# **Modeling Perceptual Bistability: Impact of Neuronal Adaptation** <sup>2</sup> **and Noise on Alternation Dynamics** <sup>3</sup>

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#### **Abstract**

Perceptual bistability, characterized by stochastic alternations between two neuronal population activities, reflects the brain's processing of information that can be perceived in two distinct ways. This study investigates the dynamics of a proposed attractor network model, which identifies noise as the primary driver of these alternations. We reconstructed the rate-based version of this model using differential equations and the Euler method to systematically explore the nuanced impacts of noise, adaptation, and excitatory inputs on the model's behavior. Our results reveal that adaptation and noise critically affect the duration and distribution of temporal intervals between state transitions, profoundly influencing the model's ability to mimic experimental observations. Furthermore, we found that careful parameter selection is crucial in constructing network models that accurately capture perceptual bistability. This research not only underscores the crucial roles of noise and adaptation in the dynamics of alternation but also highlights the challenges inherent in simulating complex biological phenomena through computational models.

Keywords: Perceptual Bistability; Attractor Network; Energy Model; Differential Equations; Numerical Analysis 7

## 1. Introduction 8 and 8

In circumstances where a single perceptual stimulus allows two distinct interpretations, observers experience a phenomenon known as perceptual bistability. This occurs, for example, during binocular rivalry when each eye is presented with a different image. In such instances, the neuronal  $\mu$ populations supporting the perception of each image engage in a competitive interaction, where 12 the population with higher neural activity dominates the perception. This competition results in the observer's perception alternating over time. Although extensive experimental and theoretical <sup>14</sup> research has been conducted to understand this neural phenomenon, the precise mechanisms un- <sup>15</sup> derlying perceptual bistability remain unclear. In this project, we explore the theoretical model 16 proposed by Moreno-Bote et al. (2007) in their paper "Noise-Induced Alternations in an Attractor <sup>17</sup> Network Model of Perceptual Bistability." [\[1\]](#page-11-0) This model aims to explain the dynamics of alternation <sup>18</sup> by attributing it to ongoing noise within the system. Furthermore, we reconstruct and examine the <sup>19</sup> rate-based model outlined in the primary literature, assessing how variations in factors such as the 20 adaptation effect, feedforward input, or noise influence the model's ability to simulate perceptual 21 **bistability.** 22

## <span id="page-0-0"></span>2. Primary Literature and Report 23 April 23

In their research, Moreno-Bote and colleagues present a noise-driven attractor model of perceptual <sub>24</sub> bistability. Unlike earlier models that attributed perceptual alternations primarily to slow adapta- <sup>25</sup> tion effects acting upon the dominant population, their approach emphasizes noise in the synaptic 26 activities as the principal driver. This perspective presents a fundamentally different interpretation  $27$ of neural behavior and introduces a distinct modeling structure. The insights from this study are 28 crucial for reconstructing the theoretical model for our project and addressing our research ques- <sup>29</sup> tions. Therefore, this section delves into the experimental basis of perceptual bistability as detailed <sup>30</sup> in their work, the architecture of their model, its capacity to replicate experimental behaviors, and <sup>31</sup> the novel findings and predictions it yields.  $\frac{32}{2}$ 

To construct and evaluate a theoretical model of neural phenomenon, it is crucial to comprehend the 33 experimental properties of the behavior it seeks to capture. Levelt's 1965 study on binocular rivalry 34 provides a clear summary of important observations essential for modeling perceptual rivalry [\[2\]](#page-11-1). 35 First, his "Proposition II" indicates that weakening the stimulus strength (i.e., the image contrast) in 36 one eye does not shorten its duration of perceptual dominance. Instead, it causes the rival image  $\frac{37}{27}$ to dominate perception for longer periods. Second, "Proposition IV" suggests that strengthening <sup>38</sup> the image contrast in both eyes simultaneously decreases the dominance duration for both image  $\frac{39}{2}$ interpretations, thereby increasing the alternation rate. Lastly, multiple studies have discovered that  $\quad$ aggregating the durations during which each population dominates results in a skewed Gaussian 41 distribution [\[2,](#page-11-1) [3\]](#page-11-2). These findings are critical for determining the structure of the attractor model  $\frac{42}{42}$ and assessing the viability of various models.  $\frac{43}{3}$ 

