2006 Special Issue

Selective attention through phase relationship of excitatory and inhibitory input synchrony in a model cortical neuron

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Abstract

Neurons in area $V2$ and $V4$ exhibit stimulus specific tuning to single stimuli, and respond at intermediate firing rates when presented with two differentially preferred stimuli ('pair response'). Selective attention to one of the two stimuli causes the neuron's firing rate to shift from the intermediate pair response towards the response to the attended stimulus as if it were presented alone. Attention to single stimuli reduces the response threshold of the neuron and increases spike synchronization at gamma frequencies. The intrinsic and network mechanisms underlying these phenomena were investigated in a multi-compartmental biophysical model of a reconstructed cat $V4$ neuron. Differential stimulus preference was generated through a greater ratio of excitatory to inhibitory synapses projecting from one of two input $V2$ populations. Feedforward inhibition and synaptic depression dynamics were critical to generating the intermediate pair response. Neuronal gain effects were simulated using gamma frequency range correlations in the feedforward excitatory and inhibitory inputs to the $V4$ neuron. For single preferred stimulus presentations, correlations within the inhibitory population out of phase with correlations within the excitatory input significantly reduced the response threshold of the $V4$ neuron. The pair response to simultaneously active preferred and non-preferred $V2$ populations could also undergo an increase or decrease in gain via the same mechanism, where correlations in feedforward inhibition are out of phase with gamma band correlations within the excitatory input corresponding to the attended stimulus. The results of this model predict that top-down attention may bias the $V4$ neuron's response using an inhibitory correlation phase shift mechanism.
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Keywords: Selective attention; $V4$; Gain modulation; Gamma band synchrony; Out of phase inhibition

1. Introduction

Neural correlates of selective attention have been studied using single-unit recordings from primate extrastriate area $V4$. It was found that attention increases the neuron's firing rate in response to a single stimulus placed in its receptive field. When more than one stimulus is presented, selective attention can modulate the neuron's response based on its stimulus selectivity. When attention is directed to the neuron's preferred stimulus the neuron's firing rate is

increased; when attention is directed to the non-preferred stimulus its firing rate is decreased (Reynolds, Chelazzi, & Desimone, 1999; Reynolds, Pasternak, & Desimone, 2000; Reynolds & Desimone, 2003). This phenomenon has been conceptually explained as a biased competition (Desimone & Duncan, 1995; Reynolds et al., 1999) wherein active $V2$ input populations from multiple stimuli compete with one another to generate a $V4$ neuronal response intermediate between the responses to the individual stimuli. Attending to a stimulus can bias this competition producing a shift in the $V4$ neuron's response towards the response that would be obtained if the attended stimulus population was active alone.

Several models have been proposed to elucidate the mechanisms underlying stimulus competition and attentional bias. In a phenomenological model by Reynolds et al. (1999), attention bias was conceived as an increase in the synaptic

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weights of the inputs from the neurons that receive visual information from the attended stimulus. However, the time course of synaptic modification being generally slow, it is not clear how such synaptic biases can emerge at the time scales of attention shifts. In other network models cell populations selective to specific stimulus features such as orientation were used with feedforward and feedback connections to a global inhibitory network pool. In the presence of multiple stimuli, a principal cell's response to a preferred stimulus was suppressed by inhibitory inputs recruited from other principal cells that selectively responded to the non-preferred stimuli (Deco, Pollatos, & Zihl, 2002; Usher & Niebur, 1996). The competition was biased in favor of a particular feature/ orientation by providing an external excitatory top-down drive preferentially to the principal cells tuned to that orientation. Hence, the attention effect was modeled by modulating the total amount of input excitation and inhibition to a neuron. In a single cell multicompartmental model, stimulus competition was implemented by spatially segregating the inputs projecting onto a $V4$ neuron to different regions of its dendritic tree (Archie & Mel, 2000). The authors also modeled the attentional bias by increasing the amount of feedforward excitatory input to the attended stimulus (Archie & Mel, 2004).

