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Coding and Computation with Neural Spike Trains

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We study a simple model for the statistics of neural spike trains as they encode a continuously varying signal. The model is motivated with reference to several recent experiments on sensory neurons, and we show how analogies between the relevant probabilistic issues in neural coding and statistical mechanics can be exploited. Results are given for the information capacity of the code, for the optimal structure of code-reading algorithms, and for the time delays which arise in optimal processing of the coded signal. In addition, we show how simple analog computations can be expressed directly in terms of transformations of the spike train. The rules for reading the code and for optimal analog computation depend on the context for behavioral decision making—the relative weights assigned to different types of errors, the relative importance of different signals. We find that there is a conflict between minimizing this context dependence of the code and maximizing its information capacity; a compromise can be achieved by appropriate preprocessing (filtering) of the encoded signal. Experiments on auditory and visual neurons qualitatively confirm the predicted filtering. Similarly, the structure of the optimal "multiplier neuron" is shown to depend upon the intensity and spectral content of incoming signals, and these predictions compare favorably with experiments on a movement-sensitive cell in the fly visual system.

KEY WORDS: Neural networks; signal processing; analog computation.

1. INTRODUCTION

Neural information processing has been rather well described from an electrochemical point of view. A "spiking" neuron receives its input infor-

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mation in the form of an electrical signal $v(t)$ from the synaptic junctions on its dendrites, where $v(t)$ denotes the instantaneous electrical voltage measured in suitable units. Its output consists of a train of spikes, occurring at time $\{t_i\}$, traveling rapidly down its axon. The form of the spikes is independent of $v(t)$. Rather, information about $v(t)$ is encoded in the times $\{t_i\}$ themselves.(1) In this paper, we study neural information processing from an information-theoretic point of view. We are interested in several rather broad questions:

a. Given that we observe a set of spikes $\{t_i\}$, how much information have we obtained about the signal $v(t)$? How might one reconstruct this input signal (read the code)? How does one ensure that the rules for reading the code are not strongly dependent on the context for behavioral decision making?

b. Let $v_r(t)$ denote the signal reconstructed from spikes $\{t_i\}$. Suppose that we reencode this signal in the spike train $\{t_a\}$ of a second neuron. How much information is lost in the process of encoding, decoding, and reencoding? This is just a formal question, since such simple decoding/recoding almost certainly never occurs in the brain, but this estimate of information loss should give us an indication of whether signals are significantly degraded as they pass through successive layers of cells.

c. How can we perform simple analog computations on the spike trains, such as multiplying two signals $v_1(t)$ and $v_2(t)$ encoded in the firing of two neurons?

To approach these issues theoretically, we require a model for the encoding of $v(t)$ in the spikes $\{t_i\}$. We present the experimental motivation for such a model, and in subsequent sections we take up issues a–c in turn.

2. MOTIVATION FOR A SIMPLE MODEL

In recent years considerable attention has been given to neural models(2) in which neurons flip between saturated states of maximal or zero firing, or where the pattern $\{t_i\}$ can be replaced by a continuous rate function which saturates at rather moderate stimulus intensities. In these models the fact that neurons fire discrete impulses is viewed only as contributing an effective noise level. It has been known for some time, however, that the timing of individual spikes and spike clusters can play a significant role in neural information processing,(3) and recent evidence from the fly visual system indicates that two or three spikes from one neuron encode essentially all of the sensory information available about sudden movements across the visual field.(4) Similarly, many of the cells sensitive to sound source location in the inferior colliculus of the echolocating bat *Pteronotus parnellii* fire at most five spikes in response to each returning echo, with some cells firing as few as one or two.(5) Studies of primary neurons from a vibratory organ of the bullfrog inner car suggest that modulations of the firing rate are an essentially linear measure of stimulus amplitude over much of the behaviorally relevant range.(6) In auditory neurons of the mammalian ear the firing rate exhibits relatively soft saturation at 30–40 dB above the threshold of hearing in quiet,(7) but even this may be traced to saturation of the presynaptic signal (for review see ref. 8). In the mammalian visual cortex, many neurons exhibit nearly linear responses to spatial patterns with contrasts of up to 30%, which is typical of many natural scenes.(9)

