The time course of binocular rivalry reveals a fundamental role of noise

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When our two eyes view incongruent images, we experience binocular rivalry: An ongoing cycle of dominance periods of either image and transition periods when both are visible. Two key forces underlying this process are adaptation of and inhibition between the images' neural representations. Models based on these factors meet the constraints posed by data on dominance periods, but these are not very stringent. We extensively studied contrast dependence of dominance and transition durations and that of the occurrence of return transitions: Occasions when an eye loses and regains dominance without intervening dominance of the other eye. We found that dominance durations and the incidence of return transitions depend similarly on contrast; transition durations show a different dependence. Regarding dominance durations, we show that the widely accepted rule known as Levelt's second proposition is only valid in a limited contrast range; outside this range, the opposite of the proposition is true. Our data refute current models, based solely on adaptation and inhibition, as these cannot explain the long and reversible transitions that we find. These features indicate that noise is a crucial force in rivalry, frequently dominating the deterministic forces.

Keywords: binocular rivalry, bistable perception, noise, visual awareness, temporal dynamics, Levelt's second proposition, neural models

Introduction

When we present two discordant images to both eyes, binocular fusion gives way to binocular rivalry (e.g., Figure 1), a phenomenon characterized by ongoing perceptual alternations between the two images (Alais & Blake, 2005; Blake, 2001), similar to those occurring when viewing ambiguous figures such as the Necker cube. Understanding such bistable phenomena is important for the study of visual awareness. Arguably, they are an evident demonstration of fundamental processes underlying awareness, reflecting an ongoing effort of the visual system to select and reorganize sensory input to form consistent interpretations (Andrews & Purves, 1997; Leopold & Logothetis, 1999). In addition, because of the partial decoupling of stimulus and percept, rivalry is a valuable tool in studies into neural correlates of awareness in isolation from stimulation.

According to current ideas, binocular rivalry revolves around *cross-inhibition* and *slow self-adaptation* (e.g.,

Wilson, 2005). That is, both interpretations of an ambiguous stimulus have a neural representation, and these representations inhibit each other's activity. When one representation becomes stronger than the other, its inhibitory force on the other also increases and the situation develops to full activity (dominance) for one and to minimal activity (suppression) for the other representation. Then, slow self-adaptation gradually causes the dominant representation's activity to decline until a point is reached at which the balance tips in the opposite direction, and so forth.

Models based on these ideas can account for existing data on dominance durations (Kalarickal & Marshall, 2000; Lehky, 1988; Mueller, 1990; Stollenwerk & Bode, 2003; Wilson, 2005). Notably, they agree with Levelt's second proposition. In its original form, this proposition states that changing the strength (contrast) of one eye's stimulus, while fixing the other one, affects dominance durations only of the eye with the fixed contrast (Fox & Rasche, 1969; Levelt, 1966). More recent work (Bossink, Stalmeier, & De Weert, 1993; Mueller & Blake, 1989; see also Shiraishi, 1977) demonstrated small changes in the eye with the variable
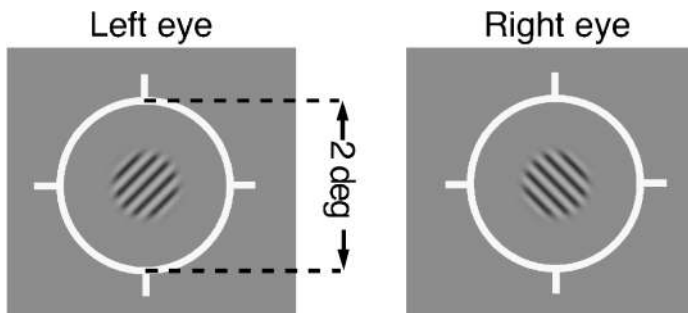
Figure 1. Our binocular rivalry stimulus.

contrast as well; thus, the currently accepted interpretation is that unilateral contrast changes *primarily* affect dominance durations in the fixed-contrast eye.

The good agreement between models and psychophysics is encouraging but somewhat misleading because the constraints posed by current psychophysical data are not very rigorous, as witnessed by substantial differences between the models cited above. It would seem, then, that current data do not allow all too specific inferences on the rivalry mechanism. Fortunately, there are indications that rivalry's alternation cycle is more diverse in its features than is usually taken into consideration and, therefore, carries more information on underlying mechanisms than the handful of rules constraining current models.

Specifically, each alternation cycle comprises not only periods with complete dominance of either percept but also substantial transition periods in which a compound of both is perceived (Blake, O'Shea, & Mueller, 1992; Bossink et al., 1993; Hollins, 1980; Mueller & Blake, 1989; Wilson, Blake, & Lee, 2001; Yang, Rose, & Blake, 1992). A further informative complication lies in the fact that, although most transitions mediate a dominance change from one eye to the other, some end up with dominance returning to the previously dominant eye (Mueller & Blake, 1989). These latter events, which we call *return transitions,* have not yet been studied systematically. Finally, what we do know of rivalry's dynamics all comes from studies that measured at a limited set of specific contrast settings (e.g., fixing one eye's contrast at a chosen value and varying the other one) and not throughout the range of contrasts that we may present the eyes with.

In this study, we aim to get a more complete view of the dynamics of binocular rivalry, including dominance durations, transition durations, and the occurrence of return transitions. We study these for a matrix of left-eye and right-eye contrast combinations spanning the entire range from near the detection threshold to the theoretical maximum. We subsequently test whether current rivalry models can account for these dynamics.

Using a conventional orthogonal grating stimulus (Figure 1), we demonstrate that dominance durations, transition durations, and the frequency of occurrence of return transitions (fraction of return transitions [FRT]) all systematically depend on stimulus contrast. This dependence is similar for dominance durations and the FRT but different for transition durations. Regarding dominance durations, we show that Levelt's second proposition (in its currently accepted form) is accurate only in a limited contrast range and may be replaced more generally by the statement that unilateral contrast changes mainly affect dominance durations of the *higher contrast* eye. These findings show that the data underlying current ideas represent only a fraction of the rich behavior of this system. The more complete characterization presented here allows new inferences on the mechanism of rivalry and poses more stringent model constraints. Indeed, we demonstrate, using simulations, that existing models cannot reproduce our findings. Specifically, systems based exclusively on cross-inhibition and slow self-adaptation cannot account for the many return transitions and long transition durations that we find. These features of the alternation cycle point toward neural noise as an essential driving force underlying rivalry.

