

# **Binocular Rivalry**

*This is Chapter 6 and the Bibliography  
from the doctoral dissertation:*

**Neural Network Models for  
Color and Brightness Perception  
and  
Binocular Rivalry**

*by*

**Karl Frederick Arrington, Ph.D.**

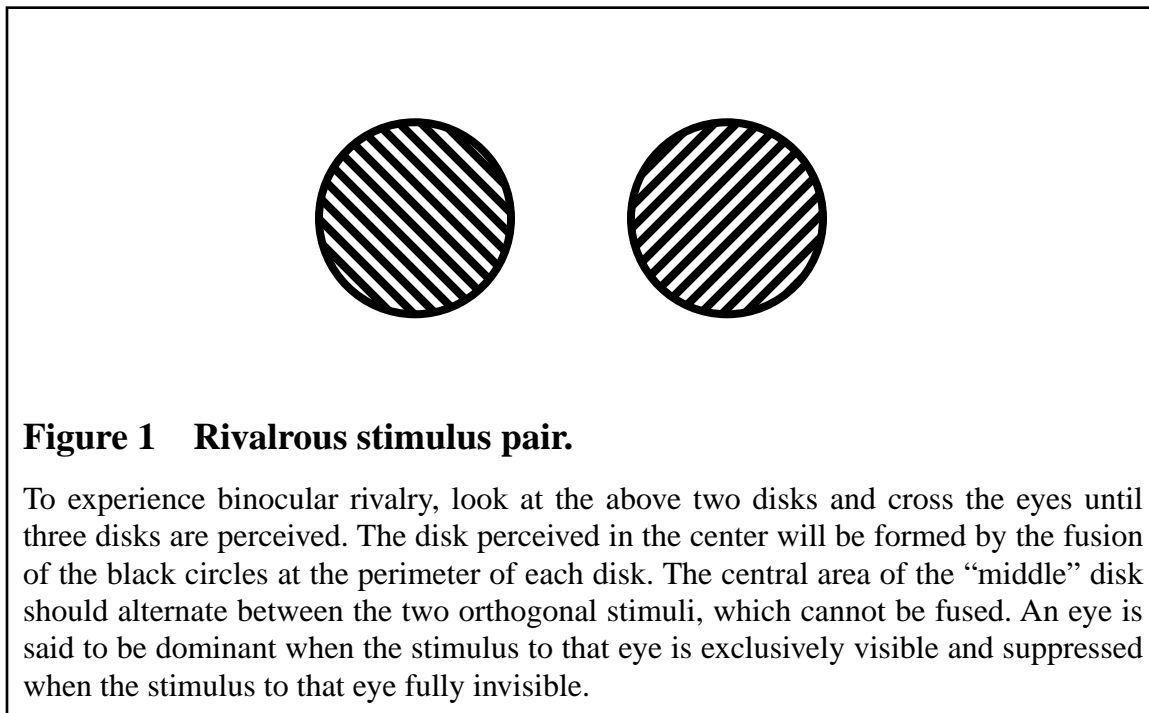
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## CHAPTER 6      Binocular Rivalry.

### 6.1 Introduction.

Binocular rivalry is the perceptual alternation that occurs when the stimuli to the two eyes are sufficiently different that they cannot be fused into a single percept. A typical dichoptic stimulus pair consists of orthogonal sine-wave or square-wave gratings, as in Figure 1. An eye is said to be *dominant* when the stimulus to that eye is exclusively visible and *suppressed* when the stimulus to that eye is fully invisible. Recently binocular rivalry has



gained attention as a tool for psychoanatomy, that is, the inference of neural circuitry from psychophysical experimentation (Wolfe, 1986a).

This chapter examines a particular type of reciprocal inhibition oscillator (RIO) based on the gated pacemaker model (Carpenter and Grossberg, 1983), which is described in Section 6.6, and evaluates the usefulness of this model in predicting the temporal dynamics of binocular rivalry. The gated pacemaker has previously shown great success in modeling circadian rhythms (Carpenter and Grossberg, 1983; Carpenter and Grossberg, 1984; Carpenter and Grossberg, 1985a), after-effects and motivational interactions (Carpenter and Grossberg, 1985b). Grossberg (1987b) has also used the model to qualitatively explain the types of data that are quantitatively simulated here. In particular, this chapter studies the behavior of the model under the binocular rivalry stimulus paradigm that was used by Mueller and Blake (1989), which is described in Section 6.8.

## 6.2 History of binocular rivalry.

Binocular rivalry was apparently first described by Dutour in the late 18th century. He used the phenomena as an argument for *suppression theory*, i.e., the thesis that every point in the visual field is only perceived with one eye at a time<sup>1</sup>. As strange as suppression theory may seem, it has retained a loyal, albeit small, following up to the present time. Recently, suppression theory has been revived by Wolfe (1986a) who proposed a four channel model of binocular vision in which *permanent rivalry* occurs inevitably whether the stimuli to the two eyes are the same (dioptic) or rivalrous (dichoptic).

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<sup>1</sup> Levelt (1965), p.1, cites Dutour (1780), as the first description.

No significant work on Binocular rivalry is found for the next 60 years after Dutoir's initial description. It was not until systematic study by Wheatstone (1838), using the then-new stereoscope<sup>2</sup>, that real scientific progress was made in understanding binocular rivalry.

Helmholtz believed that the cause of rivalry was a shift of attention. The *attentional theory* has been persuasively vitiated by Levelt's explanation of how shifts in attention can cause shifts in the eyes movements, such that retinal stimulation occurs in one eye, but not in the other eye<sup>3</sup>. This is easily understood in the case of orthogonal gratings; when the eye move perpendicular to the grating in one eye, so as to produce movement of the bars across the retina, the movement will be parallel to the bars seen by the other eye, so as to produce no additional retinal stimulation. The idea that attenuation affects rivalry has never been completely settled and is still favored by some<sup>4</sup>, though these effects are usually considered to be negligible.

### **6.3 History of reciprocal mechanisms.**

There is a rich history about the idea of reciprocal inhibition and reciprocal inhibition oscillators. It has been understood for centuries that opponent motor nerves innervate the antagonistic muscles for arms and legs, and that for one muscle to do its work by contracting the antagonistic muscle must be allowed to relax. As early as 1662, in his work *De Homine*, Descartes described the reciprocal action of the two muscles in effecting lat-

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<sup>2</sup>. The stereoscope is usually attributed to Wheatstone, but apparently a similar instrument was built by Helioth four years earlier; Kaufman (1974) refers to Dudley (1951) for this historical issue.

<sup>3</sup>. Levelt (1965), p. 6

<sup>4</sup>. As a contemporary example, Lehky (1988), refers to Walker (1978) as favoring an attenuation theory of rivalry.

eral movements of the eye<sup>5</sup>. More sophisticated experiments on inhibition have been carried out by Sherrington (1906), who advanced the idea that reciprocal inhibition can be an important mechanism for rapidly re-establishing a baseline response level.

The development of understanding the physiological mechanisms of reciprocal inhibition largely followed the development of understanding the nature of inhibition. As recently as 100 years ago the “neutral theory” of inhibition was supported. This view made an analogy to physical interference, as with light or sound waves, such that neural transmissions cancel, or neutralize, one another (Sherrington, 1906, p.195). The neutral theory was criticized because it did not account for rebound effects. It gave way to theories involving secondary mechanisms that operated on different time scales, such as catabolism and anabolism of trophic factors. These views take the actual nutritive activity of the cell as the field in which inhibition operates.

“We can imagine that a material continuously produced by a tissue, and yielding on decomposition the particular activity which is inhibited, may by an inhibition be checked in its decomposition, and accumulate, so that at the end of the period of inhibition the tissue contains more of the particular decomposable material than before. This molecular rearrangement would diminish activity for the time being, but lead to increase of activity afterwards. There would ensure a rebound effect. This is, as is well known since Gaskell’s researches, what actually happens in the pure vagus action on the heart. .... Hence Gaskell expressively speaks of the vagus as the ‘trophic nerve of the heart’.”

Sherrington, 1906, p. 196-197

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<sup>5</sup>. see von Békésy (1967), p. 22-25, for a brief history of inhibition, and Sherrington (1906), p195-206, for a historical perspective on the nature of inhibition and interference.

Macdonald hypothesized a different type of slow process that involves the effect of inorganic salts on protein, he considered a stimulus as a substance causing an approach to the condition of coagulation (Sherrington, 1906, p. 198) that manifests itself as fatigue.

The first mechanical reciprocal inhibition oscillator (RIO) mechanism for self sustaining rhythm generation is attributed to Brown (1911); it was called the half-center model because he suggested that the spinal cord contains one network for activating flexors and another for the extensors, i.e., two half centers. In general a half-center model is the same as an RIO, though some would prefer to have the former name reserved for Brown's original model (Grillner, 1985). A number of variations and implementations of the reciprocal inhibition oscillator have been studied as models for predicting bistable perceptual phenomena, for example, figure-ground reversals and Necker cube depth reversals (Attneave, 1971). McDougall (1906) may have been the first to account for the alternations of binocular rivalry with a reciprocal inhibition mechanism. Different names are employed to distinguish variations, implementations and applications of RIOs, for example "multivibrator flip-flop circuit" by Attneave (1971), "astable multivibrator circuit" by Lehky (1988), "gated pacemaker model" by Carpenter and Grossberg (1983), and as noted earlier "half-center model" by Brown (1911).

