications and Architectures*, edited by L. Vázquez, F. Tirando, and I. Martín (World Scientific, Singapore, 1997), p. 100.

[11] X. Pei, L. Wilkens, and F. Moss, Phys. Rev. Lett. **77**, 4679 (1996).

[12] M. F. Reza, *An Introduction to Information Theory* (Dover, New York, 1994).

[13] M. I. Dykman *et al.*, Phys. Lett. A **193**, 61 (1994); N. G. Stocks *et al.*, in *Fluctuations and Order—the New Synthesis*, edited by M. Millonas (Springer, New York, 1996).

[14] G. Somjen, *Neurophysiology — the Essentials* (Williams & Wilkins, Baltimore, 1983).

[15] S. Rosen, in *Scott-Brown's Otolaryngology (6th edition) Volume 2: Adult Audiology*, edited by D. Stephens (Butterworth Heinemann, Oxford, 1996).

[16] G. J. Suaning *et al.*, Aust. N. Z. J. Ophthalmol. **26**, 195 (1999).

[17] R. P. Morse and E. F. Evans, Nat. Med. **2**, 928 (1996).