Optimal information transfer in synchronized neocortical neurons[☆]

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Abstract

The output precision and information transmission was studied in a model neocortical neuron that was driven by a periodic presynaptic spike train with a variable number of inhibitory inputs on each cycle. Spike-timing precision was maintained during feedforward propagation during entrainment. The range of presynaptic firing rates and precision for entrainment was determined. During entrainment the Shannon information of the output spike phase was reduced but the amount of information the neuron transmitted about the synaptic input was increased. We quantify how robust information transmission is against intrinsic neuronal noise. We propose how neuromodulation, via entrainment, can regulate the information transfer in neocortical networks. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Electrophysiological recordings from the living brain reveal synchronized oscillatory activity in the delta (0.5–2 Hz), theta (5–12 Hz) and gamma (30–80 Hz) frequency ranges [1]. The functional relevance of these synchronized oscillations is unknown. Here we explore an alternative to the hypothesis that gamma oscillations bind
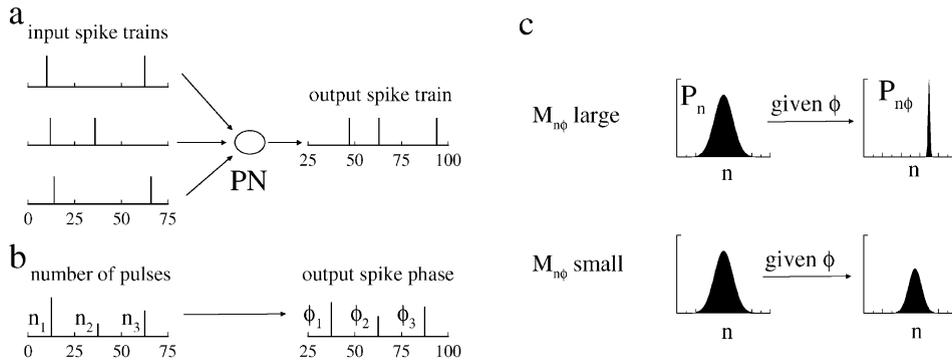
Fig. 1. Diagram of information-theoretical analysis. (a) Postsynaptic neuron (PN) receives inputs from a synchronized network of inhibitory neurons. Individual neurons fire at a fixed phase, $\phi = 12.5$ ms with temporal jitter σ_{in} and sometimes skip cycles. The postsynaptic neuron produces a spike on each cycle. (b) The number n_i of active neurons in cycle i is mapped onto a spike phase ϕ_i in the next cycle. The spike phase ϕ is the spike time modulo T. (c) Distribution P_n of n (left hand side) and distribution $P_{n\phi}$ of n conditional on ϕ (right hand side). The mutual information $M_{n\phi}$ is large (top) when the conditional distribution is sharp and small (bottom) when it is dispersed.

neurons representing the distinct perceptual features of an object. Neurons use spikes to carry information between brain areas. A commonly used information measure is the Shannon entropy of the spike times or interspike interval distribution [9,10]. During synchronized oscillations the spike times are precise, the spike time distribution is sharp, and its information capacity small. Why would populations of neurons synchronize if this reduces their information content? We report here that despite a reduced spiking variability, the neuronal output in the synchronized state conveys more information about the synaptic input: the mutual information between the synaptic input and the output spike time increases during synchronization. This result suggests that neurons can indeed support a spike-timing code during synchronization.

Tonic activation of local interneuron networks in hippocampal slices produces a synchronous synaptic drive to pyramidal cells in the gamma frequency range [14] (see also [3]). These interneuron networks may also be responsible for the long-range coherence of gamma oscillations [12]. Here we study the transmission by cortical neurons of the synchronized activity of a presynaptic network of interneurons.