Taken together, these and other experiments suggest that we study models in which the information carried by individual spikes is *not* ignored or averaged away, and saturation of the neural response does *not* play an essential role. The lack of saturation implies that spikes are typically separated by intervals long compared to the electrochemical time scales which determine the maximum firing rate. In the limit that the interspike intervals are very long, the occurrence of one spike cannot influence the generation of the next, and neural firing becomes a Poisson process, where the probability of observing N spikes at times t_i on the interval $(0, T)$ given the signal $v(t)$ is

$$P[\{t_i\} \mid v(t)] = \frac{1}{N!} \exp\left[-\int_0^T d\tau \, r(\tau) \right] r(t_1)\, r(t_2) \cdots r(t_N) \tag{1}$$

with $r(t)$ the rate function determined by $v(t)$. Evidence for the near-Poisson character of neural firing has been found in the mammalian auditory nerve,(7,8,10) and in retinal ganglion cells firing has been described as a Poisson process driven by the Poissonian arrival of photons at the retina and slightly modified by "dead time."(11) The fact that the firing rate $r(t)$ is always modulated by noise in presynaptic signal $v(t)$ may account more generally for observed deviations from Poisson behavior,(12) as seen below.

The next issues concern the relationship between the spike rate $R(t)$ and the signal $v(t)$. One way of thinking about neural firing in the Poisson regime is that noise in the cell occasionally drives the voltage through the threshold for initiation of an action potential; successive spikes are then uncorrelated because the mean time between threshold crossings is long compared to the correlation time of the noise. The noise exists on top of some bias level determined by the mean current injected into the cell, and external signals such as $v(t)$ modulate this bias. From the general theory of threshold crossings in random signals one finds that the rate of crossing depends exponentially on the difference between the bias level and the threshold level, so we expect that the firing rate in the Poisson regime will also vary exponentially with the amplitude of the external signal. This prediction has been verified in simulations of realistic models for the electrical dynamics of spiking neurons.[3] These considerations suggest that a simple first approximation for the firing rate is $r(t) = \lambda \exp[v(t)]$. Note that even when there is no signal, $v(t) = 0$, there is some spontaneous firing rate λ, as in real neurons.

3. READING THE CODE

The "exponential-Poisson" model has been applied previously to the study of neural coding and to the interpretation of statistical experiments on neural firing.(7,10) Many of the general questions outlined above, however, remain to be answered. Our basic strategy is to note that everything we know about the signal $v(t)$ by virtue of having observed the spikes $\{t_i\}$ is contained in the distribution $P[v(t) \mid \{t_i\}]$, as determined by Bayes' theorem

$$P[v(t) \mid \{t_i\}] = \frac{P[\{t_i\} \mid v(t)]\, P[v(t)]}{P[\{t_i\}]} \tag{2}$$

To evaluate this distribution, we need the *a priori* distribution for the signal, $P[v(t)]$. This is determined by the characteristics of the natural (or experimental) stimulus ensemble, suitably filtered by the response of the presynaptic cells. For simplicity we choose $P[v(t)]$ to be that of stationary Gaussian noise,

$$P[v(t)] = Z^{-1} \exp\left[-\frac{1}{2} \int \frac{d\omega}{2\pi} \frac{|\tilde{v}(\omega)|^2}{S(\omega)} \right] \tag{3}$$

with $\tilde{v}(\omega) = \int dt\, e^{+i\omega t} v(t)$ and $S(\omega)$ the power spectrum.