Methods

Four subjects, one author and three naive individuals, with normal or corrected-to-normal vision, participated. The stimulus (Figure 1) consisted of sine-wave gratings (6.5 cycles/deg) filling a circular patch ($r = 0.31°$) with constant contrast plus a surrounding region in which intensity fell off following a Gaussian profile (half-width, 0.06°), that is, a "soft stimulus edge." Average luminance of both stimulus and background was 15 cd/m^2. For fusion, we used an alignment ring ($r = 1°$; 50 cd/m^2) with four lines extending 0.27° outward in the cardinal directions and a binocular pattern of open squares (side, 0.34°; 50 cd/m^2) sparsely scattered across the screen from 13° above and below the center onward. Subjects reported percepts by pressing and holding either of two buttons corresponding to exclusive visibility of either eye's image or releasing all keys in case of a transition. Because releasing the keys is also a natural response when one is uncertain of the percept (e.g., due to temporally unaligned eyes), subjects were instructed to press a third button to indicate such episodes. We sampled a 4 × 4 matrix spanning the full domain of left-eye/right-eye contrast combinations. The four contrast values were customized per subject based on their detection threshold. We therefore determined for each subject the contrast, yielding 75% correct for gratings presented monocularly (an otherwise identical stimulus) in a two-interval, two-alternative forced-choice QUEST (Watson & Pelli, 1983) procedure. We verified that this value was similar for both eyes and orientations, and we used the average to determine the contrast range: The lowest one was 0.75 log$_{10}$ units Michelson above 75% detection, which meant 15% Michelson on average for these subjects; the highest one was 100% Michelson (the theoretical maximum), and we interpolated the other two in equal log

steps. Contrast conditions were distributed randomly over trials. Sessions consisted of four 5-min experimental trials (see the Appendix for remarks on this duration) and a 2-min control trial each. The first minute of each trial was discarded. Control trials, in which contrasts were always 100%/100% Michelson, were compared over sessions to verify subjects' constant performance, leading a fifth subject's data to be excluded from analysis. Each subject produced an average of about 180 dominance durations per condition per eye and the accompanying transition durations.

Results

Figure 2 shows the results for a typical subject (Panel A) and averaged over all four (Panel B). The top and middle charts show dominance and transition durations; the bottom ones show the FRT, that is, the fraction of transition periods after which dominance returned to the previously dominant eye instead of crossing over. Return transitions were not included in the calculation of transition durations, a choice that did not notably affect any of our conclusions. None of the subjects showed a significant eye preference; thus, data could be pooled over eyes. Consequently, regarding dominance durations, contrasts are given for the ipsilateral and contralateral eye, that is, for the eye of which durations are plotted and for the other eye, respectively. Concerning transitions, we use the terms "departure" and destination contrast, that is, in the eye that was dominant before the transition and in the other one, respectively.

Figure 2 shows that both dominance and transition durations are on the order of seconds, with dominance phases taking up the most time. Furthermore, return transitions are almost absent in some conditions, but in other conditions, they make up as much as about half of all transitions starting from a given eye. Dominance durations (top) and the FRT (bottom) show similar patterns of contrast dependence, both being enhanced by a high ipsilateral/departure contrast and attenuated by a high contralateral/destination contrast. In addition, both values increase slightly when contrast is lowered symmetrically in both eyes, but this rise is small compared to the off-diagonal effects. Transition durations (middle) show a different pattern of contrast dependence, with the roles of departure and destination contrast being largely equivalent. As a result, transition durations are largest when both contrasts are minimal (cf. Hollins, 1980).

A restriction to Levelt's second proposition

A hallmark of current ideas on rivalry, known as Levelt's second proposition, is the notion that a change in one eye's contrast has a strong effect on the other eye's dominance durations, and only a weak effect (or none, in the original formulation) on those of the eye itself. This has been shown in experiments in which one eye's contrast was fixed while
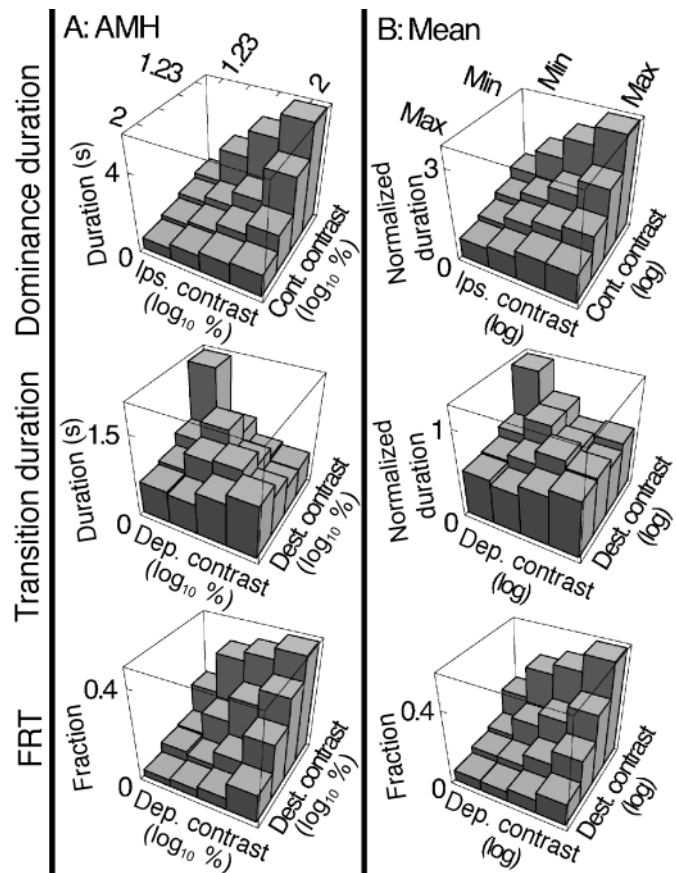
Figure 2. Dominance durations, transition durations, and the FRT as a function of the two eyes' contrasts, for one subject (A) and averaged over all four (B). Ipsilateral (ips.) and contralateral (cont.) refer to the eye whose dominance durations are plotted and to the other eye, respectively. Departure (dep.) and destination (dest.) refer to the eye that was dominant before a transition started and the other eye, respectively. Contrasts were customized for each subject, with "Min" meaning near detection threshold and "Max" meaning 100% Michelson. Durations in Panel B were normalized per subject relative to the dominance duration in the 100%/100% contrast condition (1.2, 0.9, 1.6, and 0.9 s for these subjects); hence, proportional relations between dominance and transition durations are preserved. The figure shows that dominance and transition durations are both on the order of seconds and that the FRT varies between about 0 and as much as 0.5, depending on condition. All three quantities show a systematic dependence on contrast, which is similar for dominance durations and the FRT but different for transition durations.