The above models hypothesize that a neuron must receive increased excitatory inputs to exhibit attentional modulation. This increase assumes the existence of a mechanism that can recruit new excitatory inputs, or that can selectively increase the firing rate of the input population corresponding to the attended stimulus. An alternative hypothesis is that the amount of excitatory inputs (number or rate) remains unchanged, but that attentional bias is achieved by a modulation of their correlation. Correlations imply no change in the sum total input spikes to a neuron, nor a change in synaptic strengths, but a possibly rapid change in the relative spike timing of these inputs such that spikes from different neurons arrive close together in time and have therefore a greater postsynaptic impact.

Model simulations have shown that input correlations increase the gain of a post-synaptic neuron's input–output firing rate curve (Chance, Abbott, & Reyes, 2002; Fellous, Rudolph, Destexhe, & Sejnowski, 2003; Salinas & Sejnowski, 2000, 2002). This is achieved by increased fluctuations around the spiking threshold of the neuron. Correlation in either the excitatory or inhibitory inputs can separately elicit this effect; however correlations between excitatory and inhibitory input annul this increase in gain. Physiologically, correlations have been observed as gamma frequency range oscillations in visual cortex (reviewed in Engel, Roelfsema, Fries, Brecht, and Singer (1997), Singer (1999), Singer and Gray (1995)), and neuronal assemblies that have a common orientation preference to synchronize with one another (Eckhorn et al., 1988; Gray & Singer, 1989; Gray, Engel, Konig, & Singer, 1990). More recently $V4$ neurons receiving their preferred stimulus input have been shown to have spike field coherence in the gamma frequency range in spatial attention (Fries, Reynolds, Rorie, & Desimone, 2001) as well as visual search tasks (Bichot, Rossi, & Desimone, 2005). In addition to excitatory neurons, there is vast accumulating evidence that networks of inhibitory interneurons mutually synchronize and are capable of generating gamma frequency range oscillations in the hippocampus and cortex (Deans, Gibson, Sellitto, Connors, & Paul, 2001; Fisahn, Pike, Buhl, & Paulsen, 1998; Wang & Buzsaki, 1996). Based on model simulations it was proposed that the attention effects to single stimuli could be mediated by the modulation of the synchrony of interneuron networks (Tiesinga, Fellous, Salinas, Jose, & Sejnowski, 2004). In this model when the temporal dispersion of the inhibitory inputs to the $V4$ neuron was reduced, leading to greater synchrony, the neuron displayed a firing rate gain akin to that seen when a stimulus is attended. However, increasing the synchrony of the interneuron network corresponding to an attended stimulus always increased the model response. Hence a synchrony manipulation on its own cannot account for a decrease in firing when a non-preferred stimulus is attended.

Recently Tiesinga (2005) also proposed an inhibitory correlation mechanism for biased stimulus competition termed stimulus competition by inhibitory interference. The firing rate of the postsynaptic neuron was modulated with attention to the preferred or non-preferred stimulus by changing the phase delay between two separate inhibitory populations that represented either stimulus. When the two inhibitory populations oscillating in the gamma frequency range were in phase or had constructive interference the postsynaptic neuron's firing rate was increased. A reduction in firing rate was achieved when the two inhibitory populations were out of phase. In this model excitatory inputs were modeled as asynchronous events, which may not be entirely compatible with evidence from recordings in striate and extrastriate cortex (reviewed in Engel et al. (1997), Singer (1999), Singer and Gray (1995)). Given the evidence for synchronized oscillation in both excitation and inhibition in cortex we investigate a mechanism wherein both these components are correlated to attain biased stimulus competition.

2. Methods

2.1. Model and quantitative assumptions

We used a multi-compartmental reconstruction of a layer 4 spiny stellate neuron (Mainen & Sejnowski, 1996) to represent the $V4$ neuron in our model. Voltage gated Na^+ and K^+ Hodgkin–Huxley channels were inserted in the soma and axon. The soma was also provided with a M-type K^+ current to allow for spike frequency adaptation as well as Ca^{2+} dependent K^+ after-hyperpolarizing currents that prevented excessive spike bursts to synaptic inputs. The dendrites were modeled as passive and all compartments were provided with a gradient of leak currents as determined experimentally (Stuart & Spruston, 1998).

The $V4$ neuron received stimulus driven feedforward excitatory and inhibitory synaptic input from cortical area $V2$ as well as stimulus independent synaptic inputs that represented intracortical or top-down inputs (Fig. 1). All glutamatergic inputs were distributed uniformly throughout the dendritic tree, while inhibitory inputs were located perisomatically within