It is important to realize what this assumption about the *a priori* distribution actually means. To characterize a natural stimulus ensemble, we would, for example, record the waveforms of speech signals as spoken by a wide variety of speakers in different acoustic environments as they recite different texts or engage in typical conversation. Although any particular short segment of speech could hardly be considered "noiselike," if one averages over all the possible speech sounds one would find that *the ensemble* is essentially that of random signals with some correlation

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[3] For a general discussion regarding the statistics of infrequent threshold crossings in Gaussian noise, see Rice.(13) For simulations of realistic neural models, see Bialek *et al.*(14)

structure, perhaps well approximated by the power spectrum alone. Similarly, if one examines the structure of natural scenes, it is likely that the fluctuations in contrast as viewed through the aperture of a single photoreceptor or the receptive field of a single higher-order neuron are approximately Gaussian, with some spectral density reflecting the typical velocities of movement across the visual field; some measurements of this type have been reported for natural image ensembles.(15) We recall also that a probabilistic description of the signal is necessary in an information-theoretic discussion,(16) and of course the Gaussian approximation is the simplest starting point. It is worth noting that in laboratory experiments one can always choose the distribution of signals to be Gaussian, as in ref. 4.

After much discussion, then, we have identified our problem: Our knowledge of the signal $v(t)$ as derived from $\{t_i\}$ is summarized by

$$P[v(t)\,|\,\{t_i\}] = \frac{\lambda^N}{P[\{t_i\}]N!}\exp\left[-\lambda\int_0^T dt\, e^{v(t)} + \sum_{i=1}^{N} v(t_i) - \frac{1}{2}\int\frac{d\omega}{2\pi}\frac{|\tilde{v}(\omega)|^2}{S(\omega)}\right] \tag{4}$$

It will be convenient to think of this distribution in terms of statistical mechanics or quantum mechanics, where $P[v(t)\,|\,\{t_i\}] \sim \exp\{-A[v(t);\,\{t_i\}]\}$ defines the effective action A for a particle in one dimension to take a trajectory $v(t)$ while being "kicked" at the times t_i.

One approach to reconstructing $v(t)$ from $\{t_i\}$ is maximum likelihood(17)—find the trajectory $v(t)$ which maximizes $P[v(t)\,|\,\{t_i\}]$ or, equivalently, minimizes the effective action. This procedure is optimal under certain conditions, and evidently it corresponds to finding the classical limit of our equivalent quantum mechanics problem. The extremal condition is

$$\lambda\exp[v_*(t)] + \int dt'\, v_*(t')\int\frac{d\omega}{2\pi}\frac{e^{-i\omega(t-t')}}{S(\omega)} = \sum_{i=1}^{N}\delta(t-t_i) \tag{5}$$

which we can solve iteratively for small $v_*(t)$:

$$v_*(t) = v^{(1)}(t) + v^{(2)}(t) + \cdots \tag{6a}$$

$$v^{(1)}(t) = -\int dt'\, K(t-t')\left[\lambda - \sum_{i=1}^{N}\delta(t'-t_i)\right] \tag{6b}$$

$$v^{(2)}(t) = -\frac{1}{2}\lambda\int dt'\, K(t-t')[v^{(1)}(t')]^2 \tag{6c}$$

$$K(\tau) = \int\frac{d\omega}{2\pi}\frac{e^{-i\omega\tau}}{\lambda + 1/S(\omega)} \tag{6d}$$

Thus, we see that, for small modulations in the firing rate, the reconstructed signal can be obtained as $\approx v^{(1)}(t)$ from the independent addition of contributions from each spike; as the modulation becomes larger, one must include correlations among spike pairs, triplets, and so on.

It is easy to see that, if the signal-to-noise ratio is high $[S(\omega) \gg 1/\lambda]$, then Eq. (6) is a power series expansion in which $v^{(1)}$ itself serves as the expansion parameter. At lower signal-to-noise ratios the expansion parameter is smaller than v.$^{(1)}$ Issues of convergence are complicated; to be precise, we would have to discuss convergence in a probabilistic sense, since the signals are chosen randomly from some ensemble. While these issues are interesting, we feel it would be more profitable to view Eq. (6) as a natural approximation whose applicability to real neurons can be tested experimentally, as described below.