the other one was varied. To test if our data support this notion, we reconstructed four such experimental regimes from our data, as shown in Figure 3. The bottom-right inset, depicting a schematic top view of a chart such as in Figure 2, illustrates this: Taking a section through the matrix at a given ipsilateral contrast (dashed line; e.g., purple) and combining it with the section at the same contralateral contrast (solid line; same color) yields the data for one such regime. The four reconstructions differ
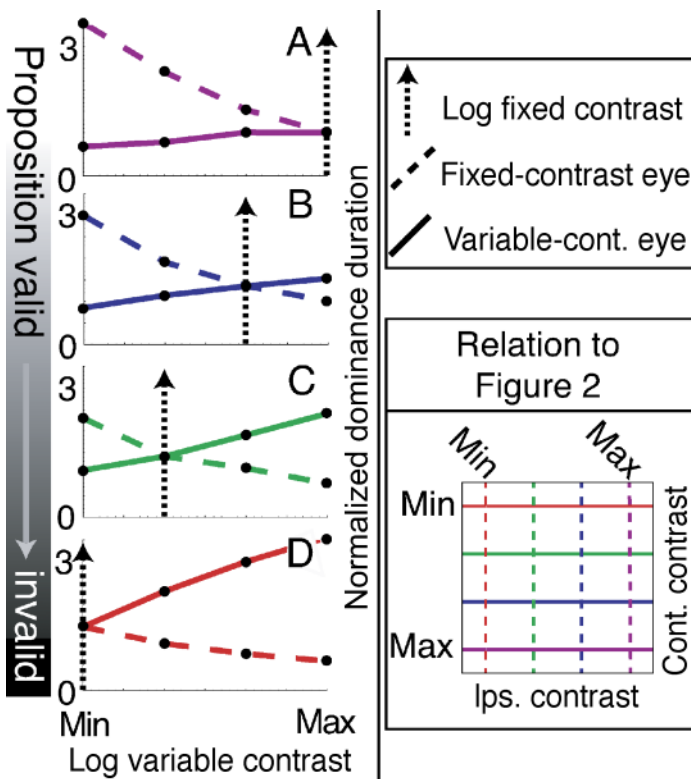
Figure 3. Levelt's second proposition. In its current form, this proposition states that a change in one eye's contrast primarily affects the other eye's dominance durations rather than those of the eye itself. It is based on experiments where one eye's contrast was fixed and the other one was systematically varied. From our data, we took four subsets corresponding to such experimental regimes, as shown in the bottom-right inset, schematically depicting our 4 × 4 ipsilateral/contralateral contrast matrix. Each color denotes one subset, with the solid lines indicating the data points for the variable-contrast eye (i.e., contralateral contrast fixed) and the dashed lines those for the fixed-contrast eye (i.e., ipsilateral contrast fixed). Panels A–D show across-subject averages, using the same colors as in the inset. (A and B) At high values of the fixed contrast (dotted arrows), we see the classic pattern. (C and D) At lower values, however, this pattern subsides and reverses. The proposition therefore applies only in a restricted portion of the contrast domain, namely, where the fixed contrast is high. Outside this domain, the opposite of the proposition becomes true.

in the level of the fixed contrast (dotted arrows in Panels A–D). Panels A–D depict the reconstructions from our across-subject averages, with colors corresponding to those in the inset. Panels A and B show the classic result: As the contrast in one eye is altered, dominance durations change mainly in the other eye. However, Panels C and, especially, D show that the pattern subsides and actually reverses for lower values of the fixed contrast: Here, the main effect is in the eye in which the contrast is changed. The validity of the proposition therefore depends entirely on the subsection of the data one considers: valid at high values of the fixed contrast but invalid at lower ones.
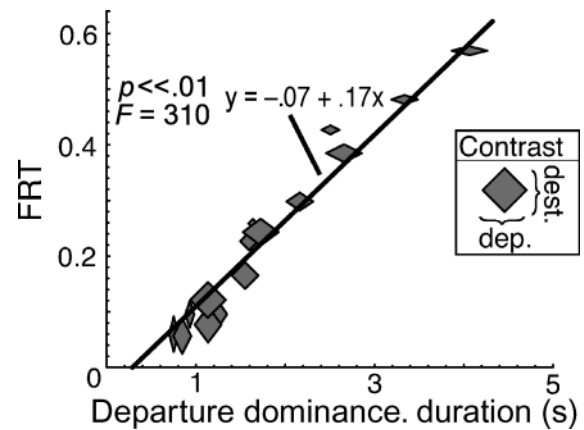

Figure 4. Relation between the FRT and mean dominance duration of the departure eye, in various contrast conditions. The width and height of the rhombi symbolize ipsilateral and contralateral contrast, respectively. Dominance durations and the FRT show a positive linear correlation, as indicated by the regression line. p is ANOVA p value; F is ANOVA F ratio. These data point toward a common underlying variable, responsible for trends in both departure dominance durations and the FRT.

Return transitions and dominance durations

Figure 2 showed similar contrast dependencies for dominance durations and the FRT. Here, we examine this similarity more closely. Figure 4 displays across-subject averages of the FRT as a function of mean dominance duration in the departure eye; that is, it shows how transitions starting from dominance for a given eye are related to dominance durations of that eye. The horizontal extent and the vertical extent of the 16 rhombi symbolize ipsilateral and contralateral contrast, respectively, with smaller values corresponding to lower contrast. There is a clear positive correlation between dominance durations and the FRT, as quantified by the regression line. It turns out that there is no *direct* causal link between the occurrence of a return transition and the occurrence of a long-lived percept (see the Appendix); that is, one does not cause the other. Instead, the correlation stems from a common dependence on an underlying variable, strongly influenced by contrast. In addition, irrespective of contrast, our data showed a tendency for subjects with long dominance durations to experience many return transitions, strengthening the notion that both quantities are connected.

Comparison with existing models

We performed simulations (see the Appendix) with three prevailing models based on adaptation and inhibition, which agree with experiments to date (Kalarickal & Marshall, 2000; Stollenwerk & Bode, 2003; Wilson, 2005). To verify if these

models can reproduce our findings, we tested their predictions on dominance durations, transition durations, and the FRT for a matrix of ipsilateral/contralateral input strengths.

To adequately cover transitions, we chose two distinct classes of models, each addressing one of the two types of transitions that may occur (see also the Discussion section). The Wilson model and the Kalarickal and Marshall model cover *superposition* transitions, during which both images are seen superimposed (Burke, Alais, & Wenderoth, 1999; Liu, Tyler, & Schor, 1992), whereas the Stollenwerk and Bode model covers *piecemeal* transitions, during which parts of both images are seen in complementary regions of the stimulus (Blake et al., 1992; Lee, Blake, & Heeger, 2005; O'Shea, Sims, & Govan, 1997; Silver & Logothetis, 2004; Wilson et al., 2001).

The models by Wilson and by Kalarickal and Marshall comprise a single oscillator formed by the two percepts' representations interacting via adaptation and inhibition. Piecemeal transitions are beyond their scope as they have no spatial dimension. We defined superposition phases as those when none of the representations strongly dominates, but instead, both are intermediately active.

The model by Stollenwerk and Bode involves oscillators similar to those described above, but several of them linked together in a 2D network, corresponding to neighboring zones in visual space. Neighboring oscillators are coupled such that they tend to follow each other's dominance states, so that once a dominance change emerges in one location, a piecemeal transition may occur. We defined transition periods as those during which less than 100% of all oscillators were in the same dominance state.

Figures 5A–C display simulation results at the original papers' parameter settings. From left to right, the charts in each panel show dominance durations, transition durations, and the FRT as a function of input strength. The white bars in the left charts reproduce the original papers' demonstrations of agreement with Levelt's second proposition. They also illustrate how we complemented the original input strength combinations to form 4×4 matrices. Aside from the white bars, the models show a striking lack of concordance, underscoring the added constraints posed by the present characterization. The charts show marked deviations from our data. First, all models predict transitions to be much shorter than dominance phases rather than of the same order and also underestimate the FRT. Second, contrast dependence of particularly transition durations and the FRT is not correctly reproduced.

