Stimulus competition by inhibitory interference

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Abstract

When two stimuli are present in the receptive field of a V4 neuron, the firing rate response is between the weakest and strongest response elicited by each of the stimuli alone. When attention is directed towards the stimulus eliciting the strongest response (preferred stimulus), the response to the pair is increased, whereas the response decreases when attention is directed to the poor stimulus. We reproduced these results in a V4 model neuron. The model suggests that top-down attention biases the competition between V2 columns for control of V4 neurons by changing the relative timing of inhibition rather than by changes in synchrony of interneuron networks.
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1. Introduction

The neural correlates of selective attention have been studied in monkeys using recordings from single neurons in cortical area V4 [5]. A key finding is that attention modulates both the mean firing rate of a neuron in response to a stimulus and the coherence with other neurons responsive to the same stimulus [2]. The increase of coherence with attention is strongest in the gamma frequency range (30–80 Hz), suggesting that interneuron networks might mediate the effects of attention. The degree of synchrony of the inhibitory inputs to V4 neurons can be characterized by their temporal dispersion, referred to here as precision. Attention could act by increasing the precision of inhibitory inputs to V4 neurons [6]. We found that the resulting modulation of the model neuron's firing rate and its coherence with the inhibitory inputs was consistent with the observed effects of attention. However, the preceding model only considered the case of one stimulus in the neuron's receptive field.

The response of a V4 neuron to two stimuli in its receptive field has also been studied [5]. One of the stimuli yielded a weak response when presented alone, whereas a more vigorous response was elicited when the other stimulus was presented alone. The latter is referred to as the preferred stimulus and the former is referred to as the poor stimulus. When both stimuli were presented at the same time there was stimulus competition: the neuron's firing rate was less than the response to the preferred stimulus but larger than the response to the poor stimulus. When attention was directed to the preferred stimulus the response increased, whereas attending to the poor stimulus decreased the response. Hence, attention biased the outcome of stimulus competition towards the stimulus that was attended. The neural circuit that underlies stimulus competition is not yet fully characterized. Our goal is to determine whether and how modulation of the activity of local interneuron networks can account for attentional modulation of stimulus competition. We find that modulating the relative phase of synchronized inter-neuron networks rather than the degree of synchrony can account for the competition between V2 columns for the control of V4 neurons.

2. Methods

The following framework is used to study the behavior of the V4 model neuron (Fig. 1A). We used a single compartment neuron with Hodgkin–Huxley voltage-gated sodium and potassium channels, a passive leak current,

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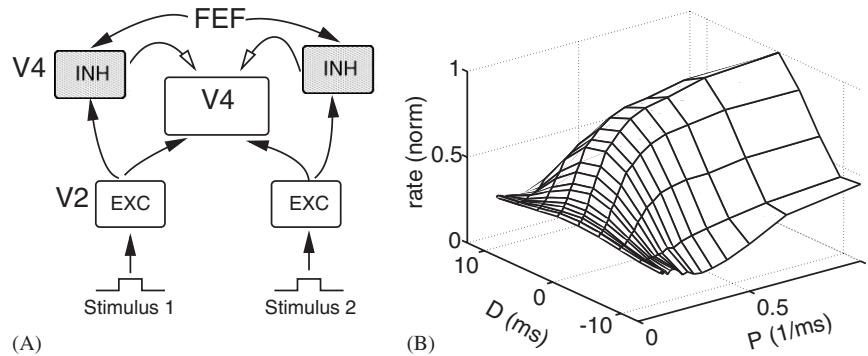E-mail address: tiesinga@physics.unc.edu.

Fig. 1. (A) The Model Network. The model neuron receives feed-forward inputs from two excitatory pools in area V2 and it receives inhibition from two local interneuron networks in V4. The interneuron network is modulated by inputs from the frontal eye fields (FEF). (B) Stimulus competition is robust against modulation of the precision of interneuron networks. We plot the normalized firing rate (see text) in response to stimulus 1 and 2 presented together versus the delay between inhibitory volleys, D, and the precision P.

