The role of lateral inhibition in binocular motion rivalry

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It is generally believed that percept alternations in binocular rivalry result from the interplay between mutual inhibition and slow adaptation of the competing percepts. This view is supported by growing evidence that dynamic changes in adaptation indeed support percept alternations in binocular rivalry. Empirical evidence for the involvement of mutual inhibition, however, is still scarce. To fill this gap, we presented human subjects with dichoptic random-dot motion stimuli and manipulated the angle between the monocular directions of motion from pure opponent horizontal motion to pure vertical motion in the same direction. We hypothesized that this decrease in motion–direction disparity increases the cross-inhibition gain due to lateral inhibition between neurons in the brain that are coarsely tuned to adjacent directions of visual motion, which predicts the largest changes in dominance at the smallest instead of the largest motion–direction disparities. We found that decreasing the angle between the two monocular directions of motion indeed systematically increased the predominance and mean dominance durations of the motion pattern presented to the ocular dominant eye (as identified by the hole-in-card test). Moreover, this effect was stronger if the contrast of the stimuli was lowered. Simulations showed that these features are indeed hallmark of weighted lateral inhibition between populations of directionally tuned motion-sensitive neurons. Our findings thus suggest dominance and suppression in binocular rivalry arises naturally from this fundamental principle in sensory processing. Interestingly, if the two monocular directions of motion differed <60°, the percept alternations also included transitions to in-between (vertical) motion percepts. We speculate that this behavior might result from positive feedback arising from adapting disinhibitory circuits in the network.

Introduction

Binocular rivalry is a phenomenon which occurs when our eyes receive a pair of stereo-incompatible inputs at the same retinal location. Even though both stimuli are constantly present, one generally perceives only one image at a time, with switches between the two percepts occurring every few seconds (for reviews, see Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006). This apparent dissociation between the visual input and the perceptual output is of interest because it may provide insight into the origin of visual awareness. For example, the fact that under most circumstances the two stimuli are never seen together (e.g., transparently or as a summed image) points to a central role for inhibition. However, the exact mechanisms underlying binocular rivalry are not fully understood. Most current models of binocular rivalry assume that the alternations between dominance and suppression result from the interaction between feedback cross-inhibition and slow self-adaptation (e.g., Blake, Yu, Lokey, & Norman, 1998; Freeman, 2005; Lehky, 1988; Noest, van Ee, Nijs, & van Wezel, 2007; Wilson, 2003) (Figure 1A). Feedback cross-inhibition implies that neurons representing the competing percepts inhibit each other through their output, resulting in suppression of the initially weaker percept while the other one becomes dominant. The inhibitory influence of the dominant population on the suppressed cells then slowly decays as a result of adaptation of the dominant population, allowing the suppressed cells to (re)gain dominance. This, in turn, allows the previously dominant population to recover from adaptation. In this way, the adapting reciprocal-inhibition model of binocular rivalry explains both suppression and alternation (but...
see, e.g., Ashwin & Lavric, 2010; Hohwy, Roepstorff, & Friston, 2008; Moreno-Bote, Rinzel, & Rubin, 2007; Sundareswara & Schrater, 2008, for a different perspective).

Studies in which the level of adaptation was manipulated have indicated that adaptation plays a significant role in binocular rivalry alternations (Alais, Cass, O’Shea, & Blake, 2010; Blake, Sobel, & Gilroy, 2003; Carter & Cavanagh, 2007; Kang & Blake, 2010; van Ee, 2011). Evidence for reciprocal inhibition originates from Levelt’s (1965) influential study on binocular rivalry dynamics, which showed that increasing the contrast of the image in one eye did not increase the dominance duration of that image but instead decreased the dominance duration of the image in the other eye (Levelt’s Second Proposition). This relationship seems counterintuitive at first glance but is easily explained within the framework of reciprocal inhibition where a given stimulus generates not an isolated response but one linked to the response generated by another competing stimulus. So far, however, the nature of this reciprocal inhibition remains elusive. Recent studies indicate that there is a specific and feature-tuned element to rivalry suppression (Stuit, Cass, Paffen, & Alais, 2009), which suggests that reciprocal inhibition between neighboring feature-tuned neuronal populations could be at the heart of the competition mechanism driving binocular rivalry. Such lateral inhibition has also been implicated in the