2. Methods

The activity of the synchronized interneuron network can be accurately described using three parameters: the cycle length $T = 25$ ms of the population discharge, the temporal dispersion σ_{in} of the network spike time distribution in each cycle, and f_{pre}, the number of inhibitory postsynaptic potentials (IPSPs) generated by the network per second [11]. We generated the presynaptic spike trains using the method described in [11]. Example spike trains are shown in Fig. 1a. Each presynaptic spike

produced an exponentially decaying conductance pulse in the postsynaptic cell, yielding a current $I_{syn} = g_i \exp(-t/t_i)(V - E_{GABA})$. In this expression t is the time since the pulse arrival, $t_i = 10$ ms is a decay constant, $g_i = 0.002$ mS/cm^2 a conductance, V the membrane potential, and $E_{GABA} = -75$ mV, is the reversal potential. The total synaptic conductance cannot exceed $g_{max} = 0.1$ mS/cm^2. The resulting time-series of conductance pulses drives a single compartment neuron with Hodgkin–Huxley voltage-gated sodium and potassium channels, a passive leak current, the synaptic currents described above, and an applied current representing the membrane depolarization caused by neuromodulators. A detailed description of the model neuron and its implementation is given in [11,13]. This formulation accurately represents the spike generation in fast and regular spiking cortical pyramidal cells [8].

For the purpose of information-theoretical analysis we map the input spike trains into a single variable, n_i pulses in cycle i, or for brevity, n pulses per cycle (Fig. 1b). The input capacity is the entropy S_n of the input distribution P_n, and the output capacity is the entropy S_ϕ of the phase histogram P_ϕ (the bin width is 1 ms). The neuron maps a particular value of n_i into a spike phase ϕ_i. The joint probability distribution $P_{n\phi}$ is obtained by counting the data points (n_i, ϕ_i) in a two dimensional set of bins. The mutual information is the entropy of this distribution

$$M_{n\phi} = S_n + \sum_{\phi_j} P_\phi(\phi_j) \sum_n P_{n\phi}(n|\phi_j) \log_2 P_{n\phi}(n|\phi_j)$$

and measures, on average, how much the uncertainty in the input is reduced by knowing the output [2]. The mutual information $M_{\phi\phi}$ between consecutive spike phases is calculated similarly.

3. Results

For the synaptic strength used here the output jitter σ_{out} is only smaller than the input jitter σ_{in} on entrainment steps [11]. The 1:1 entrainment step, when the neuron produces one spike per cycle, is the most stable. We show in Fig. 2a an example of this resonance for $\sigma_{in} = 1$ ms and presynaptic firing rate $f_{pre} = 2500$ Hz. At $I = 1.0$ μA/cm^2, σ_{out} is still above 5 ms. Increasing the current drives the neuron into entrainment, and σ_{out} drops below 1 ms. The output entropy, S_ϕ, is closely related to the width of the phase distribution, and it drops from 4.2 to less than 1 bit per spike. The mutual information $M_{n\phi}$, however, goes from a value close to zero, to approximately $\frac{1}{2}$ a bit per spike (for other parameter values $M_{n\phi}$ could reach 2 bits). We investigated this result in more detail by comparing the map of ϕ versus n when the neuron was entrained, to when it was not (not shown). In the latter case a given ϕ is reached from a large range of n values. Therefore knowing a particular ϕ value reveals little about the input that produced it. Hence the mutual information in this case is low (Fig. 1c, bottom). During entrainment the input n is mapped onto a small range of ϕ values, hence leading to high precision. Furthermore, observing a low value of ϕ implies that the input n was also small. Thus, observing a certain value of ϕ reduces the uncertainty about the input, leading to a higher mutual information (Fig. 1c, top).
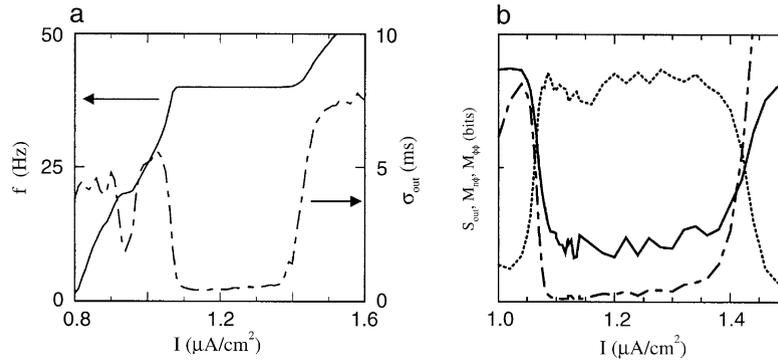
Fig. 2. (a) Firing rate (left hand side scale) and output jitter σ_{out} (right hand side scale) as a function of neuromodulator current I. The neuron produces one spike per cycle at high precision for $I = 1.15$–1.30. (b) S_{out} (solid line), $M_{n\phi}$ (dotted line), and $M_{\phi\phi}$ (dot-dashed line) as a function of current. The curves have been scaled, $S_{out} : M_{n\phi} : M_{\phi\phi} = 5 : \frac{1}{2} : \frac{3}{2}$, to fit in the figure. Here, $\sigma_{in} = 1$ ms and $f_{pre} = 2500$ Hz.

