



# A low-dimensional model of binocular rivalry using winnerless competition

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## ABSTRACT

We discuss a novel minimal model for binocular rivalry (and more generally perceptual dominance) effects. The model has only three state variables, but nonetheless exhibits a wide range of input and noise-dependent switching. The model has two reciprocally inhibiting input variables that represent perceptual processes active during the recognition of one of the two possible states and a third variable that represents the perceived output. Sensory inputs only affect the input variables.

We observe, for rivalry-inducing inputs, the appearance of winnerless competition in the perceptual system. This gives rise to a behaviour that conforms to well-known principles describing binocular rivalry (the Levelt propositions, in particular proposition IV: monotonic response of residence time as a function of image contrast) down to very low levels of stimulus intensity.

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## 1. Introduction

One of the perceptual phenomena that have intrigued researchers over the years is that of “binocular rivalry” – when the stimuli presented to the two eyes are different, perception alternates between the two stimuli roughly every few seconds [1]. The stimulus contrast is known to affect the predominance (average proportion of time spent perceiving one stimulus) and the dominance length/residence time (average time interval perceiving that stimulus). An influential synopsis of the relationship between stimulus contrast on the dynamics of rivalry was proposed by Levelt [2] in his four propositions:

- (I) “increase of the stimulus strength in one eye will increase the predominance of the stimulus”;
- (II) “increase of the stimulus strength in one eye will not [affect] dominance length for the same eye”;
- (III) “increase of the stimulus strength in one eye will increase the alternation frequency”; and
- (IV) “increase of the stimulus strengths in both eyes will increase the alternation frequency”.

To account for the empirical data on the role of stimulus properties in binocular rivalry [2–4], as well as on its neurophysiological correlates [5–8], a number of models have been put forward, most of which have been based on a reciprocal inhibition architecture, whereby the parts of the system that code for the two competing

percepts suppress each other [9–15,30]. Dominance switching is typically instantiated via slow negative feedback (e.g. population adaptation or synaptic depression variables). This negative feedback reduces inhibition exerted by the dominant side over the suppressed one. Some of the modelling efforts have been directed at the Levelt propositions outlined above. For example, Laing and Chow [12] developed a population rate model (derived from a network model of Hodgkin–Huxley-type neurons) containing two populations of neurons coding the competing percepts with reciprocal inhibitory connections between the two populations. In the model, the activity of the populations is sustained by recurrent excitation and reduced by population adaptation variables; the model also incorporates synaptic depression variables, which modulate the strength of recurrent excitation and that of reciprocal (mutual) inhibition between the competing populations. Laing and Chow [12] reported the model to be consistent with all the Levelt propositions, along with other empirical phenomena.

However, recently Shpiro et al. [16] showed that the Laing and Chow model and other models based on mutual inhibition do not always conform to the Levelt propositions. In particular, [16] set out to examine the models’ behaviour in relation to proposition IV (see above). Four models were subjected to scrutiny: the Laing and Chow model [12], two modified versions of this model (one without population adaptation and one without synaptic depression), and the model by Wilson [15]. Although the latter is mathematically different from the Laing and Chow model, the two share some important qualitative features: mutual inhibition between the model components representing the competing stimuli and the presence of a slow population adaptation process that is essential for the switching of dominance. Shpiro et al. [16] examined dominance durations for different stimulus contrasts, while also varying

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the values of the inhibition strength parameter. In addition, they assessed the effects of noise on the contrast–dominance duration relationship, the role of recurrent excitation (by omitting its term in the modified Laing and Chow models) and the effects of having a separate inhibitory population (present in the Wilson model and absent in the Laing and Chow model and its modifications).

The principal result was that none of the four models showed a monotonic dependence between stimulus contrast and dominance durations. The most common behaviour across models and inhibition strengths can be summarised as follows. For high stimulus contrast values, dominance duration decreased with increasing stimulus contrast as posited by the Levelt proposition IV (we will henceforth adopt Shpiro et al.’s terminology and refer to this as decreased duration, or DD, behaviour). For intermediate stimulus contrast values, no switching occurred, with one population active and other inactive indefinitely (“Winner Takes All” behaviour). For low stimulus contrast values, dominance durations increased with increasing stimulus contrast (increased duration, or ID, behaviour [16]). The “Winner Takes All” mode for intermediate stimulus contrast values was not found when the cross-population inhibition parameter had low values or when random white noise was introduced. However, the non-monotonic dependence between stimulus contrast and dominance duration was still observed (ID behaviour for lower contrasts and DD behaviour for higher contrasts). The presence of recurrent excitation (in the Laing and Chow model [12]) or that of a separate inhibitory population (in the Wilson model [15]) did not seem to influence the (non-monotonicity of the) relationship between stimulus contrast and dominance durations.