## **6.4 Temporal behavior: Oscillation frequency & duty cycle.**

The two dynamical behaviors of primary interest in an oscillator model of binocular rivalry are: oscillation frequency and oscillation duty cycle. The *full cycle duration* or *period* is measured as the average length of time it takes to complete one alternation, that is, the time it takes for each eye to complete both one dominant and one suppressed phase,

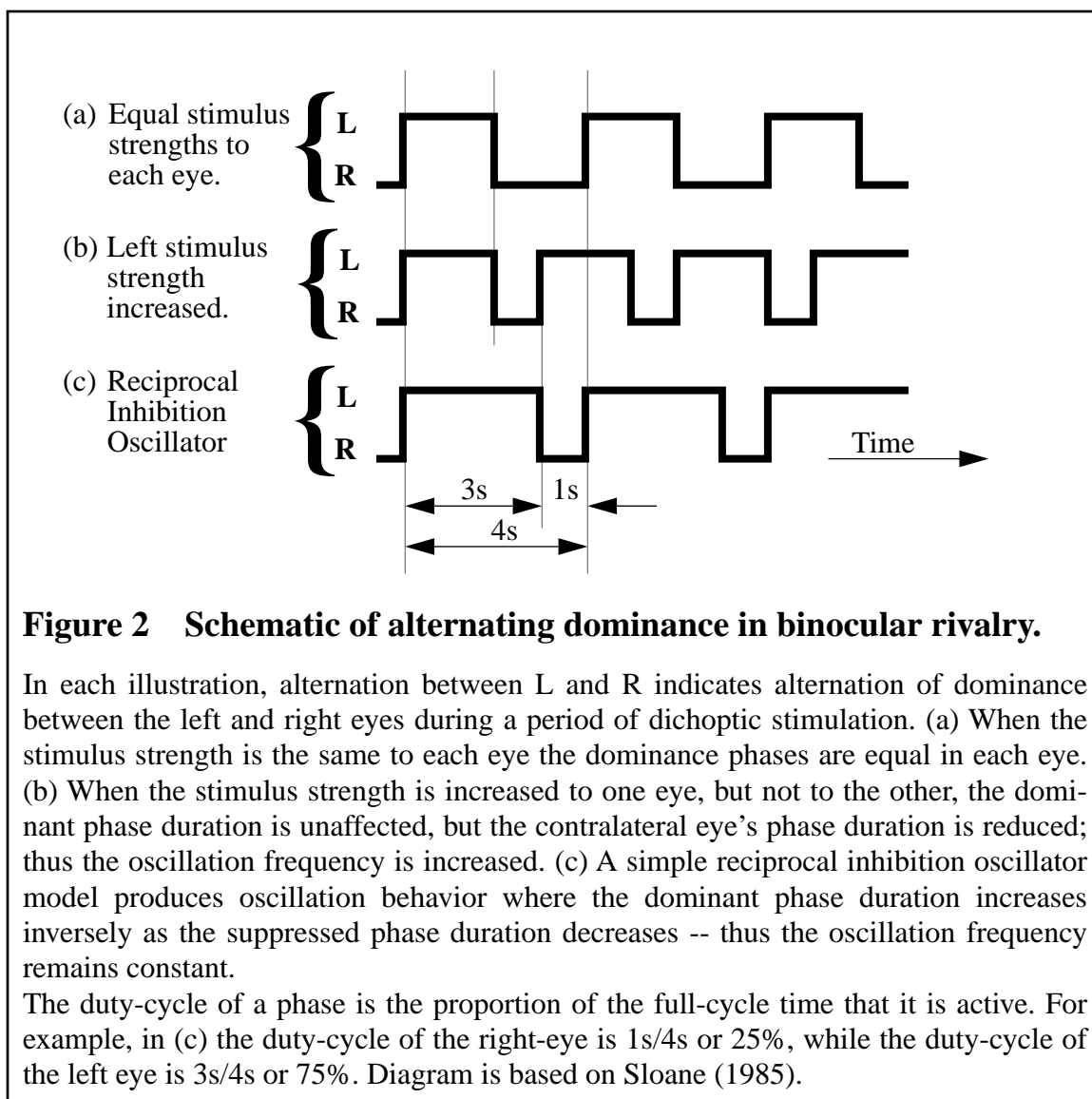
e.g. 1/2 second per cycle. The *oscillation frequency* is the reciprocal of the full cycle duration time, e.g. 2 cycles per second. *Duty cycle* is the ratio of the average<sup>6</sup> amount of time spent in each of the two states. When the stimulus intensity is the same to each neuron, the duty cycle is 50%, which means that each cell is active 50% of the time, on average. However, as will be shown later, when the stimulus intensity is different, one may be dominant a larger percentage of the time than the other one is dominant; e.g. left eye dominant 70% of the full-cycle time and right eye dominant 30% of the time. Figure 2 illustrates how duty-cycle is calculated.

The degree to which a stimulus can effect binocular rivalry is a measure of the salience that stimulus has to the visual system. Contrast is one of the most salient factors and probably the major determinant of stimulus strength (Alexander and Bricker, 1952; Levelt, 1965), changes in luminance have weaker effects and the presence of sharp contours is significant (Alexander and Bricker, 1952; Levelt, 1965; Lehky, 1988, p. 216). With weak stimuli to both eyes the *depth of suppression* is less and the perception of a mixture of the two stimuli, called *incomplete suppression*, will occur more frequently (Hollins, 1980). Also, the depth of suppression will diminish as the visual system adapts to the dichoptic stimuli (Hollins and Hudnell, 1980). When viewing an orthogonal gratings, as illustrated in Figure 1, incomplete suppression will result in the appearance of a plaid percept<sup>7</sup>.

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<sup>6</sup>. The average is used because there is a significant stochastic component to the alternations in perception. This stochastic behavior has been modeled by Lehky by adding random walk noise to the inhibition signal of the RIO system (Lehky, 1988, p. 222).

<sup>7</sup>. The plaid percept can also occur if the dichoptic pair is flashed very briefly, this is called *abnormal fusion* by Wolfe (1984), which seems to imply a delay of the inhibitory circuitry. Also, during the first 3.5 month of infancy, before the ocular dominance columns are segregated and before stereopsis appears, summation of the dichoptic stimuli into a plaid percept seems to be normal (Held, 1991; VanSluyters, et al, 1990).



Binocular rivalry can occur in different stimulus dimensions such as color, direction of motion, spatial frequency, and orientations. For example, Treisman (1962) reported that dichoptic orthogonal gratings with complementary background colors may yield rivalry where color alternation and orientation alternation are independent (Sloane, 1985, p.212).



The nature of the underlying mechanism of binocular rivalry can be explored psychophysically by manipulating the stimuli presented to each of the two eyes. The psychophysical effects of increasing stimulus strength in one or both eyes is summarized by Levelt's four propositions<sup>8</sup> (Levelt, 1965):

1. Increase of the stimulus strength in one eye will increase the predominance of that stimulus.
2. Increase of the stimulus strength in one eye will not effect the mean duration period for that eye.
3. Increase of the stimulus strength in one eye will increase the alternation frequency (i.e. decrease the full-cycle duration).
4. Increase of the stimulus strengths to both eyes will increase the alternation frequency.

Grossberg discussed these parametric properties qualitatively, using gated dipoles, in Section 27 of Grossberg (1987b).

## **6.5 Is an RIO a good model for binocular rivalry?**

Fox and Rasche (1969) objected to using a reciprocal inhibition oscillator as a model for binocular rivalry, because their experience with RIOs showed that when the stimuli to one channel of an RIO is increased, the duration of dominance changes in both channels, which is contrary to Levelt's proposition two. Figure 2 illustrates this problem. This objection against the RIO model has been met by several researchers including Lehky (1988) and Mueller (1990). A different objection to using RIOs as a model for binocular rivalry comes from Fox and Check (1972). Their psychophysical data showed that the sensitivity to a test probe during suppression remains constant over the duration of the suppressed phase (Fox and Check, 1972), i.e., the phases are relatively flat, as with a

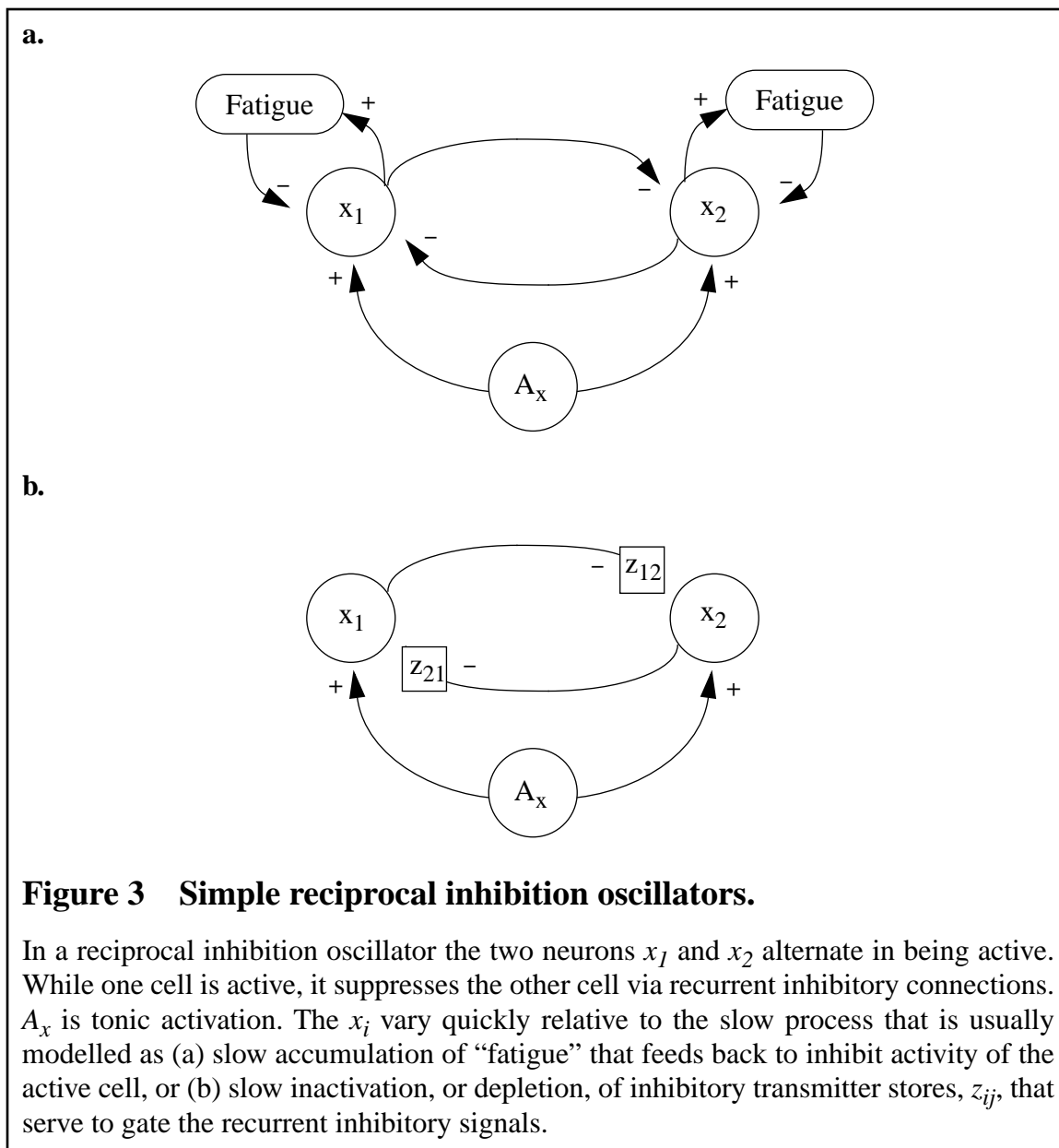
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<sup>8</sup>. Levelt's seminal book, *On Binocular Rivalry*, is probably the most widely cited work on binocular rivalry.