The difference in transmitted information between the two cases can be understood by determining the mutual information $M_{\phi\phi}$ between the phase ϕ_i in the present cycle and ϕ_{i+1} in the next cycle. The mutual information in this case quantifies the reduction in the uncertainty about the next phase knowing the present phase. During entrainment the observed phases are essentially independent, the mutual information is close to zero (Fig. 2b), and the phase fluctuates around a well defined average. In contrast, without entrainment there is more structure in the return map (not shown). A given value of ϕ_i maps onto a distribution of ϕ_{i+1} values that is different from the total distribution (and also has a different mean). The mutual information of this distribution can be higher than 1 bit per spike.

The neuron can thus be in two states. One in which the phase variation from cycle to cycle reflects the variation in the input, and one in which the variation mostly reflects the internal correlations. Decreasing or increasing the current drive can switch the neuron from the entrained state to a non-entrained state.

4. Discussion

We explored how well the information present in the presynaptic drive is transduced to the output spike times. That is, we determined how well the neuron can convey the number of pulses in a cycle by the phase of the output spike. The output entropy is not a good indicator of the useful information content for this particular task. Indeed, outside entrainment the output entropy is high and the mutual information is low, whereas during entrainment the output entropy is small, but the mutual information is increased. The mutual information limits the maximum amount of information any postsynaptic neuron can infer about the presynaptic input of the emitting neuron. In the first case the neuron produces a lot of information, but that

information does not tell the postsynaptic neuron anything about the emitting neuron's input. In the second case the emitting neuron produces a small amount of information, but most of it is useful.

Subcortical projections originating in the basal nucleus of the forebrain release the neuromodulator acetylcholine (ACh) in cortex and hippocampus. The ACh concentration varies between waking and sleep. The known physiological effects of ACh include blockade of the slow afterhyperpolarization current (AHP) and an increased excitability [7]. Application of the cholinergic agonists can induce synchronized gamma-frequency oscillations in hippocampal slices [4,5]. In our model neuron a higher ACh concentration corresponds to a higher driving current, making the neuron more excitable. A higher ACh concentration could switch the model neuron from a non-entrained to an entrained state. The information flow in cortex can therefore be dynamically gated by neuromodulators released by ascending subcortical projections.

These results point toward a new view of the role of oscillations in information processing. Without entrainment a cortical neuron is a traditional integrator and transmits information through changes in its firing rate; during entrainment, which is promoted by neuromodulators and characterized by gamma band activity, a cortical neuron can transmit information about its inputs more efficiently by the relative spike timing within the cycle, as suggested by Hopfield [6]. Experiments in vivo need to be carried out to test this possibility.

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