Fisher Information for Spike-Based Population Decoding

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(Received 5 January 2006; published 30 August 2006)

We evaluate the Fisher information of a population of model neurons that receive dynamical input and interact via spikes. With spatially independent threshold noise, the spike-based Fisher information that summarizes the information carried by individual spike timings has a particularly simple analytical form. We calculate the loss of information caused by abandoning spike timing and study the effect of synaptic connections on the Fisher information. For a simple spatiotemporal input, we derive the optimal recurrent connectivity that has a local excitation and global inhibition structure. The optimal synaptic connections depend on the spatial or temporal feature of the input that the system is designed to code.

DOI: 10.1103/PhysRevLett.97.098102 PACS numbers: 87.19.La

Information from the environment is encoded in the noisy activity of a population of neurons. Reading the neural code is a fundamental problem in neuroscience. In particular, attention has been paid to the role of precise spike timing in addition to the spike count information [1,2] and that of correlation between neurons [3–5] on the information coding. However, a large amount of data is required to evaluate the amount of information in a real population of neurons [1,2]. Moreover, it is difficult, with this approach, to understand the role of neuronal parameters such as recurrent connectivity on the information coding. In this study, we calculated the Fisher information of a network of spiking neurons, which limits the accuracy of any unbiased estimate of a stimulus [6,7]. In contrast to the literature, where Fisher information is evaluated based on firing rates (rate-based Fisher information) [3–8], we evaluated the Fisher information when the individual spike timings of all the neurons were available (spike-based Fisher information). Interestingly, under the assumption of independent noise, the expression of the spike-based information has a simple analytical form. We estimated the amount of information included in the precise timing of spikes by comparing the information in the two cases and studied the role of synaptic connectivity on stimulus estimation. We also calculated the spike-based information for a spatiotemporal input, where rate decoding fails, and derived the optimal recurrent connectivity for spike-based information representation.

Stochastic firing neuron model. From the noisy spiking activity of N recurrently connected neurons in time duration T, we decode a parameter θ of a stimulus, which is, for example, the orientation of a light bar. Neuron $i (i = 1, \ldots, N)$ receives stimulus-dependent external input potential $h_i(t, \theta)$ and recurrent spikes from neighboring neurons. A spike from neuron j at time $t_j^{f_j} (f_j = 1, \ldots, n_j)$ provokes a postsynaptic potential of amplitude w_{ij} and time course $\epsilon(t - t_j^{f_j}) = e^{-(t-t_j^{f_j})/\tau_m} \Theta(t - t_j^{f_j})$, where $\tau_m = 10$ ms is the leak time constant and Θ is the Heaviside step function which takes the value 1 for a positive argument and 0 otherwise. Hence, the total input potential of the neuron is described by $u_i(t) = h_i(t, \theta) + \sum_{j=1}^{N} w_{ij} \sum_{f_j=1}^{n_j} \epsilon(t - t_j^{f_j})$. Depending on u_i, the neuron emits a spike with instantaneous firing probability density $\rho_i(t) = g(u_i(t))R(t - \hat{t}_i)$, where $g(u) = g_M[1 + e^{-\beta(u-u_c)}]^{-1}$ is a sigmoid function with parameters $g_M = 500$ Hz, $\beta = 8$, and $u_c = 1$, and $R(t - \hat{t}_i) = \frac{t-\hat{t}_i}{\tau_r+t-\hat{t}_i}$ is a refractory factor with the last spike time, $\hat{t}_i$, of neuron i and refractory time constant τ_r. Note that we sometimes use the abbreviation $g_i(t) = g(u_i(t))$. Because u is not reset after an output spike, the refractory factor may correspond to the integration time until the next spike for a noisy leaky integrate-and-fire model. The current model is a special case of the spike response model [9]. We assume conditionally independent instantaneous firings of neurons given the history of spikes and the input, neglecting common noise shared among neurons for simplicity.