Previous theoretical approaches have leveraged models driven by adaptation effects to explain these 44 experimental observations. As validated by our own model findings in Section [4,](#page-5-0) Subsection [4.1,](#page-5-1) 45 these oscillator models produce a perfectly periodic alternation in the absence of noise, due to the  $\frac{46}{6}$ deterministic nature of adaptation. In a state plane that displays the firing rates of the two neuronal  $\frac{47}{47}$ populations, each axis representing one population, the perceptual alternation under the oscillator <sup>48</sup> model appears as a cyclic trajectory. In this scenario, noise plays a limited role, contributing just <sup>49</sup> enough randomness to introduce some degree of variability, but not enough to disrupt this limit cycle. Most importantly, the removal of noise from the system does not stop the perceptual alternations  $\frac{51}{100}$ under the oscillator model.  $\frac{52}{2}$ 

On the other hand, the noise-based attractor model features two stable attractor points within the 53 state plane, each representing the dominance of a different neuronal population. In this model, <sub>54</sub> alternation occurs due to a force that helps the system overcome the energy barrier between the two ss attractors. Noise acts as the primary driving force in this process, and alternations between states <sub>56</sub> cease entirely when noise is removed. Although adaptation effect is also present in this model, it  $\frac{57}{10}$ alone is not a sufficient factor to induce state transitions, a topic that will be explored further later ss in our discussion.

This attractor-based framework utilizes energy functions designed to align with experimental ob-  $\approx$ servations of perceptual bistability.  $\epsilon$ <sub>51</sub>

$$
E(\Delta r) = \Delta r^2 (\Delta r^2 - 2) + g_A (\Delta r - 1)^2 + g_B (\Delta r + 1)^2
$$
 (1)

Primarily, the model's energy function includes two local minima, representing the attractor points.  $\epsilon_2$ A key modification, diverging from the standard energy function, is implemented to adhere to Levelt's Proposition II. Here, input strengths are cross-coupled, allowing increased input strength to one 64 neuronal population to lower the energy barrier for the other, leading to the desired effect of short- <sup>65</sup> ening the perceptual dominance duration of the rival image instead of extending its own [\[4\]](#page-11-3). Addi-  $\epsilon$ tionally, compliance with Levelt's Proposition IV is achieved by introducing a local inhibitory subpopulation structure. These subpopulations gather all external stimulus input to both populations  $\frac{68}{100}$ and exert inhibitory effects to each, proportionate to their activity levels. This arrangement ensures 69 that increasing overall image contrast reduces dominance durations for both eyes, thus facilitating  $\eta$ rapid alternation. Along with these main features, the model incorporates further enhancements  $\pi$ 1 such as strong recurrent excitatory connections to accurately replicate the experimental behaviors  $\frac{72}{2}$  $\alpha$  observed. The set of  $\alpha$  is the set of  $\alpha$ 

Although the attractor model denies the role of adaptation in driving alternations, it acknowledges  $\frac{74}{14}$ its significance in shaping model dynamics. Adaptation ensures that the distribution of dominance  $\frac{1}{15}$  durations reflects the skewed Gaussian pattern observed in experimental results. As confirmed by  $\frac{1}{76}$ our findings in Section [4,](#page-5-0) Subsection [4.2,](#page-6-0) noise-driven alternation without adaptation leads to an  $\pi$ exponential distribution of dominance durations [\[5\]](#page-11-4). However, incorporating adaptation resolves  $\frac{1}{18}$ this by gradually reducing the depth of minima in the energy function, thus facilitating the transition  $\eta$ across energy barriers over time. As a result, shorter dominance durations are less frequent, aligning  $\bullet$ with the skewed Gaussian distribution noted in the primary literature and verified by our analysis in  $\frac{1}{10}$ Section [4,](#page-5-0) Subsection [4.4.](#page-9-0) Furthermore, comparing dominance durations across different adaptation <sup>82</sup> levels revealed that the optimal degree of adaptation is when it is weak—having enough effect to <sup>83</sup> produce a skewed Gaussian distribution, yet not so strong as to create a less variable distribution or  $\frac{84}{100}$ destroy the energy minima.  $\frac{1}{35}$  and  $\frac{1}{35}$  and

In summary, the energy equation structures and components discussed above are essential for constructing an accurate attractor network model of perceptual bistability and have been integrated  $\frac{87}{87}$ into the network dynamics as follows:  $\frac{88}{100}$ 

$$
\tau \frac{d}{dt} r_A = -r_A + f[\alpha r_A - \beta r_B + g_A - (g_A + g_B)r_A + n_A]
$$
 (2)

$$
\tau \frac{\mathrm{d}}{\mathrm{d}t} r_B = -r_B + f \left[ \alpha r_B - \beta r_A + g_B - (g_A + g_B) r_B + n_B \right] \tag{3}
$$

Here,  $g_A$  and  $g_B$  represent the input strengths,  $r_A$  and  $r_B$  are the firing rates of neuronal populations,  $\bullet$  $n_A$  and  $n_B$  denote noise with zero mean and deviation  $\sigma$ , and f is a function that calculates the firing  $\sim$ rate of a population based on its input. Further discussion of this equation and its implementation  $\frac{91}{100}$ in our project can be found in the Methods section (Section [3\)](#page-3-0).

