Generation of and Role for Cortical Traveling Waves

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Introduction

Experimental evidence shows a relationship between cortical phase waves and faint visual stimulus detection.

Oscillations in the cortex become spatial phase gradients, which travel in alpha and theta waves[1]. Voltage fluctuations go through the cortex as waves, which, based on the wave phase, have regions of hyperpolarization and depolarization. Faint visual stimuli are sometimes, but not consistently, detected. A study on the detection of faint visual stimuli in marmosets reported that waves should be depolarized above a threshold just before the onset of the stimulus for the stimulus to be detected by the animal[2].

In this study, models are proposed to mathematically show the generation of waves and the effect of phase of an oscillation on the likelihood of stimulus detection. We used the experimentally-derived suggestion that varying frequencies give way to wave generation to inspire our model.

Model

The Wilson-Cowan firing rate model represents spatial distribution of excitatory and inhibitory neurons in the primary visual cortex.

Frequency Gradient for Wave Generation:

The Wilson-Cowan model generates waves in a cortical layer.

$$\frac{\partial u}{\partial t} = -u(x,t) + f(a_{ee}((1-\lambda_e)u(x,t) + \lambda_e(K(x) \star u(x,t))) - a_{ei}v(x,t) - \theta_e + de(x))$$

$$\tau_i \frac{\partial v}{\partial t} = -v(x,t) + f((a_{ie}(1-\lambda_i)u(x,t) + \lambda_i(K(x) \star u(x,t))) - a_{ii}v(x,t) - \theta_i$$

where u is an excitatory neuronal population, v is an inhibitory neuronal population, $f(u) = \frac{1}{1+e^{-u}}$ is a nonlinear gain function representing firing rate, a_{bc} is the strength of projection from network c to b, $\lambda_{e,i}$ is the coupling factor between the local circuit and the rest of the network, $\theta_{e,i}$ is a threshold for firing. $K_{e,i}(x)$ is a kernel describing the weights of excitatory and inhibitory connections and is defined as $K(x) = \frac{1}{2\sigma}\exp(\frac{-|x|}{\sigma})$. The drive force to create variation in frequencies is defined as $de(x) = \frac{x}{100}(de_1 - de_0) + de_0$.

Single Oscillation for Faint Stimulus Detection:

We first model a single oscillation throughout a cortical layer.

$$\frac{du}{dt} = -u(t) + f(a_{ee}u(t) - a_{ei}v(t) - \theta_e + de + c_{ee}\,us)$$

$$\tau_i \frac{dv}{dt} = -v(t) + f(a_{ie}u(t) - a_{ii}v(t) - \theta_i + c_{ie}u\,s)$$

We then introduce noise and a stimulus from a sensory cortical layer where b_{cd} is the strength of projection from network d to c in the stimulating layer, d_{ab} is the strength of projection from network b to a in the wave layer, and $nz_{u,v}$ determine the amplitude of the noise.

$$\frac{dus}{dt} = -us(t) + f(b_{ee}us(t) - b_{ei}vs(t) - \theta_e + stim + d_{ee}u(x,t) + nzu\,yu(t)$$

$$\tau_{is}\frac{dvs}{dt} = -vs(t) + f(b_{ie}us(t) - b_{ii}vs(t) - \theta_i + stim + d_{ie}u(t) + nzv\,yv(t)$$

Low pass filtered noise:

$$\tau_y \frac{dyu}{dt} = -\frac{yu(t)+\mathcal{N}(0,1)}{\sqrt{dt*\tau_y}} \text{ and } \tau_y \frac{dyv}{dt} = -\frac{yv(t)+\mathcal{N}(0,1)}{\sqrt{dt*\tau_y}}$$

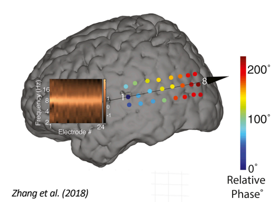
We measure the response due to the stimulus where ton is the time of stimulus onset and wid is the width of the Heaviside function.

$$\frac{\partial resp}{\partial t} = \frac{us(t)}{wid} H(t-ton)\,H(ton+wid-t)$$

The stimulus is a step function at time ton of width wid and height amp where H is a Heaviside function.