rectangular wave. However their experimental experience with RIOs indicated that a reciprocal inhibition model must produce more triangularly shaped phases due to the gradual decrease of suppression (Lehky, p.218). Lehky has countered this objection by demonstrating the generation of rectangular waves by his electronic astable multivibrator circuit; however, concern has been expressed by Mueller about the biological plausibility of this circuit (Mueller, 1990, p.76). Mueller suggests that his own model that uses pre-synaptic inhibition meets the objection of Fox and Rasche in a more biologically plausible way. It should be noted however that Mueller's model does not produce particularly rectangular phases, which are required to meet the objection of Fox and Check. The model described here meets both objections using a biologically plausible mechanism that gates the recurrent excitatory and inhibitory signals by habituating transmitters. This model is described in the next section.

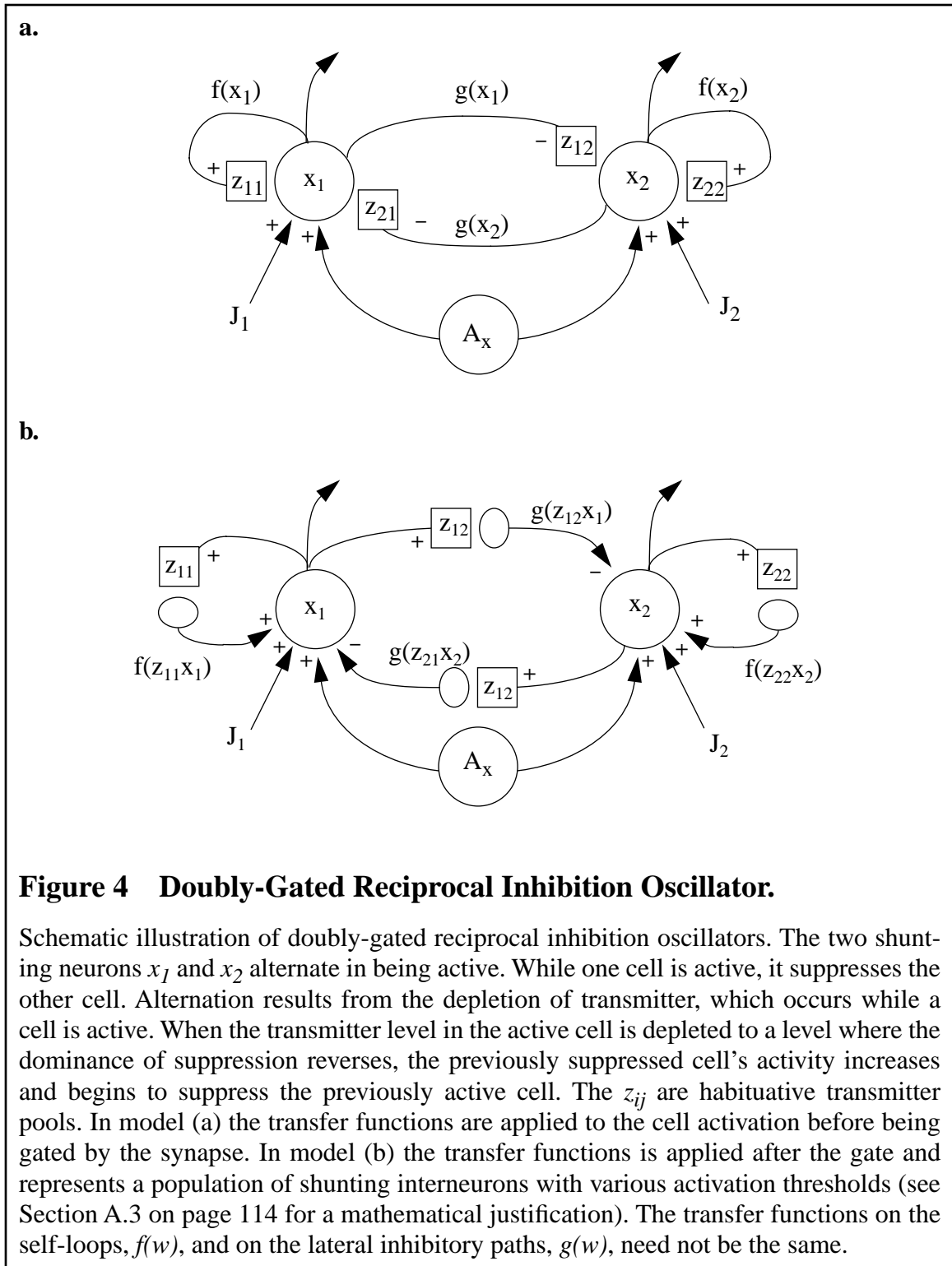
## **6.6 The model.**

The basic reciprocal inhibition oscillator typically consists of two neurons (usually considered to be representative of two neural populations) that are coupled by lateral inhibition. This is illustrated in Figure 3. As mentioned in Section 6.3, oscillation is typically produced by incorporation of a slow process that is usually modeled as fatigue, shown in Figure 3a, or as transmitter inactivation, shown in Figure 3b. It is the latter mechanism that will be developed here.



A more elaborate RIO involves excitatory self feedback<sup>9</sup>, as is illustrated in Figure 4. In the model employed here the neurons are modeled by shunting equations, es-

<sup>9</sup>. It has been shown that excitatory self feedback can eliminate the need for tonic activation (Perkel, 1976; Roberts, et al, 1985).



essentially identical to Eqn. 1, except that the passive restorative force is toward a non-zero baseline value,  $T_x$ , rather than toward zero, such that

$$\frac{dx_i}{dt} = -P_x (T_x + x_i) + (D_x - x_i)I_i^{(+)} - (x_i + H_x)I_i^{(-)} . \quad (1)$$

The input to the neurons now includes (1) an external arousal or suppression<sup>10</sup> source,  $A_x$ , that is the same to each neuron, (2) the external stimuli,  $J_i$ , and the recurrent feedback signals that are gated by depletable, but self replenishing, transmitter stores. The recurrent processes include (3) excitatory feedback,  $f(x_j)z_{ji}$ , and (4) inhibitory recurrent coupling,  $g(x_j)z_{ji}$ , from the opponent cell, such that

$$I_i^{(+)} = J_i^{(+)} + \mathbf{f}(x_j) z_{ji} + A_x^{(+)} , \quad (2)$$

and

$$I_i^{(-)} = J_i^{(-)} + \mathbf{g}(x_j) z_{ji} + A_x^{(-)} . \quad (3)$$

Alternatively, since recurrent signals are frequently delivered via interneurons, it is sometimes chosen that the transfer function is applied after the transmitter has gated the signal, such that

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<sup>10</sup>. To avoid the need for an external arousal source, the opponent neurons of the oscillator were designed to be tonically spontaneously active. In the initial experiments a fundamental design problem arose: either the system would not oscillate with simultaneous stimulation, or if it did, it would not spontaneously cease oscillation when the input was removed. A solution is to add tonic external inhibition,  $A_x^{(-)}$ , to the system that wanted to constantly oscillate. This simple addition prevents spontaneous oscillations until the presentation of a positive stimulus that overrides the inhibition, though the victory seems Pyrrhic.

$$I_i^{(+)} = J_i^{(+)} + f(x_i z_{ii}) + A_x^{(+)} \quad (4)$$

and

$$I_i^{(-)} = J_i^{(-)} + g(x_j z_{ji}) + A_x^{(-)}, \quad (5)$$

which is the mechanism that was chosen here.

Each of the recurrent processes is gated by a *bouton terminal* whose transmitter dynamics obey

$$\frac{dz_{ij}}{dt} = P_z(T_z - z_{ij}) - x_i z_{ij} \quad (6)$$

(Grossberg, 1968, 1969) where parameter  $T_z$  is the transmitter accumulation level<sup>11</sup>, and  $P_z$  is the passive rejuvenation coefficient. The rate of accumulation,  $P_z(T_z - z_{ij})$ , varies only as a function of the current level of available transmitter; however the rate of depletion,  $x_i z_{ij}$ , varies as a function of both the current level of available transmitter,  $z_{ij}$ , and the level of neural activity,  $x_i$ . This distinction will become important later, when analyzing the simulations results.