Spike-based and rate-based information. The output spike train of neuron i is represented by $x_i(t) = \sum_{f_i=1}^{n_i} \delta(t - t_i^{f_i})$, where δ is the Dirac delta function. The history of the spike activity until time t is described by $X(t) = \{x_i(t') | i = 1, \ldots, N, 0 \leq t' < t\}$. Given a realization of history $X(t)$, the spiking probability of the next very short interval Δt is written by using the binary variables $\Delta x_i(t) = \int_t^{t+\Delta t} x_i(t')dt'$, where we formally define the integral of a delta function by $\int_0^1 \delta(t' - t)dt' = 1$ for $0 \leq t < 1$ and 0 otherwise. Because we assume instantaneously independent firing, the spike probability is given as a product of individual firing probabilities, i.e., $P(\{\Delta x_i(t)\}_{i=1}^N | X(t)) = \prod_{i=1}^N P(\Delta x_i(t) | X(t))$, with the individual binary firing probabilities $P(\Delta x_i(t) | X(t)) = (\rho_i(t)\Delta t)^{\Delta x_i(t)}(1 - \rho_i(t)\Delta t)^{1-\Delta x_i(t)}$. However, each conditional firing probability depends on the past spike trains of all neurons through ρ. The Fisher information, given spike trains of duration t, is defined by $J^{\text{spike}}(t) = -\langle \partial^2 \log P(X(t))/\partial\theta^2 \rangle_{X(t)}$, where $\langle\cdot\rangle_{X(t)}$ is the average with respect to $P(X(t))$. Applying $P(X(t+\Delta t)) = P(\{\Delta x_i(t)\}_{i=1}^N | X(t)) P(X(t))$, we define the Fisher information rate by

$$\begin{aligned}\dot{J}^{\text{spike}}(t) &= \lim_{\Delta t\to 0}[J^{\text{spike}}(t+\Delta t) - J^{\text{spike}}(t)]/\Delta t \\ &= -\lim_{\Delta t\to 0}\frac{1}{\Delta t}\left\langle \frac{\partial^2 \log P(\{\Delta x_i(t)\}_{i=1}^N | X(t))}{\partial\theta^2}\right\rangle_{X(t+\Delta t)} \\ &= \left\langle \sum_{i=1}^N \frac{1}{\rho_i(t)}\left(\frac{\partial\rho_i(t)}{\partial\theta}\right)^2\right\rangle_{X(t)}. \qquad (1)\end{aligned}$$

Except for the average over the spike history, $X(t)$, the above result is well known as the Fisher information rate of independent Poisson neurons [7]. The total spike-based information from spike trains of duration T is given as an integration of the information rate, i.e., $J^{\text{spike}} = \int_0^T \dot{J}^{\text{spike}} dt$. Particularly, for a low firing rate (if $g \ll g_M$ always holds), we can approximate the sigmoid g by an exponential function $g_M e^{\beta(u-u_c)}$. This approximation gives

$$\begin{aligned}\dot{J}^{\text{spike}}(t) &= \sum_{i=1}^N \left\langle \left[h_i'(t)\frac{g_i'(t)}{g_i(t)}\right]^2 \rho_i(t)\right\rangle_{X(t)} \\ &\approx \sum_{i=1}^N [\beta h_i'(t)]^2 \nu_i(t), \qquad (2)\end{aligned}$$

where $h_i'(t) = \frac{\partial h_i(t,\theta)}{\partial\theta}$, $g_i'(t) = \frac{\partial g}{\partial u}|_{u=u_i(t)}$, and the mean firing rate is $\nu_i(t) = \langle\rho_i(t)\rangle_{X(t)}$. Equation (2) shows the relations of the Fisher information rate to the number of neurons, N, to the mean firing rate, ν, and to the square of the derivative of the input potential with respect to the parameter θ. Interestingly, the spike-based information of Eq. (2) does not explicitly depend on correlations between neurons. We should note, however, that the mean firing rates of neurons are modulated by synaptic connections between them. This kind of spike-based information has been investigated for a single neuron [1,10]. The amount of information lost by applying rate decoding and abandoning individual spike timing is an issue of interest [2]. However, several previous studies on population coding assumed only the rate decoding paradigm [3–8]. We restricted ourselves to a simple case of a constant stimulus for a fair comparison and investigated the role of model parameters on the information loss.