and excitatory and inhibitory synaptic currents [8]. The model's parameter settings were as described in [7]. The neuron received inputs from two excitatory pools. The first pool is exclusively activated by the poor stimulus (stimulus 1) and provides weak excitation to the neuron. The second pool is exclusively activated by the preferred stimulus (stimulus 2) and provides strong excitation to the neuron. For most cases, we took a 3:1 ratio for the rates of preferred and poor excitatory inputs, respectively. The total excitatory rate, when both stimuli were present was 2400 inputs per second. Each excitatory pool in V2 also activates a corresponding inhibitory pool in V4. When the inhibitory pools are activated they produce synchronized volleys with a precision P at a rate of 40 Hz. The precision is the inverse of the temporal dispersion of the spikes in a volley and it is expressed in 1/ms. A more synchronous inhibitory network has a higher value for the precision. We used P values between 0 and 1/ms. Each volley had on average $a_{IV} = 18.75$ synaptic inputs. The volleys produced by the networks arrive at the neuron at different times. The delay in volley arrival times is expressed in ms and denoted by D.

3. Results

The firing rate response to the poor stimulus alone and to the preferred stimulus alone is denoted by f_1 and f_2, respectively. When both stimuli are presented simultaneously the response is f_3. Stimulus competition thus implies the following inequality: $f_1 < f_3 < f_2$. Stimulus competition was obtained when the volleys from the second inhibitory network (activated by stimulus 2) were delayed by $D = 7.5$ ms compared with volleys from the first inhibitory network (activated by stimulus 1). The firing rate in response to stimulus 2 alone was higher than in response to stimulus 1 alone because the second excitatory pool provided a higher excitatory input rate. When both stimuli were presented simultaneously the response was less than

the response to stimulus 2 alone, because the two inhibitory networks were out of phase. To determine under what condition stimulus competition was present, we calculated f_1, f_2 and f_3 for D and P values on a two-dimensional grid. We assume that both interneuron networks have the same precision. The normalized pair rate is obtained by subtracting the response to the poor stimulus and dividing by $f_2 - f_1$. When the normalized rate is between 0 and 1, there is stimulus competition. For the parameter set used in this study, stimulus competition is obtained everywhere (Fig. 1B). The pair response is closer to the response to the poor stimulus for low values of the precision, whereas for higher values of the precision there was stronger modulation of the pair response with delay. For small delays and high precisions the normalized rate was close to one, hence the pair elicited approximately the same response as the strong stimulus by itself.

It was recently reported that altering the precision of the inhibitory inputs to a neuron could lead to a gain change of its firing rate response curve. An increase in input precision led to an increased firing rate, whereas a decrease led to a decreased firing rate [6]. In order to account for the experimental results, attention thus needs to have a different effect on the synchrony of the inhibitory networks depending on whether the focus of attention is on a poor or a preferred stimulus. This contextual modulation of precision is difficult to orchestrate in cortical networks. We therefore investigated whether we could model the effects of attention by varying the delay between the interneuron networks rather than by varying the precision. For attention directed to stimulus 1, the delay was increased and the firing rate decreased from the baseline condition. In contrast, for attention directed to stimulus 2, the delay was decreased and the firing rate increased from the baseline value. The attentional bias should be able to raise the firing rate to values close to f_2 and decrease the firing rate to values close to f_1. The requirements necessary to achieve this dynamic range were determined. For high

precision, the firing rate was strongly modulated by the value of the delay, but the pair response did not get close to f_1 (Fig. 1B). For low precision, there was only a weak modulation of the firing rate with delay and the pair response remained close to f_1 (Fig. 1B). Only for moderate precision, $P = 1/(3\,\text{ms})$, there was both a strong modulation with delay and a pair response that went from values close to f_1 to values close to f_2 (Fig. 1B). Hence, there is only a limited range of precision values for which attentional modulation is possible.

In the simulations performed for Fig. 1B the excitation was taken to be asynchronous. However, in response to stimuli with the optimal orientation and of high contrast, neurons in V1 can be synchronized in the gamma-frequency range [3]. As a result neurons in area V2, which provide inputs to V4, may also be synchronized. Recent results indeed indicate that neurons in the superficial layers of V1, V2 and V4 are synchronized in the gamma frequency range, whereas those in the deep layers are synchronized in the beta frequency range [1]. We therefore studied whether stimulus competition and the attentional modulation of it was robust against synchronous excitation. For the present investigation, the drive representing stimulus 1 and 2 comprised 993 volleys, each a Gaussian with standard deviation 3 ms and an amplitude that varied between volleys with a standard deviation of 10%. The sequence of volley times (the mean of the Gaussian) was generated using a separate Poisson process with a mean interspike interval of 10.05 ms. The density of this Poisson process had a gamma frequency component with a strength of 42% (quantified as the maximum minus the minimum of the phase histogram of the volley times divided by the mean of the histogram). 25% of the volleys were associated with stimulus 1 and 75% were associated with stimulus 2. The rate of the Poisson process was normalized so that on average there were 2400 inputs per second. The drive is shown in Fig. 2Ac. For this drive, stimulus competition was obtained for all values of the delay (Fig. 2Aa). The pair response can get close to the response to the preferred stimulus, but does not come as close to the poor-stimulus response. When only 50% of the inputs were from the volleys and the remainder was supplied in the form of asynchronous excitation, the pair response came closer to the poor-stimulus response (Fig. 2Ba).