Using both rate-based and cell-based simulation networks constructed with these equations, Moreno-Bote and colleagues demonstrate that the attractor model aligns closely with numerous experimental  $\frac{94}{94}$ findings. Specifically, examining the input noise averages before and after each alternation in the ss simulations revealed patterns similar to those Lankheet observed in binocular rivalry experiments so [\[6\]](#page-11-5). In both studies, researchers noted a simultaneous increase in noise in the population switch- $\frac{97}{20}$ ing from suppressed to dominant, and a decrease in the population transitioning from dominant to set suppressed. These findings were also replicated in our simulations (Section [4,](#page-5-0) Subsection [4.3\)](#page-8-0). Fur-  $\,$   $_{99}$ thermore, the authors discuss recent studies that offer significant experimental evidence that noise, 100 rather than adaptation, is the primary driver of alternation in perceptual bistability  $[4, 7, 8]$  $[4, 7, 8]$  $[4, 7, 8]$  $[4, 7, 8]$  $[4, 7, 8]$ .

The attractor network model not only reflects prior research on perceptual bistability but also offers 102 novel insights and predictions that may inform future studies. First, in their spiking cell-based neural network, the activity of the dominant population during rivalry did not increase with heightened  $_{104}$ input stimulation, contrary to expectations based on non-rivalrous conditions where neuronal activity typically correlates with input strength. Second, both the dominant and suppressed populations  $_{106}$ exhibited lower activity rates compared to scenarios without rivalrous perception. These intriguing 107 findings from the simulation could be further explored and validated experimentally using functional  $_{108}$ magnetic resonance imaging (fMRI) or electrophysiology. 109

In conclusion, "Noise-Induced Alternations in an Attractor Network Model of Perceptual Bistabil- <sup>110</sup> ity" by Moreno-Bote et al. presents a new framework for understanding the neural mechanisms 111 behind perceptual bistability by positioning noise, rather than adaptation, as the primary driver of 112 alternation in their model. The model incorporates novel structural elements in the energy function 113 and additional components in the differential equations, such as recurrent excitatory connections 114 and inhibitory populations, to ensure that the model's behavior aligns with findings from previ- 115 ous experiments. Additionally, it acknowledges the role of weak adaptation in producing a desired <sup>116</sup> distribution of dominance durations. Using this model architecture, the authors developed both fir- <sup>117</sup> ing rate mean-field and spiking cell-based models to simulate the dynamics, effectively capturing 118 experimental observations and offering predictions on previously undiscovered aspects of percep- <sup>119</sup> tual bistability. Overall, this paper provides a significant foundation for our research project, which 120 reconstructed and explored their proposed dynamical model. <sup>121</sup>

## <span id="page-3-0"></span>**3. Methods** 122

Differential Equations Moreno-Bote et al.'s work features a set of differential equations that 123 regulate model variables, thoroughly discussed in their methodology section. One such equation, <sup>124</sup> previously introduced in our literature review (Section [2\)](#page-0-0), describes the rate of change in firing rate <sup>125</sup> for each neuronal population, factoring in feedforward excitatory connections, the firing rate of  $_{126}$ the competing population, input stimulus strength, and noise. In our project, we incorporated this 127 equation to develop our rate-based model while ensuring the inclusion of an adaptation variable. A 128 notable departure from the primary literature is our focus on modeling a pair of neurons within a 129 circuit rather than larger populations. Additionally, for a more efficient design, we combined the <sup>130</sup> excitatory input terms into a single expression within the equation and removed the term  $-(g_A + 1)$  $(g_B) r_A$ .

$$
\tau \frac{ds_1}{dt}(t) = -s_1(t) + f(-ws_2(t) - ga_1(t) + b(1 + n_1(t))) \tag{4}
$$

$$
\tau \frac{ds_2}{dt}(t) = -s_2(t) + f(-ws_1(t) - ga_2(t) + b(1 + n_2(t)))
$$
\n(5)