Let us introduce some notation for rate decoding. We describe by $r_i = \frac{1}{T}\int_0^T x_i(t)dt$ the spike rate in the interval. The rate-based Fisher information, $J^{\text{rate}} = -\langle \partial^2 \log P(\{r_i\}_{i=1}^N)/\partial\theta^2\rangle_{\{r_i\}_{i=1}^N}$, is calculated based on the assumption that r_i is generated from a Gaussian distribution with mean $\mu_i = \langle r_i\rangle$ and covariance matrix $C_{ij} = \langle (r_i - \mu_i)(r_j - \mu_j)\rangle$. Because $C_{ij} \sim 1/T$ for large T, $J^{\text{rate}} \approx \sum_{i,j=1}^N \mu_i' C_{ij}^{-1}\mu_j'$, where $\mu_i' = \frac{\partial\mu_i}{\partial\theta}$ and C_{ij}^{-1} is the (i, j) component of the inverse of the covariance matrix [11]. Note that the Gaussian r_i assumption is generally not valid for recurrently connected networks, while we do not need this assumption for the calculation of spike-based information.

Independent neurons. We consider first a single neuron, or equivalently, a population of neurons without recurrent connections. A neuron receives constant input, $h = 0.1\theta$, and hence has constant $g = g(h)$. Because the neuron has the renewal property with constant drive, its spike train is completely characterized by the interspike interval (ISI) distribution, $Q(s) = gR(s)e^{-g\int_0^s R(s')ds'}$ [9], where s represents an ISI and the last spike time is set to $\hat{s} = 0$. The ISI distribution is controlled by the input strength, h, and the refractory time constant, τ_r. For any well-behaved renewal process, the probability distribution of spike rate $P(r)$ is asymptotically Gaussian with mean $\nu = \mu = 1/\langle s\rangle_Q$ and variance $\sigma^2 = \frac{\langle s^2\rangle_Q - \langle s\rangle_Q^2}{\langle s\rangle_Q^2}\frac{\nu}{T}$ for large T [12], where the average means $\langle\cdot\rangle_Q = \int Q(s)ds$. Hence, the rate-based Fisher information is written as $J^{\text{rate}} = T\frac{(\mu')^2}{\mu \text{Cv}^2}$ for large T with $\text{Cv}^2 = (\langle s^2\rangle_Q - \langle s\rangle_Q^2)/\langle s\rangle_Q^2$. All these spike statistics are derived from the moment-generating function, $\Phi(\xi) = \int_0^\infty Q(s)e^{\xi s}ds = 1 + \xi\tau_r e^{(g-\xi)\tau_r}[(g-\xi)\tau_r]^{-1-\tau_r g}\Gamma(1+\tau_r g, (g-\xi)\tau_r)$, where the incomplete gamma function $\Gamma(\alpha_1, \alpha_2) = \int_{\alpha_2}^\infty s^{\alpha_1 - 1}e^{-s}ds$ is used. Particularly, we find $\langle s\rangle_Q = \tau_r e^{\tau_r g}(\tau_r g)^{-1-\tau_r g}\Gamma(1+\tau_r g, \tau_r g)$ and $\text{Cv}^2 = 2\nu(1+\nu\tau_r)/g - 1$. Figure 1(a) shows g, ν, Cv, and information rates $\dot{J}^{\text{spike}}$ and $\dot{J}^{\text{rate}}$ of a single neuron. The Fisher information first increases with ν (cf. Equation (2)) but de-