4. Discussion

We have proposed a single cell mechanism for stimulus competition in V4 based on temporal interference of synchronous inhibition. The model used here has a number of assumptions that were introduced in order to explain the results in the simplest possible way. However, response modulation by inhibitory interference is obtained under more general conditions. The requirements for attentional modulation of stimulus competition were as follows. The feedforward excitation from V2 cannot be phase-locked to
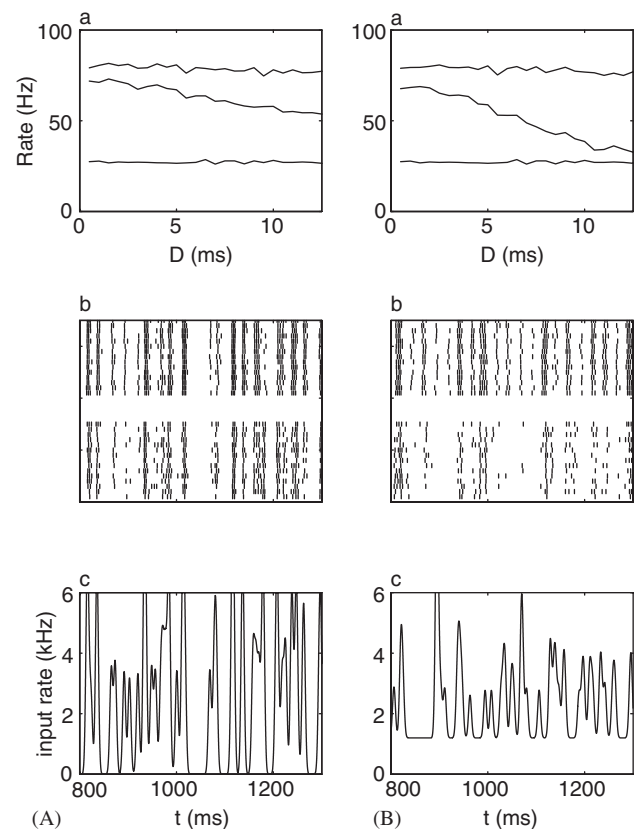

Fig. 2. Attentional modulation of stimulus competition for stimulus-locked excitation. For each panel we plot, (a) the firing rate as a function of the inhibitory delay D for, from top to bottom, stimulus 2 alone, stimulus 1 and 2 together and stimulus 1 alone; (b) the rastergram for (top) $D = 0$ ms and (bottom) 12.5 ms; (c) the density of the excitatory input. (b) and (c) have the same time scale. In (A), the density was normalized so that the mean, when both stimuli were present, was 2400 spikes/s. In (B) we multiplied the time-varying density by 50% and added a constant Poisson process with a rate of 1200 spikes/s.

the inhibitory inputs but it may consist of a sequence of precise spike volleys. The local inhibitory networks need to be synchronized. Attention-related bottom-up or top-down projections, such as from the frontal eye fields [4], need to be able to modulate the phase of synchronized interneuron networks. The power spectrum of the spike trains produced by the model has not only a peak at 40 Hz reflecting the periodicity of the inhibitory inputs, but also a second harmonic at 80 Hz. The model predicts that the relative strength of the second to first harmonic is higher for the attend-to-poor than for the attend-to-preferred condition (results not shown). This prediction can be tested experimentally.

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Paul Tiesinga studied Theoretical Physics at Utrecht University in The Netherlands. His Ph.D. thesis was on the dynamics of Josephson-junction arrays. As a postdoctoral fellow at Northeastern University and later at the Salk Institute he worked on biophysically realistic modeling of thalamus, hippocampus and cortex. Currently he is assistant professor at the University of North Carolina at Chapel Hill.