The excitatory and inhibitory feedback obey the transfer functions<sup>12</sup>

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<sup>11</sup>. The transmitter accumulation level,  $T_z$ , need not be the same for each synapse, in which case  $T_z$  becomes  $T_{ij}$  and acts as the “weight” of the synaptic connection.

<sup>12</sup>. See Appendix A for a description of this type of sigmoid transfer function.

$$f(x) = \frac{x^{\lambda_f}}{C_f + x^{\lambda_f}} \quad (7)$$

and

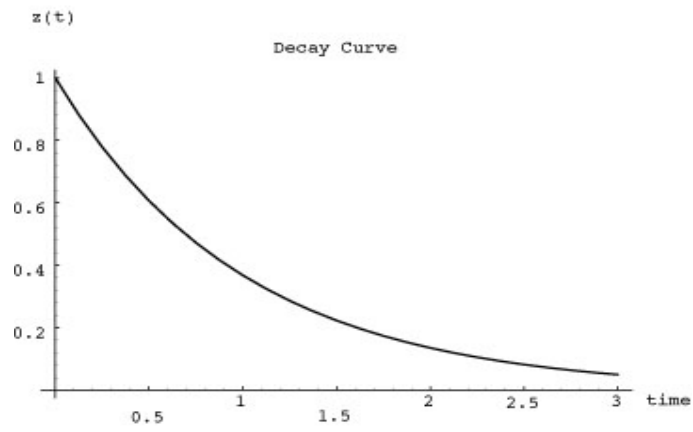
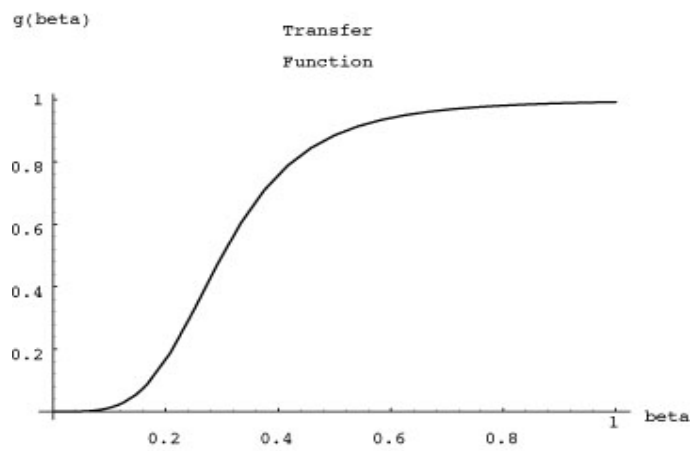
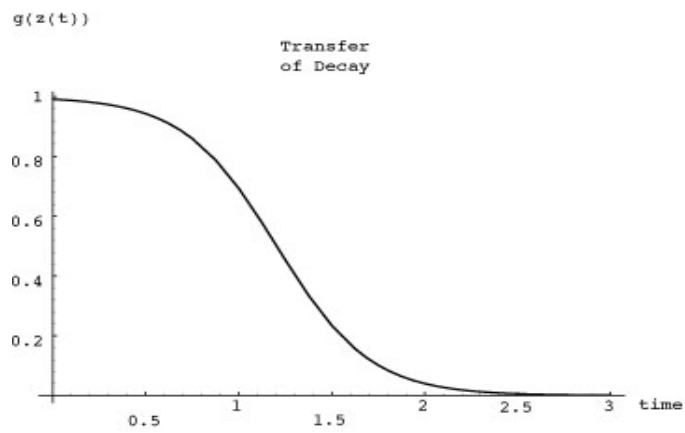
$$g(x) = \frac{x^{\lambda_g}}{C_g + x^{\lambda_g}} . \quad (8)$$

The simulations of this model, described below, take advantage of different feedback functions,  $g(x)$  and  $f(x)$ , that are used for the excitatory feedback and inhibitory feedback. The excitatory feedback function is a steeper sigmoid than the inhibitory sigmoid. It is quite reasonable to image such differences arising from the differences between excitatory and inhibitory interneurons and transmitter kinetics<sup>13</sup>. This simple and plausible asymmetry seems to be sufficient to account for the main effects of the recent psychophysical data reported by Mueller and Blake (1989), which is described below.

By associating the transfer function with an interneuron it is possible to produce a phase plateau much closer to the initial phase peak, which results in an essentially rectangular oscillation, as required to meet the objection of Fox and Check (1972), that was discussed in Section 6.4. The effect of applying the transfer function after the transmitter gate is illustrated in Figure 5. Assuming a relatively constant cellular activation,  $x_i$ , the transmitter depletion curve,  $z_{ij}(t)$ , follows the exponential decay dictated by mass action, which is shown in Figure 5a. The result of applying a sigmoid transfer function, as shown in

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<sup>13</sup>. Differences in transmitter kinetics can result from differences in binding constants, re-uptake curves, etc.

**a.****b.****c.****Figure 5 Rapid change in gated signals.**

Curve (c) is the composite function of sigmoid function (b) on decay function (a).



Figure 2b, to this decay function is shown in Figure 5c. The consequence is a sustained high signal level followed by a rapid reduction in signal strength.

## 6.7 Qualitative basis of oscillations in a simple gated-RIO.

This section develops an intuitive explanation of why an RIO oscillates, by using a simple four dimensional (two cells and two depletable gates) system, as illustrated in Figure 3b. Suppose that the system comprises two cells, an On-cell and an Off-cell, that mutually inhibit one another. The inhibitory signals are gated by transmitters that deplete as a function of the product of transmitter availability and activation level. Suppose further that the system starts out with the On-cell activation large and the Off-cell activation small, but the transmitter levels are maximal in both bouton terminals. The inhibitory signal from the On-cell further suppresses the already low activation of the Off-cell by applying its signal gated by the full inhibitory transmitter store, while the inhibitory signal from the Off-cell is negligible. Eventually however the gated inhibitory signal for the On-cell becomes small because the transmitter store becomes depleted; all the while the transmitter store in the Off-channel was not being depleted. At some point the low activity of the Off-cell gated by the full transmitter store becomes larger than that of the On-cell's inhibitory effect which is gated by a now depleted transmitter store. The dominance reverses quickly because as soon as the Off-cell gains in the balance of power it proportionally inhibits the previously dominant On-cell, which further disinhibits the Off-cell. With the On-cell depressed, the depleted transmitter has a chance to recover, while the transmitter gating the Off-channels inhibition is now slowly depleting. Before long the balance of gated inhibition will again reverse resulting in a rapid reversal of dominance. In this way the

system produces anti-phase oscillations. The frequency of oscillation varies directly as the transmitter<sup>14</sup> rate varies.

## 6.8 Stimulation paradigm.

Mueller and Blake (1989), developed a novel experimental paradigm to test for stimulus effects on the temporal behavior of binocular rivalry. The details of this paradigm are illustrated in Figure 6. In each experiment, one of the eyes was chosen as the *test eye*<sup>15</sup>. The rivalrous perceptions are labeled ipsilateral and contralateral with respect to the test eye. In the continuous contrast presentation experiments (CC), the contrast increment is constant in the test eye. In the dominance synchronized experiments (SD), the contrast increment to the test eye occurs<sup>16</sup> only while the subject reports that the percept is of the stimulus to that (ipsilateral) eye. In the suppression synchronized experiments (SS), the contrast increment to the test eye occurs only while the subject reports that the percept is of the stimulus to the non-test (contralateral) eye. This stimulus presentation paradigm is in some sense a variation of the probe procedure experiments that manipulate the stimulus during the dominant or suppressed phase to determine detection thresholds during the course of the phases (Cogan, 1982; Fox and Check, 1972).