<span id="page-3-1"></span>

#### **Table 1.** Model Parameters and Variables

This ordinary differential equation computes the synaptic activity variables, also known as firing <sup>133</sup> rates. The notations used in this equation are detailed in Table [1.](#page-3-1) The equation includes three pri- <sup>134</sup> mary inputs to the sigmoid firing rate function. Firstly,  $-ws_2(t)$  represents the firing rate of the competing neuron at a given time, scaled by a synaptic inhibitory weight, serving as a cross-inhibition <sup>136</sup> mechanism for winner-takes-all dynamics. Secondly,  $-ga_1(t)$  accounts for the adaptation effect, with  $137$  $a_1(t)$  modulated by the parameter g. The adaptation variables  $a_1(t)$  and  $a_2(t)$  are further delineated by  $\frac{138}{138}$ their respective differential equations. Lastly,  $b(1 + n_1(t))$  denotes the excitatory input, functionally  $139$ summarizing the original equation's terms  $\alpha r_A$ ,  $g_A$ , and  $n_A$ . Here, the feedforward input strength  $140$ parameter  $b$  is modulated by random noise. Collectively, these three inputs feed into the firing rate  $141$ function,  $f(x) = \frac{e^x}{1+t}$  $\frac{e^{x}}{1+e^{x}}$ , dictating the computation of neuronal firing rates in our simulation.

Additionally, the adaptation and noise variables are each regulated by their own differential equations. The adaptation equation is structured such that its effect is inhibitory and proportional to the 144 neuron's current firing rate, modulated by a time constant  $(\tau_a)$  significantly slower than the time 145  $\frac{1}{46}$  constant for the synaptic activity variables.

$$
\tau_a \frac{da_1}{dt}(t) = -a_1(t) + f(-ws_2(t) - ga_1(t) + b(1 + n_1(t))) \tag{6}
$$

$$
\tau_a \frac{da_2}{dt}(t) = -a_2(t) + f(-ws_1(t) - ga_2(t) + b(1 + n_2(t))) \tag{7}
$$

Conversely, the noise is derived from a Gaussian distribution and then refined through a low-pass  $_{147}$ filter to emulate the characteristics of noise typically observed in biological systems. <sup>148</sup>

$$
\tau_n \frac{\mathrm{d} \mathbf{n}_1}{\mathrm{d} t}(t) = -n_1(t) + \sigma \sqrt{2\tau_n} \xi_1 \tag{8}
$$

$$
\tau_n \frac{\mathrm{dn}_2}{\mathrm{d}t}(t) = -n_2(t) + \sigma \sqrt{2\tau_n} \xi_2 \tag{9}
$$

Each of these equations was implemented in MATLAB and numerically solved to simulate a circuit <sup>149</sup> of neurons in perceptual bistability.

Euler Method Our model's differential equations, defining synaptic activity, adaptation, and noise, <sup>151</sup> necessitated numerical solutions to compute the value of these variables at each time step. We em- <sup>152</sup> ployed the Euler Method for solving ordinary differential equations (ODEs). Beginning with speci- <sup>153</sup> fied initial conditions, this method iteratively approximates the solution at subsequent time points 154 by advancing along the curve's tangent. The general formula is expressed as: <sup>155</sup>

$$
y_{n+1} = y_n + \Delta t \times \left. \frac{dy}{dt} \right|_{t=t_n}
$$
 (10)

For an accurate approximation using the Euler Method, a sufficiently small time step,  $\Delta t$ , is essential; 156 our model employed a step size of 0.1 ms, thereby updating variable values every 0.1 milliseconds. <sup>157</sup>

Switch-Triggered Average (STA) The average behavior of the input stimulus around the time it 158 triggers a state switch provides valuable insight into the patterns of stimuli that affect alternation. 159 The Switch-Triggered Average (STA) computation method collects this mean input stimulus 100 mil- <sup>160</sup> liseconds before and after each state switch. In our study, we utilized the cross-correlation function 161 in MATLAB to compute the STA efficiently. The first input for our cross-correlation is a binary vec- <sup>162</sup> tor where each element corresponds to a time point and indicates whether a state switch occurred. 163 In this vector, a value of 1 signifies a transition at that specific time point, while a 0 indicates no 164 transition. The second input is the input stimulus itself, represented as  $b(1 + n(t))$  in our model, 165 with each element reflecting the exact stimulus value at corresponding time points. Employing a 166 technique similar to calculating spike-triggered averages in neural spike train studies, we computed 167 cross-correlation such that slicing the resultant vector at the desired time lags and dividing by the <sup>168</sup> total number of transitions yields the STA directly. 169

$$
STA(\tau) = \frac{1}{N} \sum_{i=1}^{N} v(t_i - \tau) = \frac{1}{N} \sum_{t} w(t) v(t - \tau) = \frac{1}{N} C_{wv}(-\tau)
$$
(11)

In this equation, N represents the total number of spikes,  $w$  is the binary vector denoting transitions, v is the stimulus vector, t denotes the time points, and  $\tau$  signifies the lag for which the  $\tau_{171}$ cross-correlation is calculated. This method allows us to observe the characteristics of the stimulus 172 that either prompts a neuron to become dominant or causes it to become suppressed.

