# A Spiking Model for Binocular Rivalry Carlo R. Laing and Carson C. Chow

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May 2, 2004

## 1 Introduction

In Laing and Chow's, "A Spiking Neuron Model for Binocular Rivalry", the authors attempt to demonstrate a biologically plausible model of the natural phenomena known as binocular rivalry [1]. When our eyes are independently presented with two significantly different images at the same time, a competition will occur between the differing visual stimuli at some location along the visual pathway. The end result is that only one of the conflicting images is perceived by the viewer (i.e. it is dominant) at a given interval of time and the other image is invisible to viewer (i.e. it is suppressed). The images will continually switch roles between being dominant and being suppressed, thus the viewer will see only one image at a given time, but the visible image will alternate between the two presented images as the stimuli compete for dominance. This switching between perceived images is called binocular rivalry, and it should be noted that the dominance of the images is not controlled by the viewer. It is easy to observe binocular rivalry, for example, look at the two images of orthogonal gratings in Figure 1. First, create a barrier between the two images with a piece of paper,



Figure 1: Two orthogonal gratings that when viewed by both eyes independently at the same time, demonstrate binocular rivalry. [2]

so only one image is visible to each eye. Then, simply look at both images, they will merge into one and you can see an alternation between the perceptions of the orthogonal gratings. There are a number of theories which try to explain what is actually rivaling during the binocular rivalry process. It was originally thought that the rivalry occurred between the eyes themselves, such that only one eye's input is perceived during a given dominance period. An experiment in favor of this theory swaps the conflicting images, while binocular rivalry is taking place, resulting in the viewer perceiving the swap in the middle of a dominance period [2]. This suggests that during a given period of dominance, the stimuli of one eye are fully perceived and the other eye's stimuli are suppressed. Recent experiments show that neurons at the site(s) of the rivalry receive information from both eyes. In this case the eyes would not be rivaling, rather the specific stimuli would be rivaling. One study supporting this theory probed the cortex of monkeys undergoing binocular rivalry, and found that it was neurons receiving input from both eyes (binocular neurons), rather than neurons receiving input from one eye (monocular neurons), that correlated with the perceptions of the rivaled images [3]. The authors then point to a study which shows that both types of rivalry, eye rivalry and stimulus rivalry, seem to occur depending on the stimulus characteristics [4].

Regardless of the details behind the rivalry process, there are five experimentally observed phenomena which characterize the binocular rivalry process. The experiments demonstrating the phenomena have been done using humans and primates, typically viewing images of oriented gratings at different angles, similar to Figure 1. The data was recorded as either direct feedback from the experiment's subject (i.e. the subject responds when the perceived image changes) or through various brain activity scanning techniques focused on the regions in the visual cortex correlated with binocular rivalry. First, there is a common distribution of the dominance durations seen in humans and primates. Second, there is no correlation between length of one dominance duration and the length of the following dominance durations. Third, changing the stimulus strength to one eye effects the mean dominance duration of the opposite eye and not the mean dominance duration of the changed eye, this is known as Levelt's second proposition [5]. Fourth, an increase in the stimuli strength to both eyes decreases the mean dominance duration (stronger stimuli switch faster). Fifth, non-orthogonal gratings have bigger mean dominance durations than orthogonal gratings (the more similar the images the longer the mean dominance duration). Any model of binocular rivalry must demonstrate these primary characteristics in order to be plausible.

The authors' aim was to create a plausibility model for binocular rivalry, which is biophysically feasible and demonstrates the the observed phenomena of binocular rivalry. This is in contrast to past models of binocular rivalry that use neural network or rate models, which the authors claim cannot be quantitatively compared with the observed phenomena of binocular rivalry. It is important to keep in mind that the models are not meant to describe any specifically known networks of neurons in the brain. There are two models presented in the paper: one models the neurons individually with Hodgkin-Huxley type neurons; the other is a spatially averaged reduced model. Both models were created on the assumption that there is a focus of active neurons that represents a specific perceptualization. So, in keeping with the oriented grating example, there are distinct groups of neurons for each discrete grating orientation. Neurons with similar orientations have excitatory connections between each other. When a group of these neurons fire, the orientation associated with them is said to be *perceived*. The connectivity of the neurons is such that when two significantly different stimuli are received only one set of orientation neurons is able to fire. A spike frequency slow process or synaptic depression would allow for the orientation neurons to switch, resulting in the perception of binocular rivalry.

