Correlated multiplicative modulation in coupled oscillator systems: a model of selective attention

Hideaki SHIMAZAKI[1] and Ernst NIEBUR[2]

[1]*Department of Physics, Kyoto University, Kyoto 606-8502, Japan*
[2]*Department of Neuroscience and Zanvyl Krieger Mind/Brain Institute, School of Medicine, Johns Hopkins University, Baltimore, Maryland 21218, USA*

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We develop an oscillator model of selective attention based on spread spectrum communication. Stimulus intensity and attention are differentially encoded in the time average of phase velocities of sender oscillators and their temporal structure respectively. Receiver oscillators are driven by a mixture of phase velocities of the sender oscillators. With the aid of top-down modulatory signals that do not change the mean rotational velocity of sender oscillators, our proposed communication scheme allows the receiver oscillators to selectively correlate their velocity with the attended stimulus.

§1. Introduction

Neural systems must select only the most relevant information among the excessive amount of detail from all stimuli available at the sensory periphery. The neural mechanisms that implement this selection process are collectively known as selective attention.1) Using a network of phase oscillators, here we develop a theoretical framework of selective attention based on the idea of spread spectrum communication.2) Different from rate-based models,3) the mechanism makes use of the temporal domain to convey and control stimulus information.

Neurophysiological studies by Mountcastle and collaborators provided the first clear insight into the visual selective attention in the dorsal ('where') pathway,4) and work by the Desimone group and others elucidated processing in the ventral ('what') pathway.5) In the latter report, when two stimuli were presented in the receptive field of a neuron in extrastriatal cortex, its firing rate varied depending on which stimulus the animal attended to. Crick and Koch proposed a framework of attention and visual awareness6) in which they hypothesized that attended features are 'tagged' by the temporal structure of neural activities, a theory later formalized in quantitative models.7) Experimental evidence that supports the use of the temporal domain for attentional selection is now accumulating.8), 9) We study here how synchronous firing can be used for successful communication within the neural system. We propose two conjectures on how stimulus information is processed in the brain.10) The first is that the representation of the physical properties of a stimulus differs from that of its attentional state:

(i) *Stimulus information in early sensory cortex is encoded in the mean firing rate; whether it is attended or not (or possibly the degree to which it is attended) is encoded in the correlational structure of spike trains.*

We emphasize that this applies to *early cortex*; there is undoubtedly a correlation between attentional state and neural firing rate extrastriate visual cortex and equivalent areas in other sensory modalities. Therefore, we propose that a temporal representation of attention in the sensory primary cortices (input) is transformed gradually into a hybrid temporal/rate code at intermediate stages, to end up as a pure rate code in motor cortex (output). We then face the problem of decoding: how synchronous activity is processed and finally transformed into a mean firing rate representation. A simple and efficient way to decode the temporal tagging modulation is by using the encryption key used for encoding. Thus our second conjecture is

(ii) *The correlated temporal structure of spike train in early cortex is introduced through attentional modulation. Selection of the attended stimulus at later stages is accomplished by using the same top-down modulatory signal.*

Based on these conjectures, we model the neural mechanism of attention using phase oscillators. Receiver neural systems (extrastriate and beyond) are synchronized with one of the sender populations (in primary visual cortex) through attentional modulation. Without changing the mean firing rates of senders, 'synchronized' receivers are selectively correlated with the attended stimulus information.

§2. An Oscillator Model of Selective Attention

We model a system of S sender oscillators and R receiver oscillators.

Sender Oscillators: Sender oscillators independently encode a stimulus intensity θ_m $(m = 1, 2 \cdots, M)$ in their rotation velocities (firing rates). We denote a set of oscillators that encode stimulus intensity θ_m by $\mathcal{S}_m$. The number of oscillators in $\mathcal{S}_m$ is denoted as s_m. We assume that the average of encoded stimulus intensities over all oscillators is approximately zero; $\frac{1}{M}\sum_{m=1}^{M} s_m \theta_m \sim 0$.