To see if model predictions would improve at other parameter settings, we performed simulations at an extensive range of values, confirming the shortcomings discussed above. There was one parameter region for the Kalarickal and Marshall model, however (Panel D), where the contrast dependence of all three variables was in qualitative agreement with our data, although both transition durations and FRT were overestimated. Interestingly, at these parameter settings, the system is in a mode entirely different from the one that was originally intended (see the
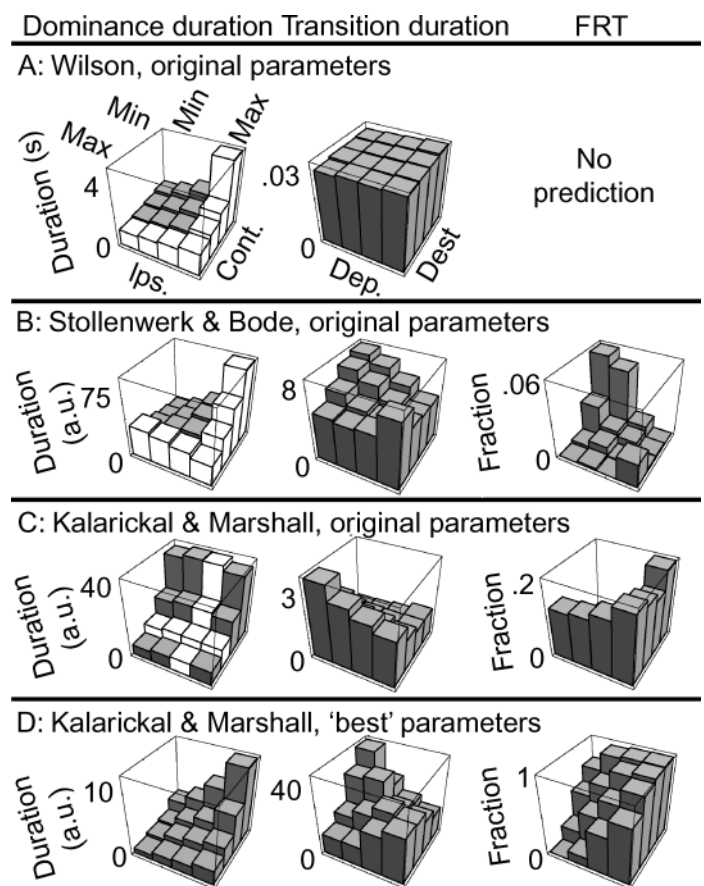

Figure 5. Validation of three existing models. The left charts of each panel show simulated dominance durations as a function of ipsilateral (ips.) and contralateral (cont.) input strength; the middle and right ones show transition durations and the FRT as a function of departure (dep.) and destination (dest.) input strength (the Wilson model produces no return transitions as it is noise-free). Durations are given in seconds for the Wilson model and in arbitrary units (a.u.) for the remaining ones. Panels A–C show results at the original parameter settings, with the white bars reproducing the original demonstrations of agreement with Levelt's second proposition. Although all three models support the proposition (for a limited range of inputs), their behavior diverges at most other points. In addition, there are marked deviations from our data. First, the models incorrectly predict at least an order difference between dominance and transition durations and underestimate the FRT. Second, none of the models reproduces the found patterns of contrast dependence of transition durations and the FRT. (D) In simulations at other parameter settings, we found one parameter region for the Kalarickal and Marshall model where the results were reminiscent of our data. Here, contrast dependencies of all three variables were qualitatively correct but were accompanied by an overestimation of both transition durations and the FRT. Further analysis (see the Appendix) shows that in this region, model dynamics are essentially stochastic: Deterministic forces keep the system in a state intermediate between both dominance states, and it is noise that causes incidental excursions into either dominance percept.

[Appendix](): Its deterministic dynamics have settled at intermediate activities for both representations, and it is purely noise that causes the oscillations manifested in the figure.

Discussion

Noise and rivalry dynamics

Our most striking finding is that current ideas on the system underlying rivalry do not agree with the observed dynamics. Broadly speaking, we show that there is much more to the alternation cycle than current models can explain, and no single adjustment will likely bridge this gap. More specifically, however, there is one aspect wherein the deviation between models and data is particularly strong and which to us indicates one necessary model addition. This aspect is the behavior of transitions: These are presently treated as brief and irreversible switches between two dominance periods, whereas the data show that they take considerable time and that return transitions are common. We will argue that the features of transitions in current models follow from an overemphasis on the role of slow adaptation and that our results point to a system in which part of this role is taken over by stochastic variations (i.e., noise) in the system components.

This is illustrated in Figure 6, schematically showing perceptual dynamics of rivalry as motions across energy landscapes (e.g., Billock & Tsou, 2003). The system state (ball) always develops toward lower energy; thus, minima in the landscapes are fixed points (attractors), corresponding to left-eye and right-eye dominance. Changes in the landscapes are due to changes in adaptation state, temporarily modifying the relative strength of the attractors. Sequence A→B→C-I shows the situation as many current models treat it. A: The ball occupies the left attractor, indicating, for example, left-eye dominance. A→B→C-I: Slow adaptation destabilizes the occupied attractor (black arrow), while recovery from adaptation deepens the other one (white arrow), until the left attractor disappears (C-I), causing the ball to move (dashed arrow) through the transition region (gray) to the remaining attractor. This transition takes place quickly, and not until considerable time has passed, allowing the left attractor to reappear, may the system return to its previous state. This separation of timescales between landscape changes and ball movement is necessary for these models to oscillate, yet it is clear that the long transition durations and particularly the existence of return transitions, corresponding to the ball moving halfway between both attractors and then returning, argue against this type of system. In Panels C-II and C-III, we show two (not mutually exclusive) alternatives to Panel C-I that do agree with our data. C-II: In this scenario, transitions are not initiated by destruction of the occupied attractor but by noise (curved arrow) tossing the system into
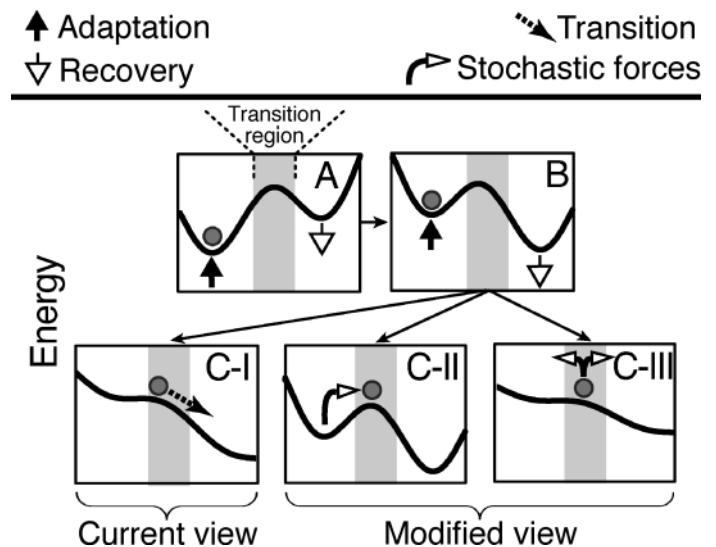
Figure 6. Schematic representation of rivalry's dynamics as currently understood (A→B→C-I) and as our data imply (A→B→C-II and A→B→C-III). Dynamical modes of the system are shown as energy landscapes. The two minima are stable states (attractors), corresponding to left-eye and right-eye dominance. (A) The ball occupies the left attractor, indicating left-eye dominance. (A→B→C-I) Adaptation (black arrow) destabilizes the occupied attractor as recovery from adaptation (white arrow) deepens the other one. Panel C-I shows transitions as treated by current models: As the occupied attractor disappears due to adaptation, the system moves to the remaining one (dashed arrow). It cannot return to the left attractor until (recovery from) adaptation has changed the landscape to the mirror image of Panel C-I. This scenario is incompatible with the slow and reversible transitions we observe, which point toward scenarios such as sketched in Panels C-II and C-III. (C-II) Transitions are initiated by noise (curved arrow), driving the system out of the still present attractor to a location in the transition region (gray) near the separation between both attractor domains. Here, deterministic forces are small and the system may develop in either direction. (C-III) The system remains in the attractor until it is gone, but the deterministic forces in the transition region are so small that the attractor may reappear before the transition is over. Again, noise may tip the system to the left or to the right. Both scenarios imply a crucial role for noise.