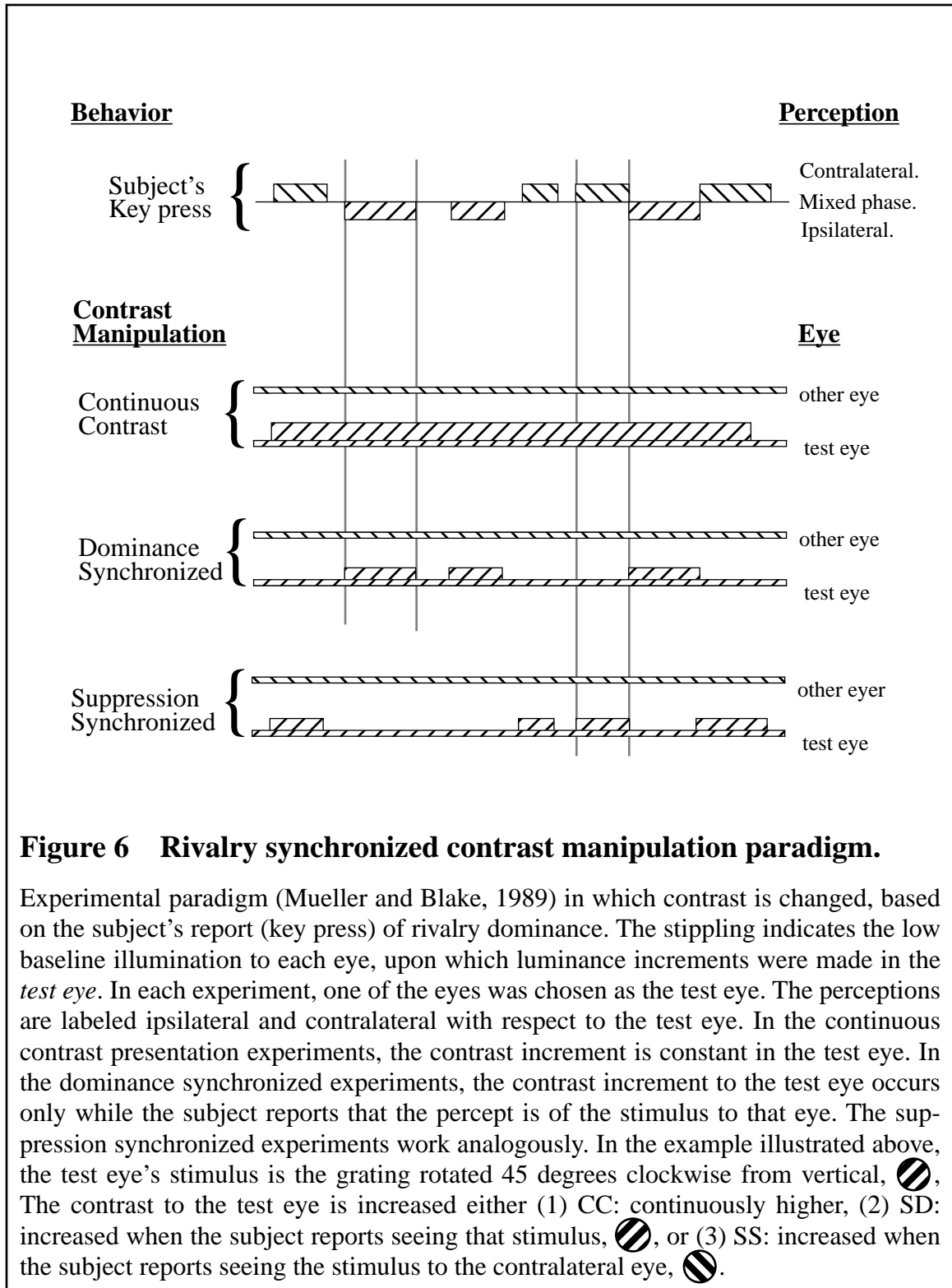
Probe experiments have shown that detection during dominance is equivalent to normal monocular viewing, but there is a factor of two to three loss of sensitivity to the

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<sup>14</sup>. The slow variable is referred to as residing on the slow manifold (Carpenter and Grossberg, 1983; Carpenter and Grossberg, 1985a).

<sup>15</sup>. The stimulus grating filled a circular field 0.8 degrees of visual angle, which essentially eliminates the appearance of a spatially different “patchwork” precept seen in dichoptic presentations that subtend more than about one degree of visual arc (Lehky, 1988, p. 215; Sloane, 1985, p. 212). The spatial frequency was 7.7 cycles/degree.

<sup>16</sup>. The stimulus increment was ramped so that the transient responses would be minimized.



test probe during suppression. Even though suppression removes the suppressed stimulus from phenomenal experience, the information in the suppressed eye may still act to facilitate the signals to the dominant eye<sup>17</sup>. Moreover a stimulus can be modified during suppression such that the change (e.g. in spatial frequency, orientation, or contrast, is not detected but, nonetheless the suppression duration will correspond to that normally obtained with the new stimulus. This indicates that the change is registered on a neural level, but not on a phenomenal level (Sloane, 1985. p.213). The results of the SD-paradigm simulation shows how a stimulus that is correlated with the suppressed phase can modify the alternation rate and duty cycles. Recall that in the SD-paradigm the energy changes to the test eye only occurs during the suppressed phase and is removed at the jump transition to the dominant phase, nevertheless the effect on rivalry is significant. The ability of the model to predict binocular rivalry is discussed in the next section.

## 6.9 Simulation Results.

The durations for the dominant and suppressed phases were recorded for various amounts of test-stimulus contrast, while the contrast to the contralateral eye was held constant. The next set of figures compare the simulation results to the psychophysical results reported by Mueller and Blake (1989). In each plot the solid line is the dominant duration of the test eye and the dashed line is the suppressed duration for the test eye (or the dominant duration for the contralateral eye). In each figure (a), at the top, is the simulation result and (b), at the bottom, is a graph of the linear regressions slopes that were made to the psychophysical data and published by Mueller and Blake (1989). Results using the CC

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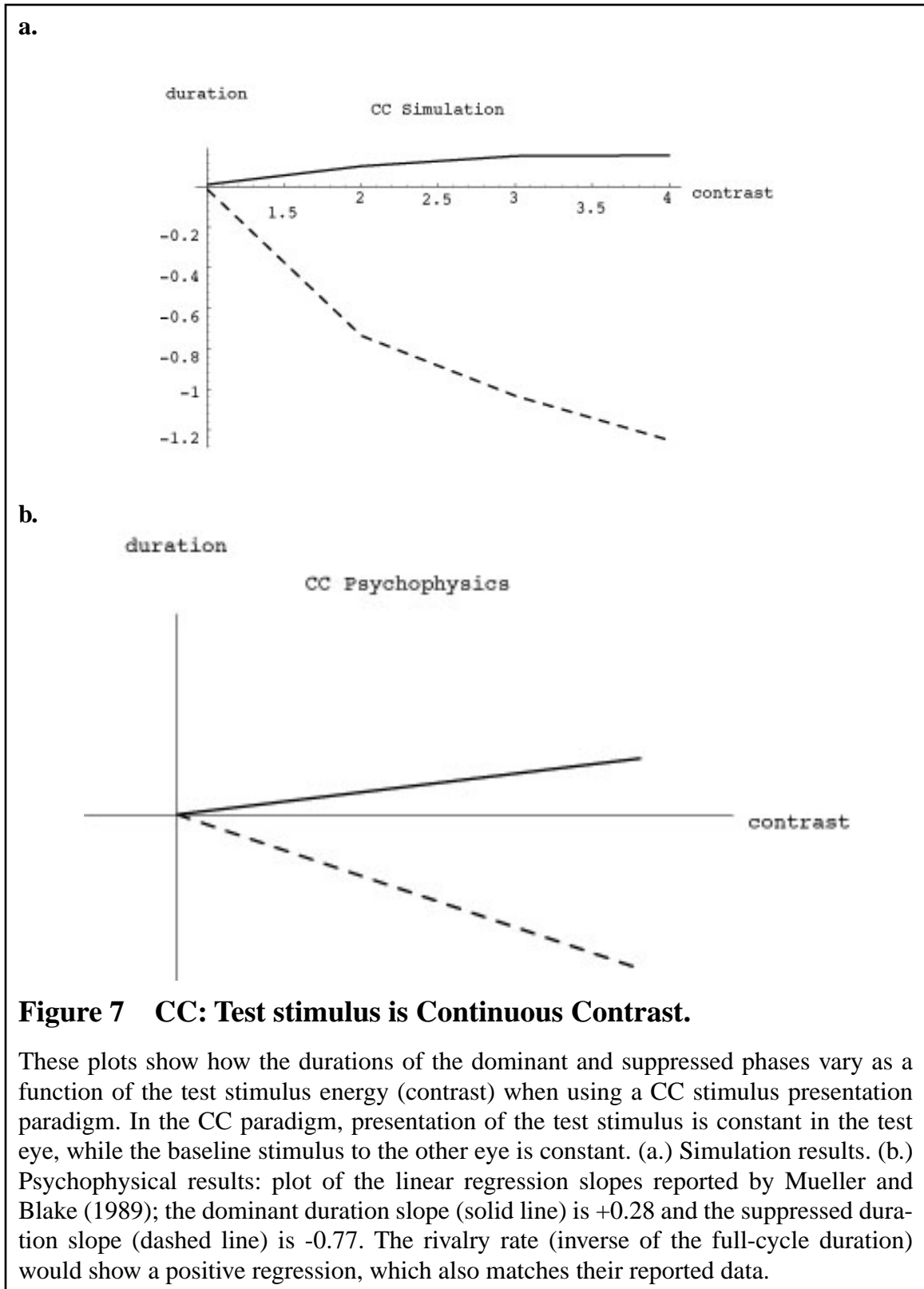
<sup>17</sup>. Sloane (1985), p. 214 cites Westendorf, et al (1982).