It is clear from Eq. (6) that the kernel $K(\tau)$ is in general acausal—a spike at t_i contributes not only to reconstruction of the signal $v(t < t_i)$, but also to *prediction* of the signal $v(t > t_i)$. This arises, of course, from correlations in the *a priori* ensemble $P[v(t)]$ as summarized in $S(\omega)$. To make use of all of the information available in the spike train, we must estimate $v(t)$ only once we have arrived at time $t + \tau_c$, with $K(\tau > \tau_c) \approx 0$, so that no future spikes can influence our estimate: Optimal decoding introduces delays.

How large is τ_c? Suppose $S(\omega)$ is a Lorentzian centered at ω_0 (and $-\omega_0$) with width Γ,

$$S(\omega) = v_{\text{rms}}^2 \left[\frac{\Gamma}{(\omega - \omega_0)^2 + \Gamma^2} + \frac{\Gamma}{(\omega + \omega_0)^2 + \Gamma^2} \right] \tag{7}$$

where

$$v_{\text{rms}}^2 = \int Dv\, v^2(t)\, P[v(t)] = \int \frac{d\omega}{2\pi}\, S(\omega) \tag{8}$$

Then we find that $\tau_c \approx (\Gamma^2 + v_{\text{rms}}^2 \Gamma \lambda)^{-1/2}$, and with the parameters discussed below this means that the decoding delays are roughly a few milliseconds. This is comparable to the delay at a single synapse,$^{(1)}$ which is often cited as limiting the speed of neural computation. Here we see that such delays are required for optimum decoding independent of the synaptic hardware. More precisely, we have a model in which the firing rate $r(t)$ instantaneously follows the presynaptic signal $v(t)$, so the synaptic delay is explicitly taken to be zero; nonetheless, the speed of processing is limited, essentially by the structure of the stimulus ensemble itself.

We emphasize that our conclusions about the need for delays in optimal decoding are in the spirit of the need for delays in higher-order processing—to understand spoken words it helps to wait until the end of the sentence. It is interesting, however, that this consideration applies at every individual stage of neural coding and processing. To continue with the case of speech, there are delays necessary in interpreting and processing the primary auditory nerve's encoding of the sound pressure waveform, long before any of the elements of speech might be recognized in higher brain centers.

Returning to the estimation problem, it should be appreciated that maximum likelihood is not always the optimal strategy. In general, one must make full use of the distribution $P[v(t) \mid \{t_i\}]$, with different features emphasized, depending on the costs and benefits in any specific task. It is reasonable to ask that, in a "good" code, reasonable changes in this behavioral context do not lead to large changes in the rules for reading the code. This is essentially guaranteed if the distribution $P[v(t) \mid \{t_i\}]$ has a single well-resolved maximum, which is the same as asking that our equivalent quantum mechanics problem actually be in its classical or correspondence principle limit.

It is well known that the difference between classical and quantum mechanics (or mean-field theory and the exact statistical mechanics) can be seen in a diagrammatic formulation of perturbation theory in terms of the loop diagrams. In Eq. (4) we expand the exponential in a power series and write the effective action as

$$A[v(t); \{t_i\}] = \frac{1}{2} \int dt \int dt' \, v(t) \, K^{-1}(t-t') \, v(t') + \int dt \, F_{\text{ext}}(t) \, v(t) + A_{\text{int}} \tag{9}$$

where K^{-1} is the operator inverse to $K(\tau)$, F_{ext} is an "external force"

$$F_{\text{ext}}(t) = \lambda - \sum_{i=1}^{N} \delta(t - t_i) \tag{10}$$

and the interaction term is

$$A_{\text{int}} = \lambda \int dt \sum_{n=3}^{\infty} \frac{v^n(t)}{n!} \tag{11}$$