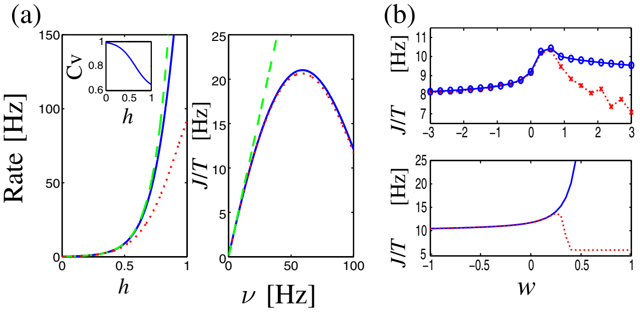

FIG. 1 (color online). (a) Left: The sigmoid function, g (solid line), its approximation by an exponential function, $g_M e^{\beta(u-u_c)}$ (dashed line), and the firing rate, ν (dotted line). The inset shows the coefficient of variation, Cv. Right: The spike-based and rate-based information rates $\dot{J}^{\text{spike}}$ (solid line) and $\dot{J}^{\text{rate}}$ (dotted line), for different ν. The refractory time constant, τ_r, is 10 ms. An approximation with the exponential g is also shown (dashed line). (b) Top: Comparison of the spike-based information rate, $\dot{J}^{\text{spike}}$ (solid line), and the rate-based one, $\dot{J}^{\text{rate}}$ (dotted line), with the sigmoid g and refractoriness, $\tau_r = 10$ ms. Bottom: The same comparison with the exponential g and without refractoriness. We set $\theta = 5$.

creases for high ν due to the sigmoid of g. The two information rates are similar with constant input but have finite differences due to the refractory factor, i.e. the observer can fix the value of $R(t - \hat{t})$ by knowing the last spike time, $\hat{t}$. The deviation of the sigmoid of g from the exponential function and the effect of refractoriness are negligible at low firing rates. In the following, we assume $\tau_r = 0$ for analytical calculations.

Effect of synaptic connection. To see the effect of recurrent connections on the information, we consider two neurons with a one-way synaptic connection and driven by constant input. The Gaussian r_i assumption is also valid in this case for large T. For the analytical calculation, we neglect refractoriness and use the exponential function $g(u) \approx g_M e^{\beta(u-u_c)}$. We investigate the effect of sigmoid g and refractoriness by numerical simulation. Two neurons receive constant inputs $h_1 = 0.1\theta$ and $h_2 = 0.1\theta$, and the output of the first neuron is fed into the second neuron with synaptic strength $w = w_{21}$. The calculation of spike-based information is straightforward from Eq. (2). We calculated the two neurons's mean firing rates and their covariance matrix to evaluate the rate-based information. Because $\tau_r = 0$, their firing probability densities are given by $\rho_1 = g(h_1)$ and $\rho_2(t) = g(h_2 + w \int_0^t \epsilon(t - t')x_1(t')dt')$. Using the fact that x_1 is a Poisson spike train and g is an exponential function, we can average ρ_1 and ρ_2 over the spike history, $X(t)$, and find the mean firing rates $\nu_1 = \mu_1 = g(h_1)$ and $\nu_2 = \mu_2 = g(h_2 + \beta^{-1}K\nu_1)$, where $K = \int \kappa(t)dt$ with $\kappa(t) = e^{\beta w \epsilon(t)} - 1$. The covariance matrix, C, is calculated as $C_{11} = \nu_1/T$, $C_{12} = C_{21} = \nu_1\nu_2K/T$, and $C_{22} = \nu_2/T + \nu_2^2L/T$, where $L = \int dt[e^{-\nu_1 \int_{|t|}^{\infty} \kappa(t')dt' + \nu_1 \int_0^{\infty} e^{\beta w \epsilon(t')} \kappa(|t|+t')dt'} - 1]$. In this way, we can also calculate the rate-based Fisher information. Taking the limit as $w \longrightarrow \infty$, we find $J^{\mathrm{rate}} \longrightarrow T(\beta h_1)^2\nu_1$, which is the amount of information from neuron 1. Hence, the output of neuron 2 does not add any additional information at this limit. Signal h_2 is buried in the noisy postsynaptic potential of neuron 1 for large w. On the other hand, within the spike decoding paradigm, neuron 2 can still transmit information on h_2 because the observer knows when neuron 1 fired. The rate-based and spike-based Fisher information is compared for a range of the synaptic strength w in Fig. 1(b). The spike-based Fisher information is significantly larger than the rate-based information for strong synaptic connectivity. This result is qualitatively similar even when we use the sigmoid g and refractoriness. One difference is that the spike-based information shows unlimited growth with the exponential g because $(g_2')^2/g_2$ is an increasing function of w. However, the spike-based information decreases for large w with the sigmoid g.