# 2 Full Hodgkin-Huxley Type Model

This model uses Hodgkin-Huxley type conductance-based excitatory and inhibitory neurons interconnected with each other. Each neuron is orientation selective, which means that it has an assigned orientation and fires rapidly in the presence of a grating with the same orientation. This model does not include neurons that fire when their orientation is suppressed or neurons that change their firing patterns depending on whether or not the stimuli are significantly different. The neurons receive orientation *input* from both eyes. To model the situation in Figure 1, where the gratings are orthogonal, current is applied to two neurons in the model with orthogonal orientations. Figure 2 shows the structure of the neurons in this model. Current is being applied to two neurons: orientation 0 and orientation 90. The



Figure 2: The configuration of excitatory and inhibitory neurons in the full model. Each neuron is labeled with its preferred orientation. Current is being injected at two orthogonal neurons: 0 and 90.

current input is modeled using a Gaussian function centered at the neuron with the matching orientation. Thus, neurons with similar orientations to the neuron where the current is focused receive some current and neurons with drastically different orientations receive very little current. Since all of the neurons in the model are interconnected the connection strengths must be modeled. The strength of the connections is a Gaussian function of the difference in preferred orientation angle. Neurons will have the most effect on other neurons with similar preferred orientations. This model is independent of the type of rivalry occurring: stimulus rivalry or eye rivalry. In the described configuration stimulus rivalry is assumed, but the model could be easily configured to show eye rivalry.

In order to get the switching behavior necessary for binocular rivalry, two slow processes are included in the model. The first is a calcium-dependent potassium current that causes spike frequency adaptation. The firing frequency of an active neuron will be slowed down, as time progresses. The second slow process is a synaptic depression in the excitatoryexcitatory synaptic connections. This will decrease the connection strength in connections between excitatory neurons and an actively firing excitatory neuron as firing time increases. To understand how the actual switching behavior is going to take place, consider two input stimuli S1 and S2. The excitatory loop in Figure 2 will cause firing activity to be centered around the neurons N1 and N2 with orientations the same as S1 and S2 respectively. The inhibitory loop will keep those firing locations from migrating around the network. The inhibitory loop is also strong enough to suppress either N1 or N2 from firing. In the case that the area around N1 is active and the area around N2 is suppressed, the spike frequency adaptation will slow down the firing of the N1 area and will increase the possible firing around N2. The synaptic depression will cause the area of firing around N1 to decrease and the possible area of firing to increase around N2. At some point the firing frequency around N1 will be low enough that N2 and its surrounding neurons will fire and immediately suppress the N1 area. This switching process will repeat and is the heart of the binocular rivalry seen in the model.

#### 2.1 Simulation Results

The actual firing pattern of the excitatory neurons in the full model, with input currents at orthogonal neurons, can be seen in Figure 3. Each dark bar corresponds to an area of neurons firing at a given time. The switching pattern can be seen clearly as the *perception* is switched between the orientation of neuron 15 and orientation of neuron 45. In the zoomed in picture on the right, there is a clear bursting pattern with the number neurons and frequency of firings greatest at the onset of the dominance period. The number of neurons and frequency dies down at the end or the dominance period, right before the other stimulus takes over, which is the expected behavior due to the two slow processes. This is more apparent in Figure 4 which is looking at the voltage of neuron 38 through two dominance periods. Furthermore, it is only possible to have one "bump" of activity at a time, and this is expected binocular



Figure 3: Excitatory neuron activity as a function of time. Orthogonal neurons 15 and 45 are being stimulated. The right plot is a zoomed in view of the left plot.



Figure 4: Voltage of the 38th neuron from Figure 3. The bottom two plots are zoomed in views of the top plot. Spike height differences are due plotting the voltage against discrete time steps.

rivalry behavior.

In Figure 5 the model's distribution of dominance durations is shown along with the biologically expected distribution of dominance durations (the dashed line). This demonstrates



Figure 5: The distribution of dominance durations for the full model. The solid line is from the reduced model. The dashed line is a Gamma distribution of the observed dominance durations.

the model's compatibility with the first observed phenomena in binocular rivalry, namely that there is a common distribution of dominance durations. The second observed phenomena, that there is no correlation in successive dominance durations, is demonstrated in the model by Figure 6. This is a plot of the correlation between successive dominance durations of a given length. Clearly, there is no significant correlation except at 0, which is expected since 0 represents no neuronal activity in the system. The authors also calculated the Lanthrop statistic, which is a specific measure of the correlation between successive values in a time series, and it turned out to be .31 (i.e. very low correlation), further demonstrating the second observed phenomena.