As usual, we develop a perturbation series in A_{int}. The simplest test of the classical approximation is to look at the one-loop correction to the propagator K:

$$K^{-1}(\omega) = \lambda + 1/S(\omega) \to \lambda + 1/S(\omega) + \lambda \int \frac{d\omega}{2\pi} \frac{1}{\lambda + 1/S(\omega)} \tag{12}$$

These "quantum-corrected" propagators have a straightforward interpretation. If we try to reconstruct the stimulus by computing the average waveform rather than the most likely (as above), we find that the reconstruction strategy has a form similar to that of Eq. (6), but the bare propagators K are replaced by the quantum dressed versions. To demand that quantum corrections be small is thus to demand that the average waveform be close to the most likely waveform, which is one way of saying that the distribution has a smooth, well-resolved maximum.

We evaluate the loop integrals in a simple picture where the spectral density $S(\omega)$ is nonzero only over a limited range of frequencies having width $\Delta\omega$. Then we find that the one-loop self-energy term in Eq. (12) is just $(\Delta\omega/\pi)/(1+z)$ with $z=\Delta\omega/\pi\lambda v_{\mathrm{rms}}^2$. Thus, the "quantum corrections" to the propagators, and hence the context dependence of the code, is minimized by narrowing the bandwidth $\Delta\omega$; we have checked that this is true for higher loop terms as well.

4. INFORMATION CAPACITY AND "NEURAL NOISE"

We now turn to determining the information coded in $\{t_i\}$, which, following Shannon,[16] we write as

$$I[t]=\int Dv\, P[v\,|\,t]\log_2\frac{P[v\,|\,t]}{P[v]} \tag{13}$$

where I is in bits and we suppress the curly bracket around t and the subscript i. While we can calculate directly with this expression, we would like to show how to manipulate it into a more compact form:

$$\begin{aligned} I[t]&=\int Dv\, P[v\,|\,t]\log\frac{P[t\,|\,v]}{P[t]}\\ &=-\log P[t]+\int Dv\, P[v\,|\,t]\log P[t\,|\,v] \end{aligned} \tag{14}$$

But $P[t]=\int Dv\, P[t\,|\,v]\, P[v]$, so

$$I[t]=-\log\int Dv\, P[t\,|\,v]\, P[v]+\frac{\int Dv\, P[t\,|\,v]\, P[v]\log P[t\,|\,v]}{\int Dv\, P[t\,|\,v]\, P[v]} \tag{15}$$

which may be written as

$$I[t]=-\left(1-\frac{\partial}{\partial\eta}\right)A(t,\eta)\big|_{\eta=1} \tag{16a}$$

$$A(t,\eta)=\log\int Dv(P[t\,|\,v])^{\eta}\, P[v] \tag{16b}$$

This last manipulation has the flavor of the replica trick used in the statistical mechanics of disordered systems.

We are able to evaluate Eq. (16) once again as an expansion in v_{rms}; the lowest-order result is

$$I[\{t_i\}] = \frac{1}{2\ln 2}\int dt \int dt'\, F_{\mathrm{ext}}(t)\, F_{\mathrm{ext}}(t') \int \frac{d\omega}{2\pi} \frac{e^{-i\omega(t-t')}S(\omega)}{[1+\lambda S(\omega)]^2} + \frac{T}{2\ln 2}\int \frac{d\omega}{2\pi}\left(\ln[1+\lambda S(\omega)] - \frac{\lambda S(\omega)}{1+\lambda S(\omega)}\right) \qquad (17)$$

with $F_{\mathrm{ext}}(t)$ as before. When we average over the spike arrival times t_i we find the mean information rate

$$R = \frac{\langle I[\{t_i\}]\rangle}{T} = \frac{1}{2\ln 2}\int \frac{d\omega}{2\pi}\ln[1+\lambda S(\omega)] \qquad (18)$$

This is just Shannon's formula[16] for the information capacity of a communication channel in which the signal has a power spectrum $S(\omega)$ and the effective noise is white with spectrum $1/\lambda$, which gives a simple intuitive picture of the "neural noise."