Attention is directed to a subset among M groups of oscillators. The set of oscillator groups which are subject to the top-down modulation is denoted by $\mathcal{A}$. For $i \in \mathcal{S}_m$, where m does not belong to $\mathcal{A}$, the ith sender oscillator encodes the stimulus intensity θ_m by its angular velocity; $\dot{\varphi}_i = \theta_m$. For $i \in \mathcal{S}_m$ where m belongs to $\mathcal{A}$, top-down signals multiplicatively randomize the stimulus intensity θ_m;

$$\dot{\varphi}_i = \theta_m \xi_m(t), \qquad (2{\cdot}1)$$

where $\xi_m(t)$ is a Gaussian random signal that satisfies $\langle \xi_m(t) \rangle = \mu$ and $\langle (\xi_m(t) - \mu)(\xi_l(t+\tau) - \mu) \rangle = \sigma^2 \delta_{m,l} \delta(\tau)$. Here $\langle \cdot \rangle$ denotes time average.

Receiver Oscillators: Receiver oscillators are driven by input from the rotation velocity of sender oscillators, and are also coupled globally with a coupling constant K. The evolution of the receiver oscillators is then given by

$$\dot{\psi}_i = \frac{K}{R}\sum_{j=1}^{R} \sin(\psi_j - \psi_i) + \Theta_i \xi_k(t), \qquad (2{\cdot}2)$$

where $\Theta_i = \frac{1}{S}\sum_{j=1}^{S} w_{ij}\,\dot{\varphi}_j$ with $w_{ij} \in \{0, 1\}$. We first assume that $w_{ij} = 1$ for all i and j. Random connectivity will be studied in section 3.

Similar to Eq. 2·1, the driving force Θ_i to the ith receiver oscillator in Eq. 2·2 is multiplied by a signal $\xi_k(t)$ which was used to modulate the kth group of sender oscillators ($k \in \mathcal{A}$). The time average of the driving force is given by

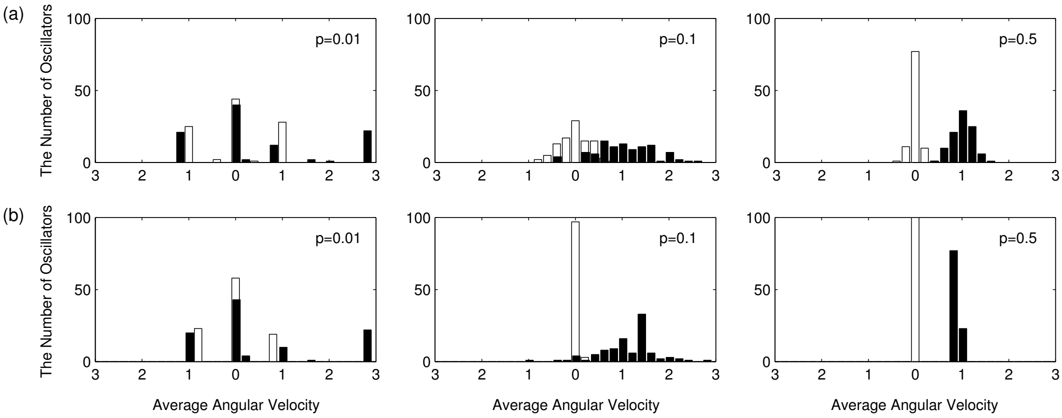

Fig. 1. Histograms of time average of angular velocity of the receiver oscillators without attention (white bars) and with attention (solid bars). There are 100 sender and 100 receiver oscillators. One-half (50) of the sender oscillators encode $\theta_1 = 1$, the other half encode $\theta_2 = -1$. The probability of random connection from sender to receiver oscillators is $p = 0.01$ (Left), $p = 0.1$ (Middle), and $p = 0.5$ (Right). For simulations shown in solid bars, a modulatory signal ($\mu = 1$ and $\sigma^2 = 2$) was applied to the sender oscillators that encode the stimulus value θ_1 and all the receiver oscillators. The time average is computed from 2000 steps with numerical step size 0.05 [s]. (a) No coupling among receiver oscillators ($K = 0$). (b) Coupling among receiver oscillators ($K = 1$) enhances the effect of attentional selection.