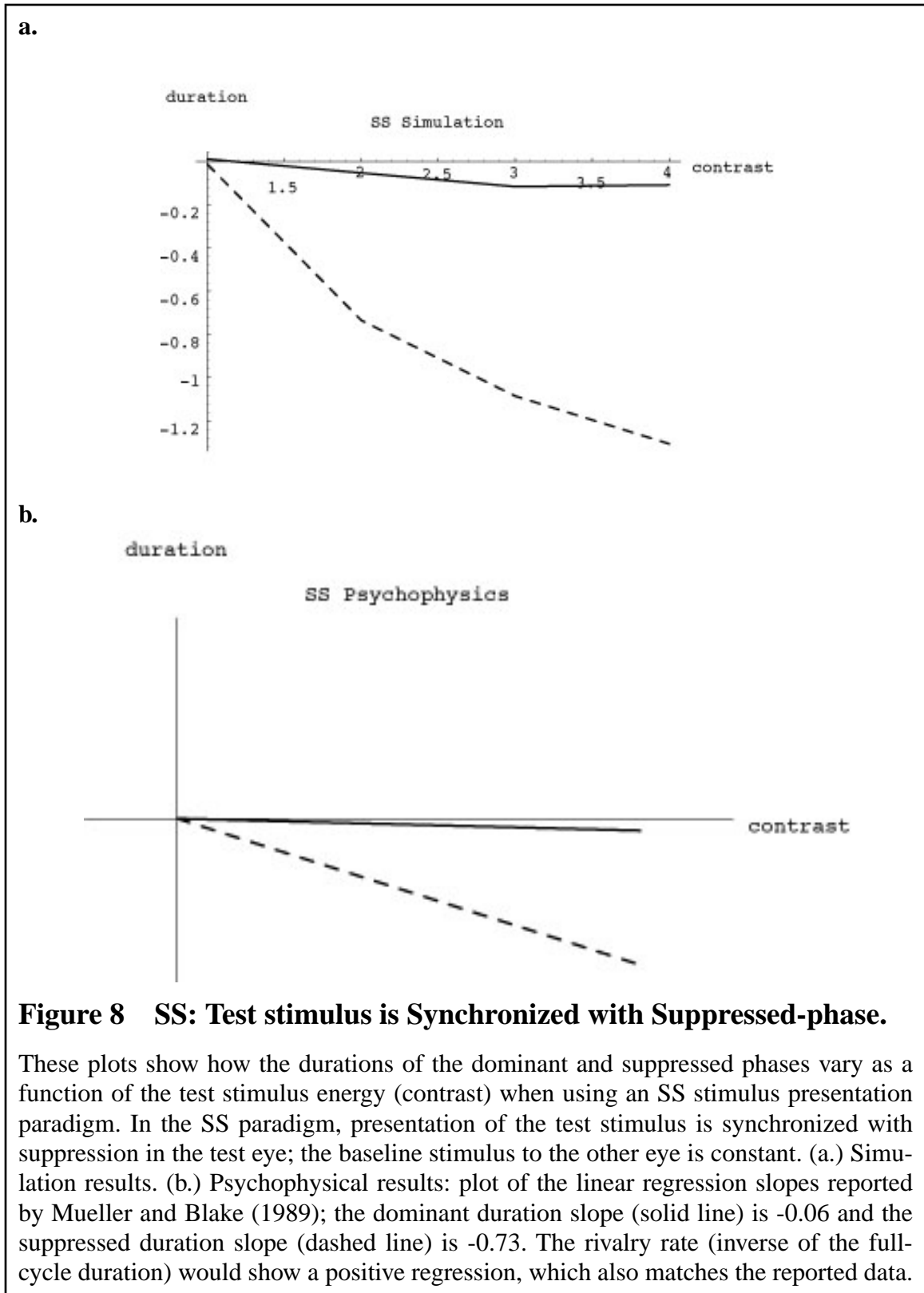
paradigm are shown in Figure 7; results using the SS paradigm are shown in Figure 8; results using the SD paradigm are shown in Figure 9.

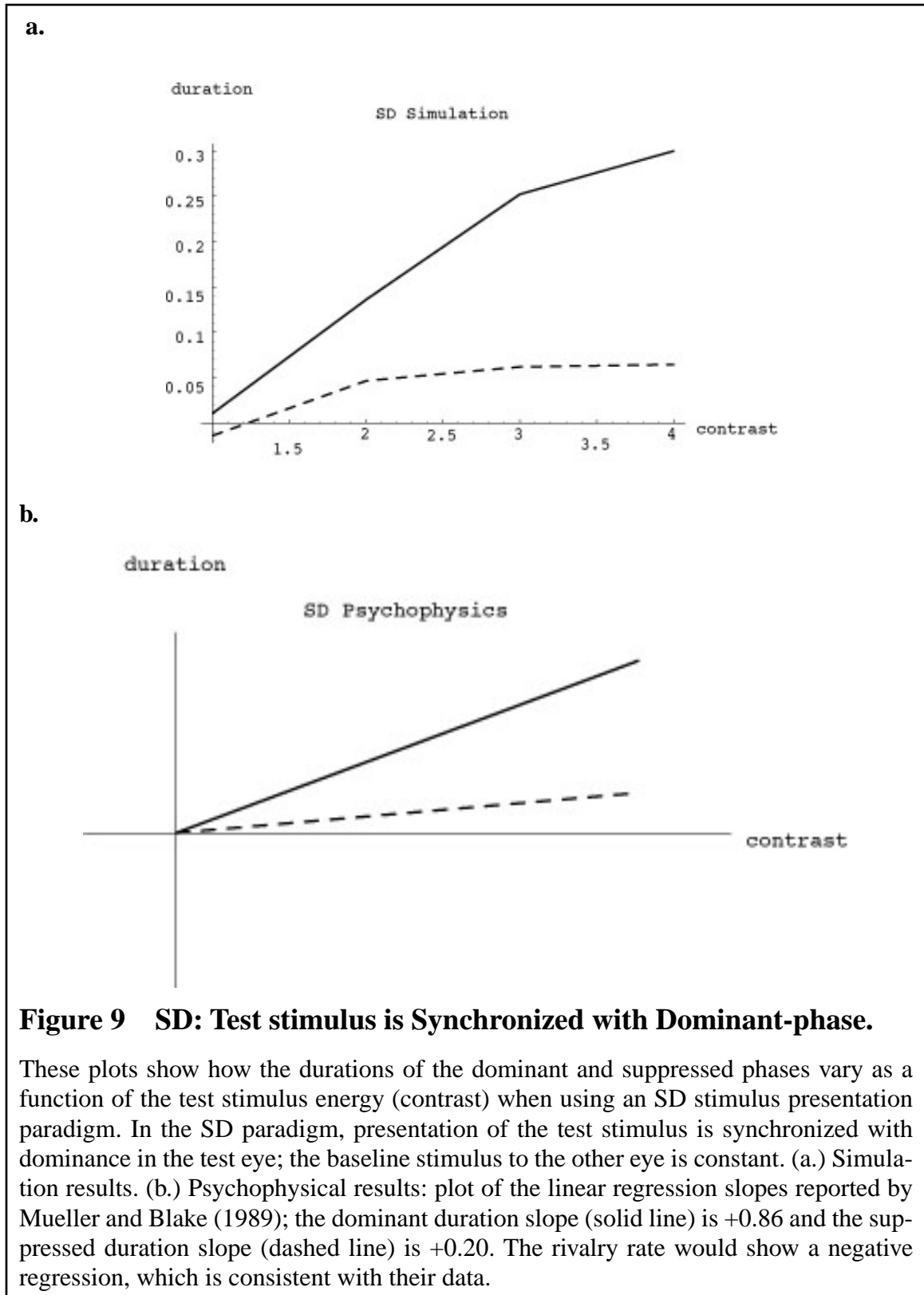
If the contrast is experimentally synchronized so that it ramps up at the onset of suppression (SS), the results are comparable to the conventional experimental paradigm (CC) in which duration is measured when presenting a continuous contrast level. However, when the contrast increase is experimentally synchronized with dominance (SD), the duration of the dominant phase increases dramatically and, even more dramatically, the duration of the suppressed phase changes from a strong negative slope to a significant positive slope.

Table 1 summarizes these results. Since the units in the simulation are arbitrary, the simulation results shown in the table are normalized to the experimentally obtained results. Each slope in the set of six,  $\{\{\text{dominant, suppressed}\} \times \{\text{CC, SS, SD-paradigm}\}\}$ , was multiplied by a constant such that the suppressed duration in the CC-paradigm was 0.77, the value obtained in the psychophysical experiment. This is the same procedure used by Mueller (1990), to facilitate comparison. As he pointed out, the scaling operation is comparable to multiplying either the stimulus energy (contrast) or the phase durations by a scaling factor.

The SS-paradigm phase durations are well match to those of the psychophysical data. The CC-suppress phase is the same by virtue of the normalization, and the dominant phase duration is in the correct direction, but corresponds more to the traditional results described by Levelt. Though the SD-paradigm phase duration slopes are not large enough, they show the correct sign and the correct ordering. Mueller (1990), reports the same









**Table 1 Slope data for different stimulus paradigms.**

Paradigm	Phase	Psychophysics	RIO Simulation
CC	Suppressed	-0.77	-0.77
	Dominant	+0.28	+0.088
SS	Suppressed	-0.73	-0.73
	Dominant	-0.06	-0.077
SD	Suppressed	+0.20	+0.045
	Dominant	+0.86	+0.179
Experimental data from Mueller and Blake (1989)			

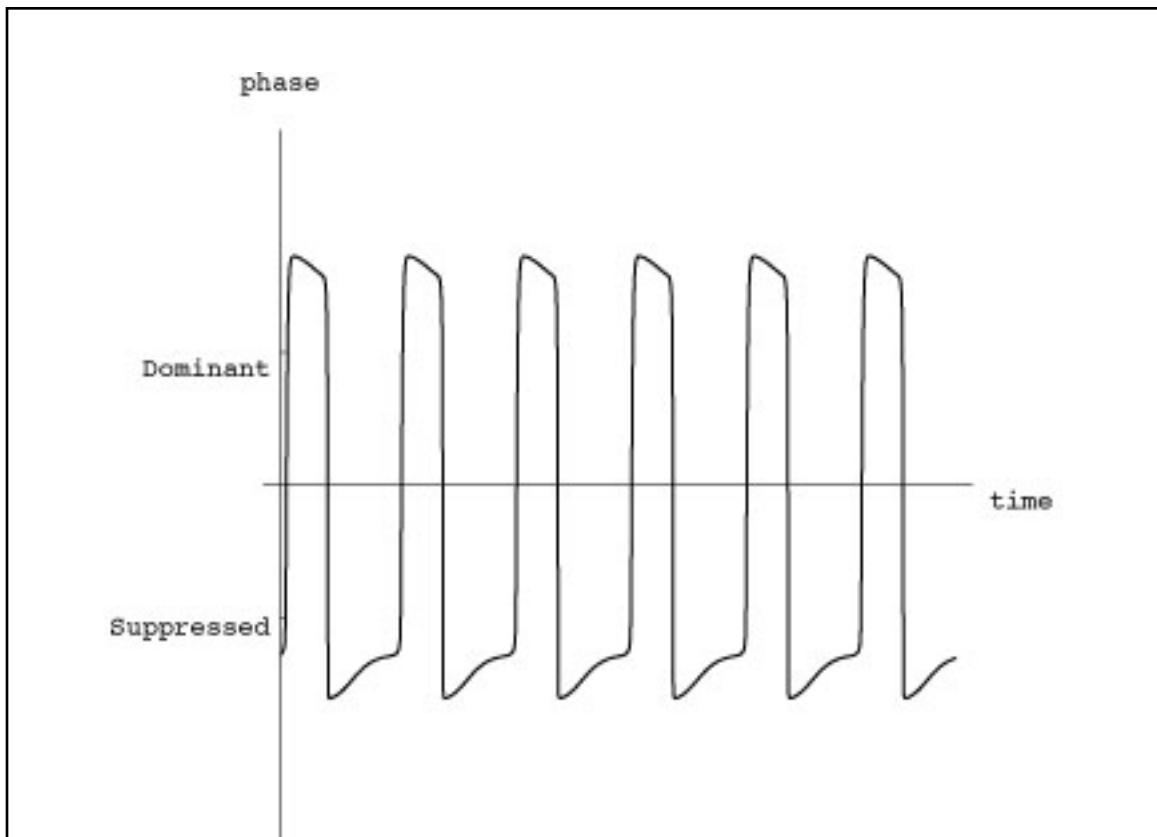
shortcomings with the presynaptic inhibition RIO that he proposes. It is not until he introduces a stimulus delay, assumed to correspond to reaction time delay in the psychophysical experiments, that the magnitude of the dominance duration slopes increases to a level comparable to the data. The introduction of this delay factor should be the focus of future work using this gated model.