Spatiotemporal input. We are most interested in seeing how the correlation among a population of neurons alters the efficacy of stimulus estimation [3–5]. The effect of recurrent connectivity on stimulus estimation has been studied mainly within the rate decoding framework [13,14], where spatially structured synaptic connections with local excitation and global inhibition are used. Moreover, calculating the rate-based Fisher information with recurrent connections is computationally hard because it requires the inverse of the output covariance matrix. In the following, we apply the spike decoding paradigm by taking account of individual spike timings, and calculate the spike-based Fisher information to estimate stimulus onsets or locations. The optimal recurrent connectivity that maximizes the spike-based information is derived under certain conditions on synaptic strength.

We consider a population, $N = 10^3$, of recurrently connected neurons evenly distributed with density $\gamma = N/(2\pi)$ on a circle $-\pi < z \leq \pi$, where z refers to a preferred stimulus of a neuron. The synaptic strength from a neuron at z' to one at z is a function of only the difference between their preferred stimuli, $\zeta = z - z'$, which is described by $w(\zeta)$. As an example of a spatiotemporal stimulus, we consider a localized pulse centered at $\tilde{z}$ injected at time $\tilde{t}$. The input potential to a neuron at z is described by a differential equation, $\tau_m \frac{dh(z,t)}{dt} = -h(z,t) + A_s[1 + \cos(z - \tilde{z})]\Theta(t - \tilde{t})\Theta(\tau_s - t + \tilde{t})$, where the stimulus strength, A_s, is 1/4 and the stimulus duration, τ_s, is 100 ms. The stimulus location, $\tilde{z}$, and the onset time, $\tilde{t}$, are the parameters to be estimated from the output spikes. The information, J_z^{spike} and J_t^{spike}, for estimating $\tilde{z}$ and $\tilde{t}$ is calculated from Eq. (1) by substituting $\theta = \tilde{z}$ and $\theta = \tilde{t}$, respectively, i.e. $J^{\mathrm{spike}} = \int_0^T dt \int_{-\pi}^{\pi} \gamma dz \langle [h_i'(z, t)g_i'(t)]^2 / g_i(t)\rangle_{X(T)}$ with $h'(z, t) = \frac{\partial h(z,t)}{\partial \theta}$. Assuming a small synaptic strength, we calculate the optimal synaptic strength, w, that maximizes J^{spike} under constraints on the first two moments of synaptic strength; i.e. excitatory and inhibitory synapses are balanced, $\int_{-\pi}^{\pi} w(\zeta)\gamma d\zeta = 0$, and the square norm of the synaptic strengths is restricted, $\int_{-\pi}^{\pi} w^2(\zeta)\gamma d\zeta = N^{-1}$. Hence, the objective function is $L = J^{\mathrm{spike}} + \lambda_1 \int_{-\pi}^{\pi} w(\zeta)\gamma d\zeta + \lambda_2 \int_{-\pi}^{\pi} w^2(\zeta)\gamma d\zeta$ with Lagrange multipliers λ_1 and λ_2. We calculate the spike-based Fisher information up to the first order of w. The zero-order term is given by the spike-based information of independent neurons, $J^{\mathrm{spike}}|_{w=0}$. The first-order term is $\int_0^T dt \eta(z, t)\nu_0(z, t) \int_{-\pi}^{\pi} \gamma d\zeta w(\zeta) \int dt' \epsilon(t - t')\nu_0(z - \zeta, t')$, where the zero-order instantaneous firing rate, $\nu_0(z, t) = g_0(z, t)$, is $g(h(z, t))$, and the coefficient $\eta(z, t) = [h'(z, t)g_0'(z, t)/g_0(z, t)]^2[2g_0''(z, t)/g_0'(z, t) - g_0'(z, t)/g_0(z, t)]$. The optimality condition is represented by a functional differentiation, $\frac{\delta L}{\delta w(\zeta)} = 0$. This leads to the optimal synaptic strength

$$w(\zeta) \propto \int_0^T dt \int dt' \int_{-\pi}^{\pi} \gamma dz \eta(z, t)\epsilon(t - t')\nu_0(z, t)\nu_0(z - \zeta, t') \tag{3}$$

up to a constant. The constant and the proportionality coefficient in Eq. (3) depend on λ_1 and λ_2, which are set