## <span id="page-5-0"></span>**4. Results**  $174$

The primary goal of our project is to reconstruct the rate-based network structure described in the 175 primary literature and to conduct an in-depth analysis of the roles and effects of various components 176 on model behavior. Initially, we will eliminate the role of noise, allowing the model's alternations  $\frac{177}{17}$ to be solely driven by adaptation. Using this oscillator model, we will explore different factors that  $_{178}$ influence the period of oscillation, which directly reflects the model's alternation rate. Subsequently, <sup>179</sup> we will evaluate a model driven entirely by noise to examine how the noise variance impacts the 180 model behavior, specifically the distribution of time intervals between adjacent alternations. Ad- <sup>181</sup> ditionally, we will employ the switch-triggered average (STA) method, as proposed in the primary 182 literature, to further investigate the impact of noise on alternations. Ultimately, using the model 183 that integrates both noise and adaptation—identified as most effective by Moreno-Bote et al.—we <sup>184</sup> will compare how the distribution of time intervals differs from the model without adaptation and 185 assess how noise variance influences this distribution.

#### <span id="page-5-1"></span>**4.1 Modeling I** and the set of the

Our initial investigation entailed removing the noise effect in our model to replicate the originally 188 proposed oscillator model of perceptual bistability. We achieved this by setting the noise standard <sup>189</sup> deviation parameter, σ, to zero. Consequently, adaptation effects and cross-inhibition mechanisms <sup>190</sup> drove the competition in synaptic activity between neurons during our 4,000-millisecond simulation. 191 The firing rates, denoted as  $s_1$  and  $s_2$ , are plotted against time in Figure [1.](#page-5-2) As expected, this setup  $192$ resulted in a periodic alternation between the firing rates of neurons 1 and 2, where each neuron <sup>193</sup> maintained a consistent period of dominance before yielding control to the other. <sup>194</sup>

<span id="page-5-2"></span>

**Figure 1.** Synaptic Activity in an Adaptation-Driven Model

We then focused on analyzing how parameters such as the strength of adaptation effect and the input 195 drive influence the oscillation period in this model. The parameter g, which scales the adaptation  $_{196}$ variables  $a_1$  and  $a_2$ , determines the extent of adaptation's impact on the neuron's firing rate. Since  $\frac{197}{197}$ adaptation—a slow force like synaptic depression—counteracts the firing efficacy of the dominant 198 neuron over time, we anticipated that a stronger adaptation effect would accelerate the reduction <sup>199</sup> in activity, resulting in frequent alternations and shorter oscillation periods. This hypothesis was 200 tested by varying g and observing the oscillation period during the bistable competition, as shown in  $_{201}$ Figure [2.](#page-6-1) Consistent with our expectations, the period of oscillation decreased as the strength of the  $_{202}$ adaptation effect rose from 10 to 30. Moreover, as we adjusted g up to 50, the mean oscillation period  $_{203}$ demonstrated a decay resembling an inverse power law. This outcome confirms that the strength <sup>204</sup> of the adaptation effect inversely affects the oscillation period in the adaptation-driven model of <sup>205</sup> perceptual bistability. 206

Next, we hypothesized that the oscillator model's strength of the input drive, denoted as b in our  $_{207}$ model and comparable to stimulus strength–that is, image contrast–in binocular rivalry experi- <sup>208</sup> ments, would have a positive effect on the oscillation period. Since feedforward input enables high- <sup>209</sup> activity neurons to sustain dominance, we anticipated that it would extend the oscillation period, <sup>210</sup> countering the adaptation effect. The results presented in Figure [3](#page-6-2) confirm that the oscillation period indeed lengthens as b is increased. However, a fundamental characteristic of perceptual bista- $_{212}$ bility is that the alternation period shortens with stronger stimuli. This discrepancy underscores 213 the limitations of oscillator models to fully replicate the behavioral dynamics observed in perceptual <sub>214</sub> **bistability.** 215

<span id="page-6-1"></span>

**Figure 2.** Dependence of Oscillation Period on the Strength of the Adaptation Effect

<span id="page-6-2"></span>

<span id="page-6-0"></span>**Figure 3.** Dependence of Oscillation Period on the Strength of the Feedforward Input