the transition region near the maximum that separates the left and right domain of attraction. Here, the slope is shallow; that is, deterministic forces are weak and may be positive or negative depending on the actual system state. This may explain both the long duration of transitions and the frequent occurrence of returns. C-III: Here, the slope in the transition region is so low (that is, the deterministic dynamics here are so slow) that the attractor may reappear before the transition is over. Again, this is in line with long transitions and provides an opportunity for noise to tip the system over in either direction. We think that this latter scenario is particularly likely at lower contrasts (see below). Both scenarios point to a strong stochastic term as a key ingredient missing from present thinking.

As such, the notion that noise plays a role in rivalry is not new, and indeed, it is obvious that no biological system is noise-free. Particularly, stochastic variations in dominance durations are well known (Brascamp, van Ee, Pestman, & van den Berg, 2005; Fox & Herrmann, 1967; Levelt, 1967) and can be reproduced by current models (Kalarickal & Marshall, 2000; Lehky, 1988; Stollenwerk & Bode, 2003; Wilson, 2005). However, to account for the stochastics of dominance durations, on the level of detail that has hitherto been considered, it suffices to add jitter to essentially deterministic systems (e.g., Lehky, 1988). The exact nature of this jitter is of little importance, and even if it is left out entirely, the dynamics are not notably affected (Wilson, 2005). Consequently, the view of noise that has dominated the literature so far is of a detail that introduces some unpredictability to a course of events that is itself governed by deterministic forces. The role that we propose for noise, on the other hand, is of quite a different order. Our data imply stochastic forces that are on a par with deterministic ones, frequently dominating them. Relevant models, therefore, require careful consideration of the nature of this noise and will display dynamics that differ fundamentally from those of current models. To put it another way, the point is not *that* noise plays a role in rivalry; the point is that it is a crucial factor for the system to function the way it does.

One recent study (Kim, Grabowecky, & Suzuki, 2006) extensively dealt with noise in rivalry, and it is important to discuss their findings in relation to ours. Like those authors, we are convinced of the importance of noise and we also endorse their assertion that more empirical constraints, like the ones presented here, are required to infer the internal workings of this system. In addition, Kim et al. take some important steps toward characterizing the relevant noise components by calculating the amount of external perturbation that is equivalent to the system noise and by showing that this amount scales linearly with stimulus contrast. We significantly add to their conclusions by providing compelling evidence that noise is indeed a dominant factor underlying oscillations in unperturbed rivalry. In addition, whereas their data did not allow them to distinguish between various models (although the data did constrain the nature of the noise component), our data indicate shortcomings in all models we tested.

Given the importance of noise, we may wonder where in the system these random fluctuations originate. There is presently no definitive answer to this question but let us consider the options. From studies dealing with noise in the context of visual detection and discrimination, we know that signal loss may arise at any level of visual processing: from retinal photoreceptors and ganglion cells to the cortex itself and both prior to and beyond binocular combination (Pelli, 1990; Raghavan, 1989). In addition, eye movements (both blinks and saccades) can influence the rivalry percept (van Dam & van Ee, 2006; Wade, 1975), providing a possible noise source on the input side (but note that Kim et al., 2006, report similar results in the absence and presence of blinks). Finally, there is the possibility of deterministic chaos (Laing & Chow, 2002; Wilson, 2005), which, although technically deterministic, is equivalent to noise on the present level of analysis. One intriguing possibility to note on the side is that, regardless of its origins, here, noise may represent more than simply a physical limit on the system's accuracy: In the context of rivalry, it may instead be of functional use. Arguably, rivalry's alternations reflect a general property of vision to continuously reorganize sensory input to reach a perceptual solution (Andrews & Purves, 1997; Leopold & Logothetis, 1999). In such a framework, noise may act to destabilize the present organization and prevent the brain from getting trapped in a single interpretation while others may have more survival value (Kim et al., 2006).

Although we emphasize the role of noise in rivalry, we do not deny the importance of deterministic forces like adaptation and inhibition. Figure 5D is instructive in this respect, showing results from the Kalarickal and Marshall model in a parameter regime (see the Appendix) where the system has only one attractory, which is permanent, that is itself moved around by noise. One definitive argument against this system, and against most purely stochastic systems, is that it produces exponential-like distributions of dominance durations, which is incorrect. Rather, all evidence points to a system characterized by an *interaction* between deterministic and stochastic forces. Specifically, deterministic dynamics likely dominate the part of the alternation cycle when the occupied attractor is deep, while noise drives the system in the temporal vicinity of a transition. This view is further supported by recent findings (Lankheet, 2006) showing that noise added externally (i.e., to the stimulus) primarily (although not exclusively) has an effect in a small time window near the transition.

Levelt's second proposition

A surprising finding of our study is the fact that Levelt's second proposition, a widespread notion considered crucial for assessing the validity of models, is not generally applicable. It should be emphasized that the present findings are qualitatively different from other demonstrations of the limits of the proposition: Previous work has already led to the attenuated view, generally accepted to the present day, that the effect of a unilateral contrast change is not *exclusively* but *mainly* in the fixed-contrast eye (Bossink et al., 1993; Mueller & Blake, 1989). Our data, on the other hand, show that, under certain conditions, the main effect is in the *variable*-contrast eye, so that one may just as accurately (and just as incompletely) claim the opposite of the proposition. The reason that this has so far been overlooked seems to be simply that the proposition had not yet been tested for the full contrast range that we considered: Levelt based the proposition on measurements in which one target was fixed at 89% contrast while the other was adjusted down to 8% (Levelt, 1966), and to our knowledge, no subsequent study

has done the converse, that is, fix one contrast at a low value and then increase the other one to near maximum, which are the conditions crucial to our conclusions. In other words, although the proposition is correct in the contrast range in which Levelt and subsequent authors measured, it does not generalize beyond this range. It is therefore not a general feature of rivalry and one should act with caution in attaching any particular significance to it. In terms of model constraints, the most appropriate description of the relation between contrast and dominance durations is probably not any single proposition but the three-dimensional surface implied by Figure 2. As a rule of thumb for experimenters, on the other hand, the most accurate alternative for the proposition may be the statement that "changes to one of the two contrasts mainly affect dominance durations in the higher contrast eye."