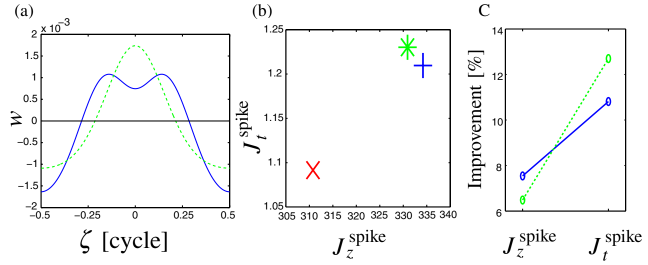

FIG. 2 (color online). (a) The optimal synaptic strengths w^{location} (solid line) for the estimation of the stimulus location, $\tilde{z}$, and w^{onset} (dashed line) for the stimulus onset, $\tilde{t}$. (b) The spike-based Fisher information, J_z^{spike} for the estimation of $\tilde{z}$ and J_t^{spike} for the estimation of $\tilde{t}$, is plotted for three types of synaptic connectivity: no synaptic connection ($w = 0$, cross), w^{location} (plus sign), and w^{onset} (asterisk). (c) Comparison of the improvement when having w^{location} (solid line) and w^{onset} (dashed line) from having no synaptic connectivity. The increases in the spike-based Fisher information, J_z^{spike} and J_t^{spike}, are plotted.

to satisfy the constraints on the synaptic strength. Moreover, Eq. (3) has the causal Hebbian property. Equation (3) is proportional to the causal pre- and post-correlation $\epsilon(t - t')\nu_0(t, z)\nu_0(t', z - \zeta)$, whose learning coefficient is given by $\eta(z, t)$ to enhance the stimulus difference. The optimal recurrent connections to estimate $\tilde{z}$ and $\tilde{t}$ are described by w^{location} and w^{onset}, respectively, and shown in Fig. 2(a). Both w^{location} and w^{onset} have local excitation and global inhibition structures, which are observed in various neural systems. However, the precise shape of w depends on the feature of the given stimulus that the system is designed to code. In Fig. 2(b), the information J_z^{spike} and J_t^{spike} is plotted for three types of synaptic connectivity: no recurrent connection ($w = 0$), w^{location}, and w^{onset}. The improvement in the information, J_z^{spike} and J_t^{spike}, due to having synaptic connections w^{location} (solid line) and w^{onset} (dashed line) is plotted in Fig. 2(c). The improvements are limited because the synapses are assumed to be small for the analytical calculation. Sharper tuning curves are known to be desirable for one-dimensional stimulus estimation with independent Poisson neurons [15]. This sharpening of tuning curves corresponds to the one by a sharper input, h, without recurrent connections. On the other hand, sharpening of tuning curves by recurrent connections does not always lead to a better estimation [13,14]. The result shows that the optimal recurrent connections are determined by the subtle interplay between the input stimulus and the response properties of neurons. The optimal recurrent connections provide, by modulating the recurrent input to each neuron, an efficient encoding of the stimulus parameter that minimizes the information loss because of the noisy spike-generation process. As is in the case of Seriès *et al.*, we can not increase the information by postprocessing a stimulus with a network of recurrently connected neurons [13]. Evaluating the spike-based Fisher information, we can identify the information in individual spike timing that codes temporal features of input, such as stimulus onset. This kind of temporal feature is difficult to decode from spike rates with wide temporal windows.

We calculated the spike-based Fisher information of a population of recurrently connected spiking neurons with independent threshold noise. Unlike the case of [16], the Fisher information is expected to give a reasonable lower bound of the estimation error because the estimation is based on a large number of independent spikes. Generalizing the spike-based Fisher information to estimate a multidimensional parameter is straightforward. Although we restricted ourselves to weak synapses for the calculation of the optimal recurrent connections, stronger synapses should also be studied to elucidate the role of nonlinearity in output firing rates and sustained activity in networks.

This work was supported by the Japan Society for the Promotion of Science, and a Grant-in-Aid No. 1806772 from JSPS and for Scientific Research on Priority Areas No. 17022012 from MEXT of Japan. We thank K. Kang, N. Masuda, and K. Hamaguchi for discussions.

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