If $S(\omega)$ is concentrated in a bandwidth $\Delta\omega$ as above, then

$$R \sim (\lambda v_{\mathrm{rms}}^2/2\ln 2)\, z\ln(1+1/z)$$

Clearly, this is maximized by letting $z\to\infty$, and hence $\Delta\omega\to\infty$. Evidently the conditions for high information capacity and context independence are conflicting. In these cases one is saved only by the fact that the context dependence (measured above as the difference between most likely and average waveforms) scales as z for small z, while the information capacity behaves as $z\ln|z|$. This means that we can cut the context dependence quite a bit while paying relatively less in information capacity. Although a detailed analysis requires assigning a numerical "value" to context independence, it is clear that for rapidly firing cells the optimal compromise will be reached at $z<1$—moderately narrow bandwidths.

To summarize, by filtering incoming signals, the presynaptic cell can reach an effective compromise between maximal information capacity and minimal context dependence of the code. The precise nature of the filtering required depends on the firing rate, and indeed, as the firing rate changes (perhaps by increasing the rms stimulus level), the filters would have to adapt to maintain optimality. In general this filtering strategy requires an array of cells tuned to different frequency bands, and this is exactly what one has in the mammalian auditory system,[8] where firing rates are $\lambda\sim 100\ \mathrm{sec}^{-1}$ and, at low sound pressures ($v_{\mathrm{rms}}<1$), $\Delta\omega/2\pi<100$ Hz. In the mammalian visual system one has arrays of cells tuned to different spatial frequencies,[(9)] but since images are always moving across the retina, this amounts to filtering in the time domain as well. The optimal bandwidth varies with stimulus level, both explicitly through v_{rms} and implicitly through λ, and this is what one observes for the actual bandwidths in the auditory system.[(8)] We emphasize that our comparison with experiment is necessarily qualitative, but it does seem that the theoretical criteria we have explored are in reasonable agreement with observation.

As mentioned in item b in the Introduction, we are interested in information transmitted in a two-stage process $v \rightarrow \{t_i\} \rightarrow v_r \rightarrow \{t_a\}$. We have to determine the convoluted probability

$$P[\{t_a\} \,|\, v(t)] = \int D\xi \sum_{N=0}^{\infty} \left(\prod_{j=1}^{N} \int dt_j \right) \times P[\{t_a\} \,|\, \xi] \, \delta[\xi(t) - v_r(t; \{t_i\})] \, P[\{t_i\} \,|\, v(t)] \quad (19)$$

where we have emphasized that v_r depends on the $\{t_i\}$. As before, we are able to evaluate this expression only as a series for small v_r. Remarkably, the lowest order result may be arranged in a rather simple form:

$$P[\{t_a\} \,|\, v(t)] = N[v] \frac{\lambda^M}{M!} \prod_{a=1}^{M} e^{v'(t_a)} \prod_{ab} e^{(1/2)\lambda L(t_a - t_b)} \quad (20)$$

where

$$\tilde{v}'(\omega) = \frac{\lambda}{\lambda + 1/S(\omega)} \cdot \tilde{v}(\omega) \quad (21a)$$

$$L(t) = \int \frac{d\omega}{2\pi} \frac{e^{-i\omega t}}{[\lambda + 1/S(\omega)]^2} \quad (21b)$$

and $N[v]$ denotes a suitable normalization factor.