The nature of transitions

As previously noted, transitions may be either local (superposition) or spatial (piecemeal) (Blake, Zimba, & Williams, 1985; Hollins, 1980; Liu et al., 1992; Yang et al., 1992). For the specific conclusion that noise is of great importance, it is not necessary to distinguish these two types: Although slow transitions may partly be explained by a series of fast local transitions adding up to a longer spatial one, the return transitions in our data form a compelling argument for noise regardless of transition type. Ultimately, however, binocular rivalry cannot be understood without a clear view of the nature of transitions because the two types correspond to entirely different system states. Specifically, the occurrence of piecemeal transitions points toward parallel rivalry in a number of separate (but linked) modules as in the Stollenwerk and Bode model (Blake et al., 1992; Stollenwerk & Bode, 2003; Wilson et al., 2001). A powerful paradigm to study such transitions in isolation has recently been developed (Lee et al., 2005; Wilson et al., 2001). The occurrence of superposition, on the other hand, indicates that the system is reaching the limits of bistability and approaching fusion, as noted by Liu et al. (1992), who were able to study this perceptual state in the period directly following stimulus onset. Clearly then, it is of value to know which type dominated in our study. Because the nature of our main experiment, in which subjects tracked their percepts in real time, did not allow a distinction between the two types, which often occur simultaneously or in quick succession, we performed a control experiment (see the Appendix) to address this issue. Subjects observed 10-s binocular rivalry trials wherein a number from 1 to 5 is assigned to each trial as a whole, with 1 meaning that all transition percepts in this trial were superposition percepts and 5 meaning that they were all piecemeal. This control involved the same stimuli and subjects as the main experiment, but we used only the four symmetric contrast conditions. The outcome was clear-cut: Going from high to low contrast, all subjects had a monotonic decrease in their scores, from *mostly piecemeal* (4.1 on average) at high contrast to *mostly superposition* (2.1 on average) at low contrast. These results underscore that both local and spatial transitions play a role in rivalry, with piecemeal percepts dominating at high contrast and superposition becoming more prominent as contrast decreases. Our findings dovetail nicely with existing literature, as our transition durations at high contrast (about 0.5 to 1 s) agree well with the lower limit predicted in case of pure piecemeal transitions (the time required for a border between two regions of opposite dominance to sweep over our stimulus, calculated based on Horton and Hoyt, 1991; Wilson et al., 2001), whereas superposition periods at stimulus onset have been shown to be particularly prominent at low contrast (Liu et al., 1992).

Note that the changes in the transition phase that accompany a contrast reduction occur gradually, with the first effects, regarding both their durations and the subjects' assessment of their nature, being apparent at contrasts as high as 50%. This argues against the notion (Liu et al., 1992) that a separate neural mechanism is responsible for binocular summation at low contrast, which would be supported for instance by a discontinuity in the transitions' features near the low contrast end. A more parsimonious interpretation of the present data is that what we observe is a gradual evolution of the binocular rivalry process from one that produces abrupt perceptual flips to one that has more gradual transitions, with stable binocular summation being a limiting case at near-threshold contrasts. Such a gradual evolution is a natural property of many oscillator models, as illustrated by Panel C-III in Figure 6, which shows that shallowing of the attractors at low contrast can be accompanied by increased stability of the region in between. Hence, although the possibility of a separate summation process cannot presently be excluded, the data do not force us to invoke any such additional mechanism.

Future research

The perspective on rivalry developed here gives rise to new questions. For instance, one would like to know *how* noise affects rivalry dynamics. Conversely, rivalry's alternation cycle may, within the proper interpretative framework, offer a new handle to assess the nature of internal noise, a lively debated issue in the field of visual detection and discrimination (e.g., Gorea & Sagi, 2001; Kontsevich, Chen, & Tyler, 2002; Legge & Foley, 1980). We think that the two different roles that noise may play in the rivalry process, as illustrated in Figure 6, offer two natural starting points for exploring such issues. First (Panel C-II), noise plays a role in terminating dominance phases by pushing the system out of an attractor corresponding to exclusive dominance. Second (Panel C-III), noise in part determines when and in which direction transition phases end by affecting the path of the system in the transition region. The observable outcome of these two processes is formed by distributions of dominance and transition durations, respectively.

With this in mind, we are currently developing models (Brascamp, Noest, van Ee, & van den Berg, 2006; Noest & van Ee, 2006) of dominance and transition phases separately, allowing us to interpret the shapes of these distributions in terms of neural interactions and to further our understanding of the rivalry process, particularly of the role played by noise.

Conclusion

We have investigated binocular rivalry's alternation cycle in terms of both mean dominance and transition duration and the FRT, in relation to stimulus contrast. Both dominance and transition durations were on the order of seconds; the FRT varied between about 0 and as much as 0.5. We found systematic patterns of contrast dependence for all three variables, similar for dominance durations and the FRT but different for transition durations. Regarding dominance durations, we show that Levelt's second proposition is valid only in a limited portion of the contrast domain and may be replaced more generally by the proposition that changes in one eye's contrast mainly affect dominance durations in the *higher contrast* eye. We found a strong correlation between the FRT and mean dominance duration of the departure eye, which shows the presence of a common variable underlying both quantities.

Our data allow inferences regarding rivalry's mechanism not allowed by previous data and provide more stringent model constraints. They refute prevailing models driven by adaptation and inhibition as these underestimate both transition durations and the FRT and predict incorrect patterns of contrast dependence. The data imply a crucial influence of stochastic variations in the neural circuitry mediating rivalry, which these models overlook.

Appendix

Trial duration and fatigue

Our experimental trials were longer than usual in the literature (5 min), and it is important to rule out the possibility that subject fatigue played any role in our results. Figure A1 shows what Figure 2 would have looked like, had we analyzed only the first 2 min of every trial rather than the last 4 min. Clearly, there are no important differences between this figure and Figure 2, indicating that trial duration is not a crucial factor.