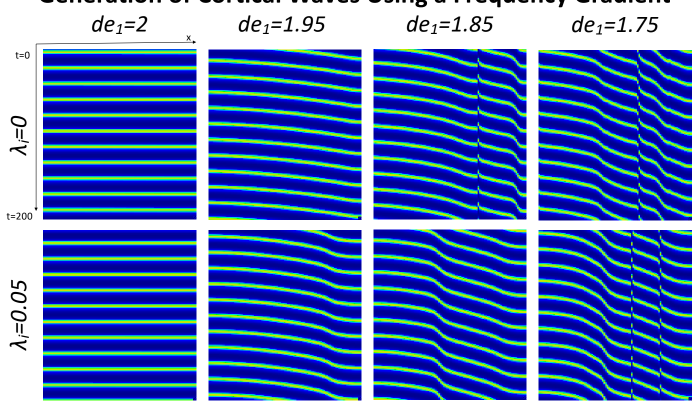
$$stim = amp\,H(ton+wid-t)H(t-ton)$$

Traveling Waves Due to Oscillation Clusters in the Human Cortex



Using electrodes measuring narrowband 8.3-Hz oscillations, the direction and relative phase of a traveling wave in a surgical patient was measured. Larger phase shifts are positively correlated with the length of time of travel for an oscillation. Using circular statistics, it was determined that 67% of oscillation clusters have consistently traveling waves and that waves occur in both hemispheres.

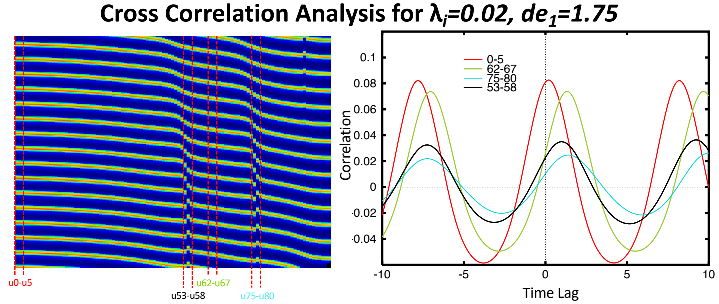
Generation of Cortical Waves Using a Frequency Gradient



Parameters: a_{ee}=20; a_{ei}=40; a_{ie}=8; a_{ii}=1; de_0=2; λ_e=0.02; σ=5; ϑ_e=4; ϑ_i=5; τ_i=2; amp=0; ton=100; wid=5

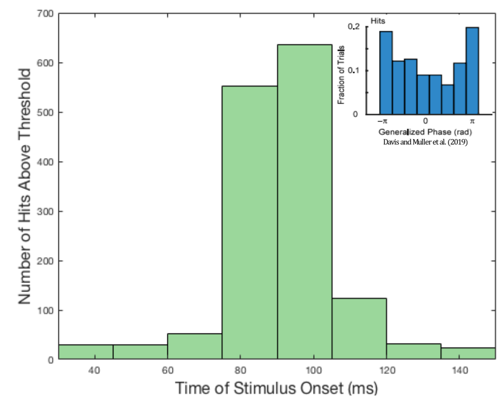
We decreased de_1 in order to decrease the drive force de(x). As the drive force decreases, cortical waves are generated, as can be observed due to the presence of frequency jumps and plateaus.

Cross Correlation Analysis for λ_i=0.02, de_1=1.75



Using the Wilson-Cowan model to generate waves, we look at the cross correlation between neurons connected across frequency plateaus versus across frequency jumps. The time scale for this analysis was increased to show greater variance in phase gradients.

Number of Oscillation Peaks above Threshold



We conducted 6,426 trials of an oscillation paired with a stimulus. Looking at the response as a function of time of stimulus onset, we set a threshold for "hits," or trials at which the response was above a baseline and the stimulus would be detected, at resp = 0.15. Given that the period of the oscillation was about 80 ms, the peak of responses occurred about halfway through the period.

Discussion

In varying de from de_0 to de_1 across the domain, we demonstrated that a phase shift occurs across the population, yielding the propagation of waves across a network of weakly coupled cortical neurons. To further expand upon this, we then showed that neurons that are across a plateau, therefore similar in phase at a given time, are closely correlated whereas neurons that are located across a frequency jump are less correlated, thus quantifying the propagation of the waves.

Once wave propagation via a frequency gradient was generated, the likelihood of a response above a threshold to faint visual stimuli was shown to be correlated with the time of onset of a stimulus and therefore the phase of the oscillation. This model also agreed with the experimental data.

References

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