The authors demonstrated that their model also conforms to Levelt's second proposition



Figure 6: Autocorrelation of successive dominance durations for the data in Figure 5.

(third observed phenomena), that changing the strength of the stimulus to one eye primarily effects the mean dominance duration of the other eye in Figure 7 The signal strength for both inputs, x and o, starts at .4 and then the signal strength of x is reduced and the signal strength of o stays the same. This results in an increase of o's mean dominance duration and x's mean dominance duration to stay fairly steady, which is precisely Levelt's second proposition. The authors do not explicitly show the full model demonstrating the fourth observed phenomena in binocular rivalry, increasing both stimuli strengths at the same time decreases both mean dominance durations. However, they do demonstrate the fifth observed phenomena, non-orthogonal gratings have a higher mean dominance duration than orthogonal gratings, in Figure 8. It is clear the the full model does a good job at reproducing many of the observed phenomena from binocular rivalry.



Figure 7: The effect of changing the strength of one input on the mean dominance duration. Both inputs start with a strength of .4. The x's strength was decreased while the o's strength remained the same. Notice that only the o's mean dominance duration significantly changed. The dashed lines are the results of the reduced model.



Figure 8: The effect of changing the difference in the angle of grating orientation on the mean dominance duration. Smaller angles do not work well with the model.

### 3 Reduced Model

At this point the authors decided they needed a simpler mathematical model, to compute a distribution of duration times with respect to signal intensity. Levelt's second proposition states that the dominance durations of one eye are only affected by the intensity of the image in the other eye, and not the intensity in itself. Massive computational time is required to model 60 Hodgkin-Huxley neurons for a significant amount of time. So the authors developed a reduced model, splitting the neurons into two hemispheres. They assume that the behavior of each half of the neurons can be represented by a few differential equations shown in Figure 9. In this reduced model, u is assumed to be directly correlated with the perception of its

$$\frac{du_1}{dt} = -u_1 + f(\alpha u_1 g_1 - \beta u_2 g_2 - a_1 + I_1) \quad (1)$$

$$\frac{du_2}{dt} = -u_2 + f(\alpha u_2 g_2 - \beta u_1 g_1 - a_2 + I_2) \quad (2)$$

$$\tau_a \frac{da_1}{dt} = -a_1 + \phi_a f(\alpha u_1 g_1 - \beta u_2 g_2 - a_1 + I_1) \quad (3)$$

$$\tau_a \frac{da_2}{dt} = -a_2 + \phi_a f(\alpha u_2 g_2 - \beta u_1 g_1 - a_2 + I_2) \quad (4)$$

$$\tau_d \frac{dg_1}{dt} = 1 - g_1 - g_1 \phi_d f(\alpha u_1 g_1 - \beta u_2 g_2 - a_1 + I_1) \quad (5)$$

$$\tau_d \frac{dg_2}{dt} = 1 - g_2 - g_2 \phi_d f(\alpha u_2 g_2 - \beta u_1 g_1 - a_2 + I_2), \quad (6)$$

Figure 9: Equations for the reduced model.

respective image. Constants are chosen to exclude steady states from this model. For example, when both percepts are active, or both are inactive. For clarity, they first ignore the last two equations, letting g1=g2=1. u1 and u2 represent "averages" of the spatially averaged net excitatory of each population. The chaotic dynamics of the spiking network are not represented in this model. a, the population adaptation variable, depends on: I, its respective input current; g, the synaptic depression variable; time constants  $\tau$  of the adaptation and depression; a Heaviside function f for the gain (i.e. turning the adaptation and depression on and off), constants  $\alpha$  and  $\phi$ .

The plots of u1, a1 vs time and u2, a2 vs time are shown in Figure 10. The authors observed that when a1 exponentially approaches  $\phi$ , a2 exponentially approaches zero. Meanwhile, u1 is on and u2 is off. This will decrease the total inputs to a and increase the



Figure 10: Solutions of Eq 1-4 of the reduced model from Figure 9. The top is u1 and a1, the bottom is u2 and a2.

total inputs to a2. Eventually, this causes the inputs to a2 to cross the threshold, making u2 increase and simultaneously increasing inhibition to cause u1 to decrease. The process then repeats and oscillations ensue.