Dominance durations and return transitions

The correlation between departure dominance duration and FRT shown in Figure 4 can have either of two expla-
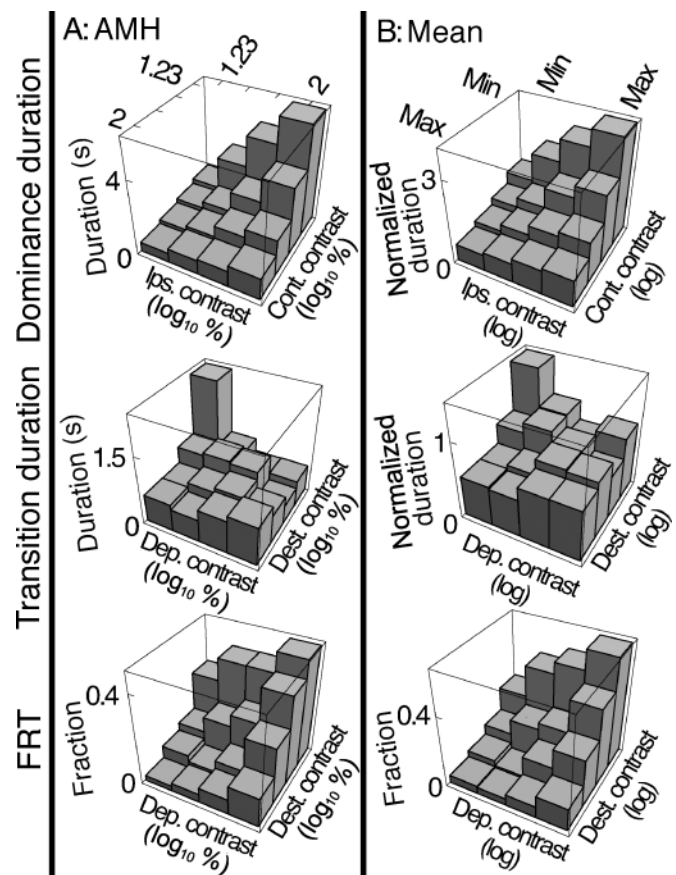

Figure A1. Same as Figure 2, using data from only the first 2 min of every trial. This figure and Figure 2 are almost identical, demonstrating that trial duration did not crucially influence our results.

nations. First, both may depend on a common underlying variable (an indirect causal link), or second, the occurrence of a return transition may cause a long duration or vice versa (a direct causal link). Figure A2 unconfounds these options. For every return transition away from and back to a given eye, we considered the 10 last dominance durations (normalized per trial and eye separately) of that eye preceding the return transition and the 10 first ones occurring afterward, rank numbering in time from −10 to −1 and from 1 to 10. This enabled us to calculate the average dominance duration per rank number. A direct causal link would show up as a positive deflection near the return transition in this event-related average. Figure A2 shows no such deflection; thus, the correlation is instead due to a common factor causing both phenomena. Strikingly, there is even a *negative* deflection at rank numbers −1 and 1. This may be explained as follows. Subjects employ some decision criterion as to the amount of suppressed-eye contamination in a dominant percept that will cause them to report the onset of a transition. If, as we propose, a transition is a gradual, errant process, then there are occasions on which a dominant percept is temporarily disturbed by some *near-criterion* amount of contamination before it restabilizes. On some of these occasions, subjects
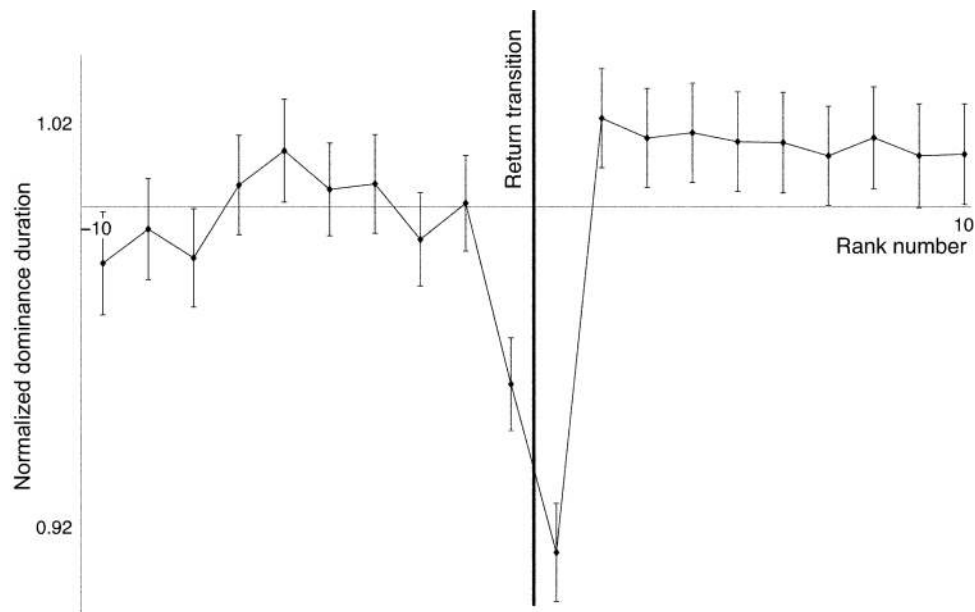
Figure A2. Event-related average dominance duration for the departure eye, relative to the occurrence of a return transition. The absence of a positive deflection for dominance durations near the return transition excludes the option that the positive correlation shown in Figure 4 arises because return transitions cause long dominance durations or vice versa. Instead, the correlation must be due to a common underlying variable. The *negative* deflection that is evident instead is not unexpected if we consider a transition as a gradual, errant process (see text). Error bars indicate standard errors.

will report a return transition and thereby cut the present dominance duration into two shorter ones, whereas on other occasions, they will not. This would explain the deflection in the figure.

Simulations

The results in Figures 5A–C are for the parameter settings used by the original authors. For the input strengths, we took four values equidistant in log space, with the smallest and largest ones based on the original papers: 0.9 and 1.5 for Stollenwerk and Bode, 0.853 and 1 for Wilson, and 0.3 and 0.7 for Kalarickal and Marshall. For the single-oscillator models, we defined transitions as those periods during which both pools' activities lay within a factor of 4 from each other; for the multiple-oscillator model, the criterion was that less than 100% of the oscillators should be in the same dominance state, that is, have the strongest activity for the same percept. For the single-oscillator models, we explored the surrounding parameter space by varying all parameters from half to twice their original values in three (Kalarickal and Marshall) or four (Wilson) equal log steps. For the multiple-oscillator model, simulation time did not allow this; hence, instead, we fixed the two parameters defining the sigmoid nonlinearity involved in the model and varied the remaining six variables from 2/3 to 3/2 times their base values in two equal log steps. For these latter simulations, we reduced the number of coupled oscillators to 10×10 to fit our stimulus, based on the assumption that one oscillator covers about $0.1°$ of

visual angle: roughly the maximum stimulus size for which rivalry is non-piecemeal (Blake et al., 1992). Along with the lattice size, we reduced the base value for ρ_0, the spatial extent of noise, by a factor of 2 because Stollenwerk and Bode tuned that value for a 20×20 lattice. For all simulations, we used an explicit Euler iteration scheme, with step sizes of 0.1 (Stollenwerk and Bode), 0.02 (Kalarickal and Marshall), and 0.001 (Wilson). Note that in the Kalarickal and Marshall model, noise is applied to the adaptation *state,* rather than to its *rate* as implied by the original equations (G.J. Kalarickal, personal communication).