### **4.2 Modeling II** 216

This time, we removed the influence of adaptation to assess an attractor model's behavior, where  $217$ alternation is solely due to noise. Unlike the periodic alternations of the purely adaptation-driven <sup>218</sup> model discussed in Section [4,](#page-5-0) Subsection [4.1,](#page-5-1) noise-driven model yields irregular fluctuations be- <sup>219</sup> tween the two neurons' firing rates, demonstrating stochastic alternations as shown in Figure [4.](#page-7-0) 220 This matches the highly stochastic patterns observed in binocular rivalry experiments [\[9\]](#page-11-8). Using  $_{221}$ the noise-driven model, we further analyzed the distribution pattern of the temporal intervals be-  $_{222}$ tween successive alternations as well as their average.  $223$ 

<span id="page-7-0"></span>

<span id="page-7-1"></span>**Figure 5.** Distribution of Time Intervals Between Adjacent Switches in a Model without Adaptation

Also known as dominance duration distribution, the distribution of temporal intervals between alternation events serves as a critical measure of a model's biological fidelity. Experimental stud- <sup>225</sup> ies have shown that this distribution typically follows a skewed Gaussian, a finding successfully  $_{226}$ replicated by Moreno-Bote and colleagues in their noise-driven model with the inclusion of weak <sub>227</sub> adaptation  $[2, 3]$  $[2, 3]$  $[2, 3]$ . In our study, we recorded the temporal intervals between alternations during a  $228$ 40,000-millisecond simulation and found that, without the influence of adaptation, the distribution <sup>229</sup> tends to an exponential form, as depicted in Figure [5.](#page-7-1) <sup>230</sup>

Furthermore, we examined the impact of noise standard deviation, denoted by the parameter  $\sigma$ ,  $\sigma$ <sub>231</sub> on the average duration of a single neuron dominating the perception. With our noise variables <sub>232</sub> normally distributed around a mean of zero, a higher  $\sigma$  introduces greater variability in  $n_1$  and  $n_2$ , 233 increasing the likelihood of randomly surpassing the energy barrier between two states. Conse- <sup>234</sup> quently, we hypothesized that a larger  $\sigma$  would lead to shorter average temporal intervals between  $\frac{235}{2}$ alternations. Our results, as depicted in Figure [5,](#page-7-1) confirmed this hypothesis. However, while stan- <sup>236</sup> dard deviation values below 5 noticeably conformed to this trend, the differences in mean temporal <sub>237</sub> intervals became less pronounced as  $\sigma$  increased beyond 5. This suggests a diminishing impact of  $\sigma$  238 noise standard deviation on facilitating state alternations past a certain threshold. 239 In summary, a model that relies solely on noise to transition between two bistable states produces <sub>240</sub> irregular alternation patterns, in contrast to those generated by an adaptation-driven model. This <sub>241</sub> discrepancy opened an avenue to analyze how temporal intervals between alternations are dis- <sup>242</sup> tributed—an analysis unfeasible in oscillator models with their inherently periodic intervals. As <sup>243</sup> anticipated, without the influence of adaptation, the dominance durations in our model followed an <sup>244</sup> exponential distribution, deviating from biological reality. Additionally, we observed that increased <sup>245</sup> noise variability reduced the average dominance durations by facilitating the transition over the <sup>246</sup> energy barrier. 247

### <span id="page-8-0"></span>**4.3** Analysis I  $_{248}$

Moreno-Bote and colleagues investigate noise patterns immediately before and after each state transition to understand how noise facilitates the perceptual shift from one neuronal population to an- <sup>250</sup> other. They describe this analysis as the switch-triggered average (STA). The findings suggest that <sup>251</sup> alternation typically occurs when there is a sharp increase in noise to the previously suppressed <sub>252</sub> population concurrent with a sharp decrease in noise to the dominating population. We replicated 253 this analysis in our entirely noise-driven model to verify these findings.

It is important to highlight that our model simplifies the excitatory inputs to the neuron using the 255 term  $b(1 + n(t))$ , in contrast to the model described in the primary literature. This term encompasses  $256$ feedforward excitation, input stimulus, and noise. Our objective was to investigate how these ex- <sup>257</sup> citatory inputs influence state transitions. We simulated neuronal activity for 40,000 milliseconds, <sup>258</sup> capturing the value of  $b(1 + n(t))$  100 milliseconds before and after each perceptual state transition. Then, this data was analyzed using STA computation methods to assess the overall trends in excita- <sup>260</sup> tory inputs. A detailed discussion of the STA calculation, employing cross-correlation, is provided <sup>261</sup> in the Methods section [3.](#page-3-0)