Were it not for the presence of the factor involving $L(t)$, which measures the correlation among the t_a, $P[\{t_a\} \,|\, v]$ would have been Poisson as in Eq. (1). However, the "would-be" Poisson distribution is not controlled by $v(t)$, but by $v'(t)$, a filtered version of $v(t)$. The correlations $L(t)$ may be thought of as arising from a "fictitious" noise added to $v'(t)$; averaging over this noise induces the interspike correlation. More explicitly, let the effective signal be $v'(t) + \psi(t)$, with $\psi(t)$ a Gaussian noise term. Averaging the Poisson distribution over the noise, we find

$$\left\langle \exp\left[\sum_a v'(t_a) + \psi(t_a) \right] \right\rangle = \prod_a \exp[v'(t_a)] \prod_{ab} \exp[(1/2)\langle \psi(t_a)\, \psi(t_b) \rangle] \quad (22)$$

Comparing with Eq. (20), we identify $\langle \psi(t_a)\,\psi(t_b)\rangle = \lambda L(t_a - t_b)$. Undoing the filtering by $L(\tau)$, we see that this fictitious noise is equivalent to a noise in $v(t)$ having spectral density $1/\lambda$, in agreement with our interpretation of the information capacity above.

5. MULTIPLIER NEURONS

Finally, we comment on the multiplication problem c. If the encoding of the signals $v_1(t)$ and $v_2(t)$ is reasonably reliable, then the optimal estimate of their product can be obtained by first estimating the two signals individually and then multiplying. As the noise level increases, there are corrections to this simple algorithm, but they do not affect the qualitative points we would like to make here. In terms of the two spike trains, a "multiplier neuron" should compute

$$v_1(t)\,v_2(t) \sim \int d\tau_1 \int d\tau_2\, K(t-\tau_1)\, K(t-\tau_2) \left[\lambda - \sum_{i=1}^{N} \delta(\tau_1 - t_i^{(1)})\right] \times \left[\lambda - \sum_{j=1}^{N} \delta(\tau_2 - t_j^{(2)})\right] + \cdots \tag{23}$$

Thus, there are terms which approximate naive "coincidence detection" $\sim \delta(t - t_i^{(1)})\,\delta(t - t_j^{(2)})$, but true coincidence detection is *not* optimal. The optimal multiplier neuron evidently encodes a signal formed by smoothly weighting all of the near-misses to coincidences between the spike trains. Put another way, apparent sloppiness in the detection of coincidences may actually reflect optimal multiplication.[4]

It is clear from Eq. (23) that the multiplication process, like the reconstruction algorithm discussed above, is acausal. Again this means that any real multiplier neuron must have an output which lags the true signal if we are to make full use of the available information. What is significant here is that the magnitude of this lag (see above) depends on the intensity of the signal v_{rms}. Thus, we expect that an optimal multiplier or correlator neuron would have a temporal impulse response which adapts to changes in stimulus ensemble, quickening as the signal strengthens. If the fly visual system there is a movement-sensitive cell whose behavior has been described quite accurately as a spatiotemporal correlator, and recent experiments demonstrate that the impulse response of this cell quickens at increasing movement velocities, just as we expect.(20)

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[4] This may have significant consequences for experiments on the neurophysiology of binaural acoustic processing, where cross-correlation (delayed multiplication) is believed to play a central role (e.g., ref. 18), although one often talks about coincidence detection. Similar comments apply to electroreception in fish.(19)

6. DISCUSSION

To summarize, we have studied a very simple model of neural encoding which nonetheless has some support in experiment. We find that this model already has a number of important consequences: the need for time delays in optimal processing; the use of presynaptic filtering to remove context dependence of the code and optimize the information capacity; the role of "sloppy coincidence" in analog computation; and the need for adaptive filtering. Some of these results seem to have clear experimental correlates. One of the most important conclusions is that, under certain conditions, it should be possible to literally decode the neural spike train, recovering the optimal estimate of the incoming stimulus, using a simple linear filter. If it is really true that spike trains can be converted back to analog signals by simple filters, then it may be possible to understand analog computation in the nervous system using very simple models, in the spirit of our discussion of multiplier neurons.