Another important finding of Shpiro et al. [16] concerned asymmetric input to the two eyes, which is relevant for the Levelt propositions I–III (see above). For the range of stimulus contrasts for which models showed DD behaviour, Shpiro et al. found that increasing stimulus contrast for one eye reduced dominance durations for the other eye’s percept, without affecting the dominance durations of the stimulus whose contrast was changed (consistent with propositions I–III). However, for the range of stimulus contrasts associated with ID behaviour, the effect of increasing stimulus contrast for one eye was inconsistent with propositions I–III, leading to an increase in dominance durations for the same eye’s percept.

The non-monotonic contrast–dominance relationship in all four models led [16] to highlight the mismatch between models and the Levelt propositions, particularly proposition IV. Our main contribution here is to produce a similarly motivated minimal model that nevertheless does produce “Levelt IV”-type (DD) behaviour all the way down to arbitrarily small stimulus contrasts. The model also shows behaviour compatible with propositions I–III in conditions of asymmetric stimulus contrast. This is achieved by means of “Winnerless Competition” between perceptual states.

### 1.1. Winnerless competition models for cognitive processes

Models of neural dynamics tend to be variational (i.e. they have an energy landscape that is explored by the dynamics). However, there is no *a priori* reason why they should be, other than this leading to an elegant understanding of their dynamics in terms of minimization on the landscape. In particular, there may be novel dynamical mechanisms for neural processes that do not fit into the energy landscape paradigm. A particular example of non-variational dynamics called “Winnerless Competition” (WLC) [17–19] was introduced by Rabinovich, Huerta and co-workers to explain a variety of switching-type responses and sequence generation for low-level neural microcircuits. Such dynamical models have robust attractors that are composed of a network of unstable states of ‘saddle type’ connected by their unstable

manifolds. The individual saddles appear to attract for a certain time, but any small components in the unstable directions grow, leading to eventual “switching” between saddles. In terms of nonlinear dynamics, such attractors have been studied for some time as *heteroclinic networks* and there is an extensive literature on their robustness, their stability (attractiveness) [19–21] and structure [22,23].

Although WLC has been primarily developed for low-level modelling (with few exceptions, e.g. [19]), it may be very useful for the modelling of higher-level cognitive processes [24]. This paper presents a case study of a model for binocular rivalry that is built on heteroclinic cycles. The model’s architecture shares some common characteristics with the models discussed above. It contains two components which represent neuronal populations each of which responds to one of the two stimuli. Based on single-cell neurophysiological data showing more dominance switching responses in binocular cells in areas V4 and MT [7], we are inclined to assume that these model components are not groups of monocular cells in the Lateral Geniculate Nucleus or the primary visual cortex, but populations of binocular cells in higher visual areas that code the perceptual features present in a given stimulus (which happens to be presented to one eye). However, they could equally represent competing groups of monocular neurons, which would be more consistent with recent neuroimaging evidence of low-level inter-ocular competition in binocular rivalry [5,8]. As in the models discussed above [12,15], in our model the neuronal populations corresponding to the two stimuli compete via reciprocal inhibition; like these models, ours also incorporates an adaptation process, which leads to saturation of activity in the two populations. However, unlike the above-mentioned models, our model also contains a third, “arbitration”, component. It could represent either a neuronal population that synthesises the inputs from modules specialised for particular stimuli/configurations, or the difference in activity between such specialised modules. In either case, the dynamics of the “arbitration” component underlies the perceptual state experienced (and reported) by the subject.

## 2. A simple winnerless competition model of binocular rivalry

We consider a simple model in  $\mathbf{R}^3$  of the perceptual processes involved in binocular rivalry, with connectivity as illustrated in Fig. 1. In this model we consider three dynamical variables that model the underlying population dynamics:

- The variables  $x$  (resp.  $y$ ) represent an activity pattern associated with the stimulus presented to the left (resp. right) eye.
- The variable  $p$  represents the activity in the “arbitration” component, which underlies the reported perceptual state.

We assume in the absence of  $x$  or  $y$  input that the dynamics of  $p$  has two stable states, one where the left eye is dominant and one where the right eye is dominant. We assume that the dynamics of  $x, y$  are usually at rest but, depending on input and currently perceived state, they can undergo a dynamical process (such as edge detection or comparison with a stored pattern) to attempt to recognize that particular pattern. If there is an input  $I_x, I_y$  that indicates the presence of one of the “perceivable” states associated with  $x, y$ , then this results in growth of that variable.

In particular, if the input does not conform with the currently perceived pattern (represented by the current value of  $p$ ) then the system dynamics will switch between the two possible states as shown schematically in Fig. 2. The system we consider is:

$$\begin{aligned} \dot{p} &= h(p) + x^2(1-p) + y^2(-1-p) + \eta_p \\ \dot{x} &= f(p, x, y) + I_x x + \eta_x \\ \dot{y} &= g(p, x, y) + I_y y + \eta_y. \end{aligned} \quad (1)$$

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