<span id="page-8-1"></span>

**Figure 6.** Switch-Triggered Average of the Stimulus

The results are presented in Figure [6.](#page-8-1) The left plot shows the average excitatory inputs to neurons  $1_{263}$ and 2 during in-to-out transitions, where neuron 1 is displaced by the increasing synaptic activities  $_{264}$ of neuron 2. The right plot displays the excitatory inputs during the reverse transitions. In both <sup>265</sup> cases, the neuron gaining dominance undergoes a sudden increase in excitatory input arising from <sup>266</sup> noise fluctuations. Concurrently, a notable decrease in the STA indicates a sharp decline in input to  $_{267}$ the neuron losing dominance. Therefore, our model demonstrates that perceptual alternation occurs <sub>268</sub> when random noise fluctuations produce simultaneous increased and decreased input to previously <sub>269</sub> suppressed and dominant neurons, aligning with findings from Moreno-Bote et al. and experimental  $_{270}$ results by Lankheet [\[6\]](#page-11-5). 271

#### <span id="page-9-1"></span><span id="page-9-0"></span>**4.4 Analysis II** 272



<span id="page-9-2"></span>**Figure 7.** Distribution of Time Intervals Between Adjacent Switches in a Model with Adaptation and Noise



**Figure 8.** Comparison of Time Interval Distributions in Models With and Without Adaptation

We further refined our model to incorporate both adaptation and noise. As discussed in the primary 273 literature, incorporating adaptation effects enabled our model to generate dominance duration dis- <sup>274</sup> tributions that align more closely with a skewed Gaussian (Figure [7\)](#page-9-1), rather than the exponential 275 distribution observed in Section [4,](#page-5-0) Subsection [4.2.](#page-6-0) The mechanism of slow adaptation adds a time- <sup>276</sup> dependent persistence to dominance states, gradually increasing the likelihood of transitions as time  $277$ progresses. Adaptation moderates the depth of the energy function's minima for the dominant pop- <sup>278</sup> ulation just enough to facilitate transitions without eliminating the energy barrier, thus achieving  $275$ a distribution of dominance durations that conforms to experimental data. This contrast is clearly <sub>280</sub> depicted in Figure [8,](#page-9-2) which compares temporal interval distributions from models with and without <sub>281</sub>  $\frac{1}{282}$  adaptation.

An interesting research question is how noise standard deviation,  $\sigma$ , influences the distribution of  $\sigma$  283 dominance durations in the presence of adaptation. We investigated this by plotting the temporal <sup>284</sup> interval distributions at four different  $\sigma$  values ranging from 1 to 20, as shown in Figure [7.](#page-9-1) Notably,  $_{285}$ the skewed Gaussian distribution becomes more pronounced with higher σ values. At very low σ,  $286$ such as 1, the dominance durations are heavily skewed towards shorter intervals, resembling an 287 exponential distribution more than a skewed Gaussian. This likely occurs because low  $\sigma$  values  $\frac{288}{288}$ minimize noise impact, allowing adaptation to take over the alternation process. Conversely,  $\sigma$  289 values above 5 produce a skewed Gaussian distribution, which aligns with expectations for a model that incorporates both adaptation and noise and is consistent with experimental data.

### 5. Discussion 2022

By reconstructing a simplified version of the originally proposed attractor model, we examined the 293 functional impacts of various model components on alternation dynamics. Initially, we developed <sup>294</sup> an oscillator model of perceptual bistability, confirming our hypothesis that stronger adaptation 295 effects shorten the oscillation period (Figure [2\)](#page-6-1). Conversely, increased strength of the feedforward <sup>296</sup> input extended the oscillation period (Figure [3\)](#page-6-2), highlighting the limitations of oscillator models in  $_{297}$ accurately representing biological systems. We then explored the model's noise-driven counterpart, 298 demonstrating that dominance duration distributions form an exponential function in the absence of <sup>299</sup> adaptation (Figure [5\)](#page-7-1). Our findings also revealed that larger noise standard deviations significantly 300 reduce average dominance durations, though their impact stabilizes beyond a certain threshold. 301 Further, we replicated the switch-triggered average analysis from the primary literature to assess <sub>302</sub> how noise triggers state transitions in our model (Figure [6\)](#page-8-1). Lastly, using an ideal model structure  $\frac{303}{200}$ that includes both noise and adaptation, we found that only with a sufficiently high noise standard  $\frac{304}{2}$ deviation does the model produce the desired skewed Gaussian distribution of dominance durations 305 (Figure [7\)](#page-9-1). Overall, our project underscores the crucial roles of noise, adaptation, and parameter <sup>306</sup> selection in crafting a model that accurately reflects the dynamics of perceptual bistability.