Although neural coding has been studied for roughly 50 years, we know of no instance in which a systematic decoding of the spike train has been attempted, so our prediction that such decoding should be possible by such simple means comes as quite a surprise; for a review see ref. 4. Since we first obtained this result it has been possible to mount an experimental test, and our prediction has been confirmed.(21)

The motivation for many of our arguments is some principle of optimization, such as finding the best estimate of the stimulus given an example of the spike train. To the extent that theoretically optimal strategies predict the behavior of real neurons, these optimization principles should be viewed as having relevance to the "design" of the nervous system. There exist several examples(22) of sensory systems whose functions have been optimized by evolution, such as the ability of the retina to count single photons, and so it seems reasonable to search for comparable optimization principles in neural coding and computation.

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REFERENCES

1. D. Aidley, *Physiology of Excitable Cells*, 2nd. (Cambridge University Press, Cambridge, 1980).
2. J. J. Hopfield, *Proc. Natl. Acad. Sci. USA* **79**:2554 (1982); **81**:3088 (1984).
3. D. H. Perkel and T. H. Bullock, *Nueorosci. Res. Program Bull.* **6**:221 (1968).
4. W. Bialek, R. R. de Ruyter van Steveninck, and W. H. Zaagman, Santa Barbara Preprint NSF-ITP-86-105, and submitted; R. R. de Ruyter van Steveninck, Academisch Proefschrift, Rijksuniversiteit Groningen (1986); R. R. de Ruyter van Steveninck and W. Bialek, *Proc. Soc. Lond. B* **234**:379 (1988).
5. J. J. Wenstrup, Z. M. Fuzessery, and G. D. Pollak, *J. Neurophys.*, in press.
6. E. R. Lewis, in *Auditory Frequency Selectivity*, B. C. J. Moore and R. Patterson, eds. (Springer-Verlag, Berlin, 1987), and personal communication.
7. D. H. Johnson, Thesis, Massachusetts Institute of Technology (1974).
8. E. R. Lewis, E. L. Leverenz, and W. S. Bialek, *The Vertebrate Inner Ear* (CRC Press, Boca Raton, Florida, 1985).
9. R. L. DeValois and K. K. DeValois, *Annu. Rev. Psych.* **31**:309 (1980).
10. W. M. Siebert, *Kybernetik* **2**:206 (1965); in *Recognizing Patterns*, P. A. Kohlers and M. Eden, eds. (MIT Press, Cambridge, Massachusetts, 1968), p. 104.
11. M. C. Teich, L. Matin, and B. I. Cantor, *J. Opt. Soc. Am.* **68**:386 (1978); M. C. Teich and B. E. A. Saleh, *J. Opt. Soc. Am.* **71**:771 (1981).
12. W. Bialek, in *Hearing: Physiological Bases and Psychophysics*, R. Klinke and R. Hartmann, eds. (Springer-Verlag, Berlin, 1983), p. 51.
13. S. O. Rice, in *Selected Papers on Noise and Stochastic Process*, N. Wax, ed. (Dover, New York, 1953).
14. W. Bialek, L. Kruglyak, and H. Lecar, preprint.
15. D. Field, *J. Opt. Soc. Am.* **4**:2379 (1987).
16. C. E. Shannon and W. Weaver, *The Mathematical Theory of Communication* (University of Illinois Press, Urbana, Illinois, 1949).
17. D. M. Green and J. A. Swets, *Signal Detection Theory in Psychophysics* (Krieger, New York, 1966).
18. J. Blauert, *Spatial Hearing* (MIT Press, Cambridge, Massachusetts, 1982).
19. T. H. Bullock, *Ann. Rev. Neurosci.* **5**:121 (1982).
20. R. R. de Ruyter van Steveninck, H. A. K. Mastebroek, and W. H. Zaagman, *Biol. Cybernet.* **54**:223 (1986).
21. W. Bialek, F. Rieke, R. R. de Ruyter van Steveninck, and D. Warland, preprint; in *Proceedings of the 1989 IEEE Conference on Neural Information Processing Systems*, to appear.
22. W. Bialek, *Annu. Rev. Biophys. Chem.* **16**:455 (1987).