$$\begin{aligned}\langle \Theta_i \xi_k(t)\rangle &= \frac{1}{S}\left\{\sum\nolimits_{m\in A} s_m\theta_m \langle \xi_j(t)\,\xi_k(t)\rangle + \sum\nolimits_{m\notin A} s_m\theta_m \langle \xi_k(t)\rangle\right\}\\ &= \frac{\sigma^2 s_k}{S}\theta_k + \mu^2 \sum\nolimits_{m\in A} s_m\theta_m + \mu \sum\nolimits_{m\notin A} s_m\theta_m, \end{aligned}\tag{2$\cdot$3}$$

We assume $\mu = 1$ because attentional modulation does not change the firing rate of the sender oscillators. Then the sum of the second and the third term vanishes. The time average of the receiver response is correlated with the attended stimulus intensity. Note that the selection mechanism differs from conventional spread spectrum communication in which a spread sequence with $\mu = 0$ is used.

§3. Simulation

For simplicity, we consider only two stimuli θ_1 and θ_2, and they satisfy $\theta_1 + \theta_2 = 0$. Half of the sender oscillators ($i = 1, \cdots, S/2$) encode θ_1, and the other half ($i = S/2 + 1, \cdots, S$) encodes θ_2. A modulatory signal ξ_1 is applied to the half of the sender oscillators that encodes the stimulus θ_1. All the receiver oscillators are demodulated by the same modulatory signal ξ_1. In this case, the time average of the driving force is obtained as $\langle \Theta_i \xi_k(t)\rangle = \theta_1\sigma^2/2$.

The effect of selective attention is shown in Figure 1. When attentional modulation is applied to neither sender nor receiver oscillators, the velocities of receiver oscillators asymptotically approaches zero as the connection probability increases (white bars). When attention is applied, the angular velocities of receiver oscilla-

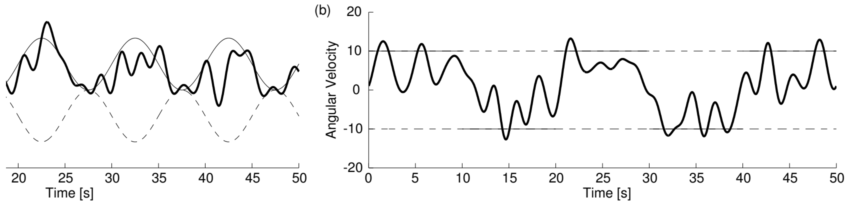

Fig. 2. The time evolution of angular velocity of receiver oscillators is shown by a bold solid line. The signal is lowpass-filtered with cutoff frequency 0.5 Hz. Other variables: $p = 0.1$, $\mu = 1$, and $\sigma^2 = 2$. (a) The sinusoidally regulated stimuli $\theta_1 = 1 + \sin(2\pi f t)$ (solid line) and $\theta_2 = -\theta_1$ (dashed line) are applied while attention is directed to θ_1 ($f = 0.1$ Hz). (b) The constant stimuli $\theta_1 = 10$ and $\theta_2 = -10$ (dashed lines) are applied. The attention is switched between them with a period 10 s (solid line).

tors are correlated with the attended stimulus value (FIG. 1-a, solid bars). Coupling among receiver oscillators both strengthens and sharpens attentional selection (FIG. 1-b, $p = 0.1$ and $p = 0.5$).

Dynamical aspects of the selection process are shown in Figure 2. Two cases, selective recovery of temporally varying intensity and switching of attention between two stimuli, are investigated. These figures show that, as long as the stimulus frequency or switching frequency of attention is slow, the attended stimulus information can be extracted from low frequency components of receiver angular velocity.

§4. Discussion and Future Topics

The present model which utilizes two different types of signals, top-down modulatory and bottom-up driving signal,[11)] is necessarily oversimplified. Nevertheless it is specific enough to explain why attention may not change the firing rate of a primary visual cortex while neurons in extrastriate cortex correlate their firing rate with attended stimulus. In this model, the average of stimulus intensities encoded in sender oscillators must be zero. Inclusion of the adaptive adjustment of the weighted average is thus an important topic of future work.

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