Besides the above simulations, we performed simulations at the original settings to verify our correct reconstruction of the models. Figure A3 shows the outcomes along with those read from the original figures. The close agreement confirms that our reconstructions were correct.

Kalarickal and Marshall model, "best" parameters

As shown in Figure 5D, there exist parameter settings at which the Kalarickal and Marshall model is in qualitative agreement with our data. It turns out that at these settings ($W_1^+ = W_2^+ = 0.315$; $W_{12}^- = W_{21}^- = 125$; $c_1 = 0.005$; $c_2 = 0.016$; $c_3 = 0.105$; $s = 0.005$), the model has not two but one attractor, and the dynamics are entirely governed by noise. This situation is illustrated in Figure A4, Panel A by a phase plane plot, displaying the states that the system may occupy in terms of both pools' activities (x_1 and x_2). For any system state, or $x_1 x_2$ combination, x_1
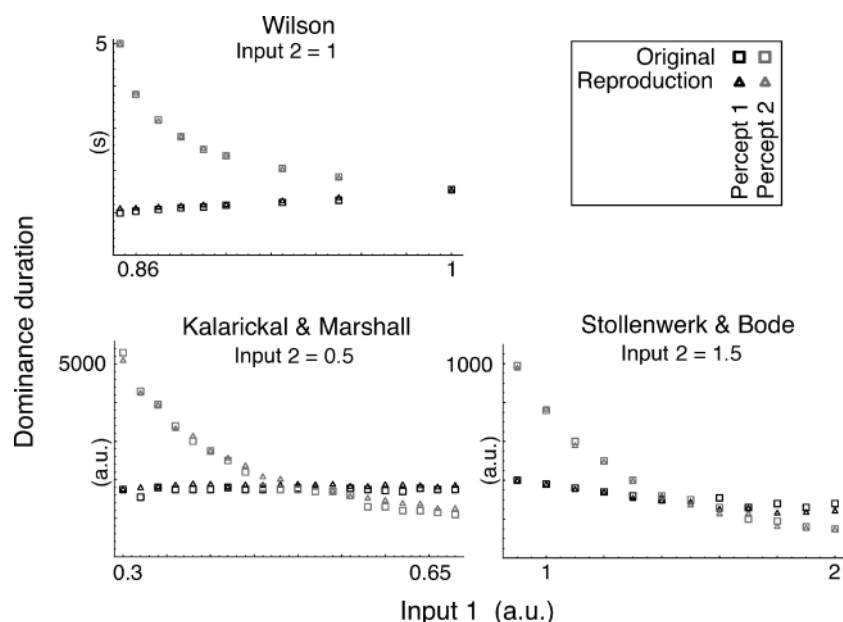
Figure A3. The original papers' simulation results (squares) and reproductions using our reconstructed models (triangles). The close agreement confirms the correct reconstruction of the models.

and x_2 develop as indicated by the flow arrows. The two curves (null-clines) however indicate the locations at which either x_1 (black) or x_2 (gray) does *not* change; hence, at an intersection between the null-clines, neither changes. At these parameter settings, contrary to the original ones, the lines have only one intersection, an attractor (plus sign), to which all flow arrows lead. The only reason the system "oscillates" is that the attractor itself is displaced by noise. It is unlikely that, in reality, binocular rivalry is entirely stochastic, as stochastic systems are generally associated with monotonically decreasing distributions of dominance durations, instead of the well-known unimodal ones observed in rivalry. Panel B illustrates this, showing a distribution of dominance durations obtained at these settings.

Superposition versus piecemeal transitions

In our main experiment, we were unable to distinguish superposition and piecemeal transitions. In this control experiment, we investigated their relative importance and how this changes with contrast. Our four subjects viewed the grating stimuli for 10 s at a time and, afterward, scored the subjective nature of the transition percepts observed during the period, on a scale ranging from 1 (*only superposition*) to 5 (*only piecemeal*). Each report was followed by another 10 s before the start of the next trial, preventing afterimages from interfering with the stimulus on the next trial. This was repeated five times per subject per condition, randomly interleaving
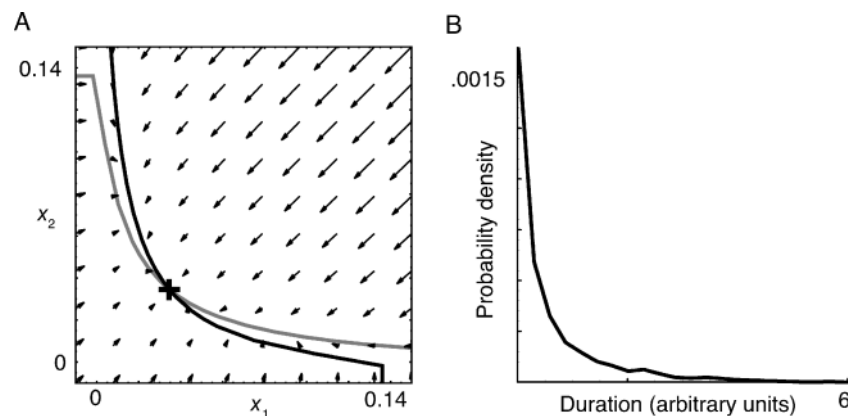

Figure A4. The Kalarickal and Marshall model in a monostable regime. At these settings, the system has not two but one attractor (A) and the dynamics are entirely governed by noise. (B) This system produces exponential-like distributions of dominance durations, rendering it an unlikely candidate for explaining rivalry, along with most other purely stochastic systems.
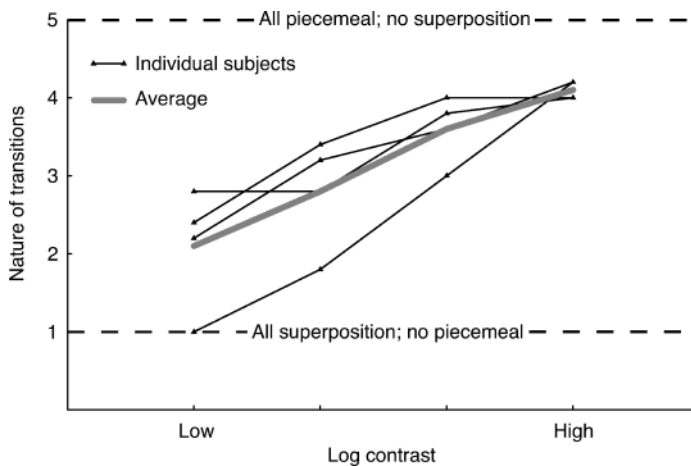
Figure A5. Relative importance of piecemeal and superposition percepts as a function of stimulus contrast. Both for individual subjects (black) and averaged over all four (gray), there is a clear shift from mainly superposition at low contrast to mainly piecemeal percepts at high contrast, although both types of percepts seem to occur throughout the contrast range.

conditions and applying only the four symmetric contrast combinations. As shown in Figure A5, there is a clear shift from mainly superposition at low contrast to mainly piecemeal percepts at high contrast, although note that both types of percepts were perceived throughout the contrast range, as neither 1 nor 5 was scored very often.

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