As noted earlier, the rate of accumulation,  $P_z(T_z - z_{ij})$ , varies only as a function of the current level of available transmitter; however the rate of depletion,  $x_i z_{ij}$ , varies as a function of both the current level of available transmitter,  $z_{ij}$ , and the level of neural activity,  $x_i$ . This causes an asymmetry between the effects of stimulus increments during dominant and suppressed phases; moreover, this asymmetry carries over into the next phase after the synchronized stimulus increment is removed. In the SS-paradigm, stimulus increment is during the suppressed phase when the transmitters are in the recovery phase, the time when cellular activation has less effect. In the SD-paradigm, stimulus increment is during the dominant phase, the time when activation can enhance depletion. The depletion is more than compensated for by the increased cellular activation during the dominant

phase, but during the suppressed phase the super-depleted transmitter allows the contralateral cell's dominance duration to increase.

### 6.9.1 Rectangular wave

From Figure 10 it can be seen that with this model the activation levels of the dominant and suppressed phases are substantially constant, that is they asymptote toward an



**Figure 10 Rectangular wave-form.**

The temporal behavior of the gated RIO model under the CC-paradigm. The dominant phases are shorter because the stimulus energy to the test cell is less than that to the contralateral cell. The oscillation is rough a rectangular wave. The percent of total activation range that shows decay (or suppression reduction) before a jump transition is small compared to the results shown by Mueller (1990) or Carpenter and Grossberg (1983).

activation plateau very quickly and remain active at that high level for the duration of the phase. The percent of the total range of activation over which decay (or suppression reduction) appears before a jump transition occurs is small compared to the results shown by either Mueller (1990) or Carpenter and Grossberg (1983). This rectangular waveform corresponds well to report by Fox and Check (1972) that loss of sensitivity to a test probe during suppression remains relatively constant over the duration of the suppressed phase.

## **6.10 Conclusion**

Mueller and Blake's novel psychophysical paradigm further probe the oscillatory mechanism underlying binocular rivalry. The trends in the data obtained using this paradigm are well modeled by applying a gated reciprocal inhibition oscillator. Also the constancy of the level of suppression is well modeled by the rectangular waveforms that are produced by this model.

## **Acknowledgments**

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## Bibliography

- Alexander, L. (1951). The influence of figure-ground relationships in binocular rivalry. *Journal of Experimental Psychology*, **41**, 376-381.
- Alexander, L. and Bricker, P. D. (1952). Figure-ground contrast and binocular rivalry. *Journal of Experimental Psychology*, **44**, 452-454.
- Arend, L. (1971). Difference information in brightness perception. *Perception & Psychophysics*, **9(3B)**.
- Arend, L. (1983). "Filling-in" between edges. *The Behavioral and Brain Sciences*. **6**, 657-658. This is the critique made by Arend of Grossberg's theory that was presented in the same volume as Grossberg (1983).
- Arend, L. E. & Goldstein, R. E. (1987). Lightness models, gradient illusions, and the curl. *Perception & Psychophysics*, **42**, 65-80.
- Arrington, K. F. and Grossberg, S. (1992). Hierarchical neural networks for monocular and binocular brightness and color perception. *In preparation*.
- Attneave, F. (1971). Multistability in perception. *Scientific American*, **225**, 61-71.
- Barlow, H. B. (1961). Der Informationswert verschiedener Reaktionstypen der Neurone des visuellen Systems. Initial Remarks. p. 375-376. In: *The Visual System: Neurophysiology and Psychophysics*. Ed. by R. Jung and H. Kornhuber. Berlin-Göttingen-Heidelberg: Springer. (Re-reference from Gerrits and Vendrik (1970)).
- Bennett, M. V. L. & Spray, D. C. (1987). Gap junctions. In G. Adelman (Ed.), *Encyclopedia of Neuroscience*, (Vol. 1, pp. 447-449).
- Bergström, S. S. (1966). A paradox in the perception of luminance gradients, I. *Scandinavian Journal of Psychology*, **7**, 209-224.
- Bergström, S. S. (1973). A note on the neural unit model for contrast phenomena. *Vision Research*, **13**, 2087-2092.
- Brown, T. G. (1911). The intrinsic factors in the act of progression in the mammal. *Proc. Roy. Soc. B.*, **84**, 308-319.
- Burt, P. J. & Adelson, E. H. (1983). The Laplacian pyramid as a compact image code. *IEEE Transactions on Communications*, **31(4)**, 5532-540.
- Carpenter, G. & Grossberg, S. (1983). A Neural Theory of Circadian Rhythms: the Gated Pacemaker. *Biological Cybernetics*, **48**, 35-59.

- Carpenter, G. A. & Grossberg, S. (1984). A neural theory of circadian rhythms: Aschoff's rule in diurnal and nocturnal mammals. *American journal of Physiology*, **247**, R1067-R1082.
- Carpenter, G. A. & Grossberg, S. (1985a). Neural dynamics of circadian rhythms: the mammalian hypothalamic pacemaker. In J. Eisenfeld & C. DeLisi (Eds.), *Mathematics and Computers in Biomedical Applications*, Elsevier Science Publishers B. V. (North-Holland) IMACS.
- Carpenter, G. A. & Grossberg, S. (1985). A Neural theory of circadian rhythms: split rhythms, after-effects and motivational interactions. *J. Theor. Biol.* **113**, 163-223.
- Cogan, A. I. (1982). Monocular sensitivity during binocular viewing. *Vision Research*, **22**, 1-16.
- Cogan, A. I. (1987). Human binocular interaction: towards a neural model. *Vision Research*, **27**(12), 2125-2139.
- Cohen, M. A. & Grossberg, S. (1984). Neural Dynamics of brightness perception: Features, boundaries, diffusion, and resonance. *Perception & Psychophysics*, (36) **5**, 428-456.
- Coren, S. (1983). When "filling-in" fails. *The Behavioral and Brain Sciences*, **6**, 661-662. This is the critique made by Coren of Grossberg's theory that was presented in the same volume, citation Grossberg (1983).
- Cornsweet, T. N. (1970). *Visual perception*. New York: Academic Press.
- Dowling, J. E. (1987). *The retina: an approachable part of the brain*. Belknap Press, Cambridge, Massachusetts.
- Dutour, (1780). Discussion d'un question d'optique. *Mém. Math. Phys. Acad. Roy. Sci. Paris.*, 3, 514-530.
- Fox, R. & Check, R. (1972). Independence between binocular rivalry suppression duration and magnitude of suppression. *Journal of Experimental. Psychology*, **93**, 283-289.
- Fox, R. & Rasche, F. (1969). Binocular rivalry and reciprocal inhibition. *Perception & Psychophysics*, **5**, 215-217.
- Furman, G. G. (1965). Comparison of models for subtraction and shunting lateral-inhibit? receptor-neuron fields, *Kybernetika*, **2**, 257-274.
- Gerrits, H. J. M. & Vendrik, A. J. H. (1970). Simultaneous contrast, filling-in process and information processing in man's visual system. *Experimental Brain Research*, **11**, 411-430.