Nonetheless, it is crucial to acknowledge the inherent limitations of our study due to the simplifica- 308 tions introduced when adapting the model from the primary literature. A significant simplification <sup>309</sup> was combining all excitatory inputs to the neurons—such as recurrent excitatory connections, stimulus input, and noise—into a single term in our equation. While this approach facilitated a more 311 straightforward analysis of excitatory input, it obscured the distinctions between crucial elements <sup>312</sup> of the original model. For example, increasing the parameter  $b(1 + n(t))$  in Section [4,](#page-5-0) Subsection [4.1](#page-5-1)  $\frac{1}{313}$ could be interpreted as either enhancing the strength of feedforward input or the stimulus intensity, <sup>314</sup> which differ as internal versus external excitation sources. Future studies should consider separating 315 these sources to allow a more detailed analysis of their impacts.  $316$ 

Furthermore, a critical behavioral component from the original attractor network model was omitted in our simplified version. In the primary literature, Levelt's Proposition IV was implemented by  $\frac{318}{2}$ incorporating a local inhibitory subpopulation, represented by the term  $-(g_A + g_B)r_A$ . This configuration allowed for an increased total stimulus to decrease the dominance durations of both neurons. 320 However, unlike other inhibitory mechanisms such as cross-inhibition from rival populations or <sup>321</sup> time-dependent adaptation, this factor was excluded in our project model. Although not central to  $\frac{322}{2}$ our research focus, its absence raises concerns about the accuracy of our analysis, as this component  $\frac{323}{2}$ could have influenced the dynamics observed in our study. For instance, this inhibitory factor, simi- $_{324}$ 

lar to adaptation in that it is proportional to the neuron's firing rate but acts more rapidly, could have  $\frac{325}{2}$ led to significantly shorter dominance durations. This highlights the ongoing challenge of balancing  $326$ simplicity and comprehensiveness in modeling to adequately reflect biological complexity.

Moving forward, it will be helpful to progressively enhance our model's complexity in a controlled <sub>328</sub> manner. By systematically reintroducing the elements we previously omitted, we can better under-  $\frac{329}{2}$ stand their individual and combined effects on the model's behavior. This approach will not only <sup>330</sup> overcome the current study's limitations but also enrich our insight into the underlying dynamics 331 of perceptual bistability. Additionally, recreating the cell-based network described in the original <sup>332</sup> research and exploring how various parameters influence its dynamics could offer valuable compar-  $\frac{333}{2}$ isons to our rate-based findings, broadening the scope of our analysis.  $\frac{334}{2}$ 

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## References 341

- <span id="page-11-8"></span><span id="page-11-7"></span><span id="page-11-6"></span><span id="page-11-5"></span><span id="page-11-4"></span><span id="page-11-3"></span><span id="page-11-2"></span><span id="page-11-1"></span><span id="page-11-0"></span>[1] Ruben Moreno-Bote, John Rinzel, and Nava Rubin. "Noise-induced alternations in an attractor <sup>342</sup> network model of perceptual bistability". In: *Journal of Neurophysiology* 98.3 (2007), pp. 1125– <sub>343</sub>  $1139.$   $344$ [2] Willem J. M. Levelt. "On Binocular Rivalry". PhD dissertation. Van Gorcum Assen, 1965. <sup>345</sup> [3] Sidney R. Lehky. "Binocular rivalry is not chaotic". In: Proceedings of the Royal Society of London. 346 Series B: Biological Sciences 259.1354 (1995), pp. 71–76. [4] Yee-Joon Kim, Marcia Grabowecky, and Satoru Suzuki. "Stochastic Resonance in Binocular <sup>348</sup> Rivalry". In: *Vision Research* 46.3 (2006), pp. 392–406. [5] Hendrik Anthony Kramers. "Brownian Motion in a Field of Force and the Diffusion Model of <sup>350</sup> Chemical Reactions". In: *Physica* 7.4 (1940), pp. 284–304.  $351$ [6] Martin J. M. Lankheet. "Unraveling adaptation and mutual inhibition in perceptual rivalry". In: <sup>352</sup>  $Journal of Vision 6.4 (2006), pp. 1–1.$ [7] Jan W. Brascamp, Raymond Van Ee, Andre J. Noest, Richard HAH Jacobs, and Albert V. van den <sup>354</sup> Berg. "The time course of binocular rivalry reveals a fundamental role of noise". In: *Journal of* 355  $Vision 6.11 (2006), pp. 8–8.$   $356$ [8] Nava Rubin and Jean-Michel Hupé. "Dynamics of Perceptual Bistability: Plaids and Binocular 357 Rivalry Compared". In: The MIT Press. Ed. by David Alais and Randolph Blake. MIT Press, 2004. 358 [9] R. Randolph Blake, Robert Fox, and Curtis McIntyre. "Stochastic properties of stabilized-image <sup>359</sup> binocular rivalry alternations". In: Journal of Experimental Psychology 88.3 (1971), p. 327.
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