The authors then calculated the length of the dominance periods, T1 and T2 in Figure 11, from the dynamics of the exponential increase and decay. They found the dependencies of the dominance duration times of each percept depend on the several parameters, including I1 and I2, the intensities of the two inputs. The equations in Figure 11 show that T1 is dependent on I2, while T2 is dependent I2. A plot of the dominance duration equations is

$$T_{1} = -\tau_{a} \log \left( \frac{I_{2} - \beta}{\beta + \phi_{a} - I_{1}} \right),$$
  

$$T_{2} = -\tau_{a} \log \left( \frac{I_{1} - \beta}{\beta + \phi_{a} - I_{2}} \right).$$
(9)

Figure 11: Dominance duration equations from the reduced model. I1 and I2 and the input strengths.

shown in Figure 12. The top graph demonstrates the strong dependence of T2, the solid line, on I1 and little dependence of T1, the dashed line, on I1. This verifies that the reduced exhibits Levelt's second postulate, which says the dominance duration of one input depends on the stimulus of the other input. The bottom graph is the average durations as a function of input when both inputs are equal (i.e. I1=I2). This shows the dominance durations decrease as the inputs increase, which is the fourth observed phenomena of binocular rivalry from the introduction.

Finally, the authors throw in the effects of synaptic depression and ignore the effects of adaptation. They find that the dynamics are similar, except they are not able to do explicit derivations for the dependence of the time duration on the other variables. Figure 5 shows a distribution of dominance durations. The bars show the data from the actual 60-neuron network, and the solid curve shows the Gaussian distribution derived from the reduced model (long derivation in the appendix of the paper [1]). They seem to match up in general, this implies that the conclusions drawn from the reduced model should comply with the dynamics of the full 60-neuron model.

The reduced model established a relationship between the input strengths and dominance duration times. Many assumptions were made in the general equations, as well as the period dependence equation. Initially, the reduced model only takes account of adaptation among the neurons. Later, it is suggested that synaptic depression should lead to similar results. The authors suggest that in reality it may be a combination of adaptation and synaptic depression that causes switching.



Figure 12: Dominance durations with only adaptation considered. In the top plot T1, dashed line, and T2, solid line, are graphed against I1, the input strength of the first input. The top plot is the dominance duration vs. the input strength to both eyes when they are the same (I=I1=I2).

## 4 Conclusions

Both models as a whole are able to account for most of the observed phenomena in binocular rivalry: they reproduce the distribution of dominance durations that have been observed in humans and primates, there is no correlation between the lengths of sequential dominance durations, the variation in stimulus strength to one eye influences the dominance duration of the other eye and not of itself, increasing both input strength decreases the mean dominance durations, and rotating the grating orientation of the neurons so that they are no longer orthogonal increases the average dominance duration. The authors did notice that the dominance durations were very sensitive to the strength of the inputs to the system, thus causing significant variations in the dominance durations. This may explain why there is a large variance in the mean dominance durations of experimental test subjects, they each experience different input strengths, which the model predicts will greatly change the dominance durations.

The models have trouble with some aspects of binocular rivalry. For example, there are times when rivalry does not occur: when stimulus contrast is low or when the angle between the gratings is too small. In the first case the model will increase the durations of each stimulus until the switching stops in either the on-on, on-off, off-on, or off-off state. In reality the images would be merged together, but there is no clear way to represent the merging in the models. In the second case the model may only show one of the stimuli as active or it may fall into an on-on. The actual perception would be of a constantly changing patchwork, spiral, or wave of both images.

One of the nice features of the models is that they do not intrinsically depend on eye rivalry or stimulus rivalry. Both forms of rivalry can be created with the models, and they can be used to model rivalrous dynamics in general. Modern research is leaning in the direction that there are many forms of rivalrous behavior that when combined cause binocular rivalry, and the authors' models can be used for each of these rivalries separately. This leads to the question, what is the significance of the models? They were created to show a plausible cortical network demonstrating binocular rivalry, and the models appear to demonstrate many of the features of binocular rivalry well. However, they are still only plausibility models and say little about the actual structure of the brain. The models tell us how they brain *might* be connected and offer insight as to how rivalrous systems, in general, can be assembled.

# References

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