- Gilchrist, J. & McIver, C. (1985). Fechner's paradox in binocular contrast sensitivity. *Vision Research*, **25**(4), 609-613.
- Graham, C. H., (1965). Visual form perception. In C. H. Graham (Ed.), *Vision and Visual Perception*, John Wiley & Sons, Inc., New York 1965.
- Grillner, S. (1985). Neurobiology of vertebrate locomotion. In *Proceedings of an International Symposium held at The Wenner-Gren Center, Stockholm, June 17th-19th, 1985*, (Chapter 18). MacMillan Press.
- Grossberg, S. (1968). Some physiological and biological consequences of psychological postulates. *PNAS*, **60**, 758-765.
- Grossberg, S. (1969). On the production and release of chemical transmitters and related topics in cellular control. *J. Theoret. Biol.*, **22**, 325-364.
- Grossberg, S. (1972). A Neural Theory of Punishment and Avoidance. II. Quantitative Theory. *Mathematical Biosciences*, **15**, 253-285.
- Grossberg, S. (1973). Contour Enhancement, short term memory and constancies in reverberating neural networks. *Studies in Applied Mathematics*, **LII**, 213-257.
- Grossberg, S. G. (1980). How does a brain build a cognitive code? *Psychological Review*, **87**, 1-51.
- Grossberg, S. (1983). The quantized geometry of visual space: The coherent computation of depth, form, and lightness. *The Behavioral and Brain Sciences*. **6**, 625-692.
- Grossberg, S. (1987a). Cortical dynamics of three-dimensional form, color and brightness perception: I. Monocular theory. *Perception & Psychophysics*, **41**(2), 87-116. Pagination references are to the reprinted version in S. Grossberg (Ed.), *Neural Networks and Natural Intelligence*, 1988, (Chapter 1, pp. 1-54).
- Grossberg, S. (1987b). Cortical dynamics of three-dimensional form, color and brightness perception: II. Binocular theory. *Perception & Psychophysics*, **41**(2), 117-158. Pagination references are to the reprinted version in S. Grossberg (Ed.), *Neural Networks and Natural Intelligence*, 1988, (Chapter 2, pp. 55-126).
- Grossberg, S. (1991). Why do parallel cortical systems exist for the perception of static form and moving form? *Perception & Psychophysics*, **49** (2), 117-141.
- Grossberg, S. & Mingolla, E. (1985a). Neural Dynamics of Form Perception: Boundary Completion, Illusory Figures, and Neon Color Spreading. *Psychological Review*, **92** (2).
- Grossberg, S. & Mingolla, E. (1985b) Neural dynamics of perceptual grouping: Textures, boundaries, and emergent segmentations. *Perception & Psychophysics*, **38**, 141-171

- Grossberg, S. & Mingolla, E. (1987) Neural dynamics of surface perception: Boundary webs, illuminants, and shape-from-shading. *Computer Vision, Graphics, and Image Processing*, **37**, 116-165
- Grossberg, S. & Todorovic, D. (1988) Neural dynamics of 1-D and 2-D brightness perception: A unified model of classical and recent phenomena. *Perception and Psychophysics*, **43**, 241-277.
- Held, R. (1991). Development of binocular vision and stereopsis. In D. Regan (Ed.), *Binocular Vision*, (Chapter 9). MacMillan Press.
- Hering, E. (1964). *Outlines of a theory of the light sense*. Translated by: Leo M. Hurvich and Dorothea Jameson, Harvard University Press, Cambridge, MA, 1964.
- Hollins, M. (1980). The effect of contrast on the completeness of binocular rivalry. *Perception & Psychophysics*, **5**, 215-217. (Re-reference from Mueller and Blake (1989)).
- Hollins, M. & Hudnell, K. (1980). Adaptation of the binocular rivalry mechanism. *Invest. Ophthalm. Vis. Sci.*, **19**, 1117-1120. (Re-reference from Sloane (1985))
- Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architectures of monkey striate cortex. *Journal of Physiology*, **195**, 215-243.
- Kaufman, L. (1974). *Sight and Mind: An introduction to visual perception*. Oxford University Press, New York.
- Land, E. H. (1977). The retinex theory of color vision. *Scientific American*, **237**, 108-128.
- Land, E. H. (1986). Recent advances in retinex theory. *Vision Research*, **26**(1), 7-21.
- Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception*, **17**, 215-228.
- Levelt, W. J. M. (1965). *On binocular rivalry*. Ph.D., Institute for Perception RVO-TNO, Soesterberg, The Netherlands.
- Livingstone, M. S. & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Proceeding of the National Academy of Sciences*, **79**, 6098-6101.
- Marr, D. (1982). *Vision*. W. H. Freeman and Co., New York.
- McDougall, W. (1903). The physiological factors of the attention-process (III.). *Mind*, **XII**, 473-488.
- McDougall, W. (1906). The physiological factors of the attention process, IV. *Mind*, **XIV**, 329-359



- Moore, A., Allman, J. & Goodman, R. M. (1991). A real-time neural system for color constancy. *IEEE Transactions on Neural Networks*, **2**(2), 237-247
- Moore, A., Fox, G., Allman, J. & Goodman, R. (In press). A VLSI neural network for color constancy. In D. S. Touretzky & R. Lippman (Eds.), *Advances in Neural Information Processing Systems 3*, San Mateo, CA: Morgan Kaufman.
- Mueller, T. J. & Blake, R. (1989). A Fresh look at the temporal dynamics of binocular rivalry. *Biological Cybernetics*, **61**, 223-232.
- Mueller, T. J. (1990). A physiological model of binocular rivalry. *Visual Neuroscience*, **4**, 63-73.
- Naka, K. I. & Rushton, W. A. H. (1966). S-Potentials from colour units in the retina of fish (*Cyprinidae*). *Journal of Physiology (London)*, **185**, 587-599. (Re-referenced from Dowling (1987))
- O'Brien, V. (1958). Contour perception, illusion and reality. *Journal of the Optical Society of America*, **48**, 112-119. (Re-referenced)
- Michael A. Paradiso & Nakayama, K. (1991). Brightness perception and filling-in. *Vision Research*, **31**(7/8), 1221-1236.
- Perkel, D. H. (1976). A computer program for simulating a network of interacting neurons. I. Organization and physiological assumptions. *Comput. Biomed. Res.*, **9**, 31-43. (Re-referenced from Roberts, et al (1985))
- Poggio, G. & Poggio, T. (1984). The analysis of stereopsis. *Ann. Rev. Neuroscience*. **7**, 379-412.
- Pollen, D. A., Gaska, J. P. & Jacobson, L. D. (1989). Physiological constraints on models of visual cortical function. In R. M. J. Cotterill (Ed.), *Models of brain function*. Cambridge University Press, Great Britain.
- Roberts, A., Soffe, S. R. & Dale, N. (1985). Spinal interneurons and swimming in frog embryos. In *Proceedings of an International Symposium held at The Wenner-Gren Center, Stockholm, June 17th-19th, 1985*, (Chapter 19). MacMillan Press.
- Ratliff, F. (1965). *Mach Bands: Quantitative Studies on Neural Networks in the Retina*. San Francisco: Holden-Day.
- Reber, A. S. (1985). *The Penguin Dictionary of Psychology*. Penguin. London
- Schiller, P. H. (1986). The central visual system. *Vision Research*, **26**(9), 1351-1386.
- Schiller, P. H. (1992). The ON and OFF channels of the visual system. *TINS*, **15**(3), 86-92.

- Sherrington, C. (1906) *The Integrative Action of the Nervous System*. Yale University Press.
- Slaughter, M. M. and Miller, R. F. (1981). 2-amino-4-phosphonobutyric acid: a new pharmacological tool for retina research. *Science*, **211**, 182-184.
- Sloane, M. E. (1985). Binocular rivalry: a psychophysics in search of a physiology. In D. Rose & G. Dobson (Eds.), *Models of the Visual Cortex*, (Chapter 21). John Wiley & Sons, Ltd.
- Todorovic', D. (1987). The Craik-O'Brien-Cornsweet effect: New varieties and their theoretical implications. *Perception & Psychophysics*, **42**(6), 545-560.
- Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. *Quart. J. Psychol.*, **14**, 23-37.
- Van Sluyters, R. C., Atkinson, J., Banks, M. S., Held, R. M., Hoffmann, K.-P. & Shatz, C. J. (1990). The development of vision and visual perception. In L. Spillmann & J. S. Werner (Eds.), *Visual Perception: The neurophysiological foundations*, (Chapter 13, pp. 349-379). Academic Press, New York.
- von Békésy, G. (1967). *Sensory Inhibition*. Princeton University Press, Princeton, New Jersey.
- von Békésy, G. (1968). Mach- and Hering-type lateral inhibition in vision. *Vision Research*, **8**, 1483-1499.
- Walls, G. (1954). The filling-in process. *American Journal of Optometry.*, **31**, 329-340.
- Walker, P. (1978). Binocular rivalry: central or peripheral selective processes? *Psychological Bulletin*, **85**, 376-389.
- Walraven, J., Enroth-Cugell, C., Hood, D. C., MacLeod, D. I. A., Schnapf, J. L. (1990). The control of visual sensitivity. In L. Spillmann & J. S. Werner (Eds.), *Visual Perception: The neurophysiological foundations*, (Chapter 5, pp. 53-101). Academic Press, New York.
- Westendorf, D. H., Blake, R., Sloane, M. & Chambers, D. (1982) Binocular summation occurs during interocular suppression. *J. Exp. Psychol.: Human Perception and Performance*, **8**, 81-90.
- Wheatstone, C. (1838). Contributions to the physiology of vision. Part I: On some remarkable and hitherto unobserved phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, **128**, 371-394.

- Wilson, H. R., Levi, D., Maffei, L., Rovamo, J. & DeValois, R. (1990). The perception of form. In L. Spillmann & J. S. Werner (Eds.), *Visual Perception: The neurophysiological foundations*, (Chapter 10, pp. 231-272). Academic Press, New York.
- Wolfe, J. M. (1983). Influence of spatial frequency, luminance, and duration on binocular rivalry and abnormal fusion of briefly presented dichoptic stimuli. *Perception*, **12**, 447-456.
- Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research*, **24**(5), 471-478.
- Wolfe, J. M. (1986). Stereopsis and binocular rivalry. *Psychological Review*, **93**, 269-282.
- Wolfe, J. M. (1986). Briefly presented stimuli can disrupt constant suppression and binocular rivalry suppression. *Perception*, **15**, 413- 417.
- Yarbus, A. L. (1967). *Eye Movements and Vision*. New York. Plenum Press.
- Zrenner, E., Abramov, I., Akita, M., Cowey, A., Livingstone, M., Valberg, A. (1990). Color perception. In L. Spillmann & J. S. Werner (Eds.), *Visual Perception: The neurophysiological foundations*, (Chapter 8, pp. 163-204). Academic Press, New York.