Figure 1. Changes in binocular rivalry dynamics as predicted by changes in cross-inhibition strength. (A) Adaptation reciprocal-inhibition model after Noest et al. (2007). The dynamics of each unit are given by a set of differential equations which specify the “local field” dynamics and “shunting-type” adaptation component of each unit. The local field activity of each unit (\(H_i\)) is converted into a spike-rate output (\(Y_i\)) via a sigmoid function \(S[z] = z^2 / (z^2 + 1)\), \(z > 0\); \(S[z] = 0, z \leq 0\), and depends on the visual input (\(X_i\)), the adaptation dynamics (\(A_i\)), and the amount of cross inhibition (\(\gamma \cdot S[H_j]\)). Parameter values were taken from Noest et al. (2007): \(\beta = 0.02\), \(\gamma = 5\). (B)–(C) Simulation of low-contrast (gray curves) and high-contrast (black curves) stimulus conditions. The strength of the feedback cross-inhibition was modulated by varying the gain, \(\gamma\), of the inhibitory interneurons. To simulate an eye preference, the inputs were chosen slightly asymmetric (\(X_2 = 1.06 \cdot X_1\)). Note that the mean dominance durations decrease systematically with decreasing strength of the cross-inhibition, and that this decrease is stronger for stimuli in the preferred eye (solid curves) versus the non-preferred eye (dashed curves). Both effects are stronger for weak (gray curves) versus strong (black curves) inputs. (C) Corresponding changes in predominance, where predominance is defined as the percentage of total stimulus time during which a given unit was dominant (i.e., had the highest activity).
propagation of rivalry dominance waves (Knapen, van Ee, & Blake, 2007; Wilson, Blake, & Lee, 2001).

Lateral inhibition is a nearly universal component of sensory processing, permitting populations of coarsely tuned neurons to support discrimination more accurately than would otherwise be possible. A byproduct of lateral inhibition is a large set of perceptual distortions such as Mach bands (Ratliff, 1965), illusory expansions of acute angles (Blakemore, Carpenter, & Georgeson, 1970; Mather & Moulden, 1980; Qian & Geesaman, 1995; Wilson & Kim, 1994), and motion repulsion (Marshak & Sekuler, 1979). Motion repulsion is the illusory enlargement of the angular separation between two targets moving in two different, but almost similar, directions. Since neither fatigue nor adaptation can explain the simultaneous influence of two motion directions on each other, motion repulsion is generally interpreted as resulting from lateral inhibition between neighboring direction-tuned channels, where the strength of the inhibition increases with decreasing angular distance between the two motion patterns. Neurophysiological studies in area MT of the macaque corroborate the notion of competitive interactions between adjacent motion directions (Kohn & Movshon, 2004; Krekelberg & Albright, 2005; Marshak & Sekuler, 1979). On the other hand, there is also clear evidence that motion opponency plays a role in visual motion processing (e.g., Heeger, Boynton, Demb, Seidemann, & Newsome, 1999).

We reasoned that manipulating the angle between the directions of motion in the two eyes would provide a means to change the strength of the inhibitory link between the two competing channels in binocular rivalry and test the nature of the competition. More specifically, if the competition relies on lateral inhibition between neighboring direction-tuned channels, decreasing the angle between two competing motion directions is expected to enhance the strength of the cross-inhibition between their neuronal representations. Alternatively, if the competition relies on opponent motion processing (i.e., if channels with opposite preferred direction inhibited each other strongest), the strength of the cross-inhibition between the two neuronal representations would be enhanced by increasing the angle between two monocular directions of motion.

Feedback cross-inhibition models predict that enhanced cross-inhibition between two perceptual representations leads to increases in dominance durations of the two competing percepts. This prediction holds because the suppressed population would need more time to recover sufficiently from its adapted state to overcome the stronger but decaying (due to adaptation) inhibition from the currently dominant population. Combined with weak inputs it could even lead, at some point, to “winner-take-all” behavior (Curtu, Shpiro, Rubin, & Rinzel, 2008; Shpiro, Curtu, Rinzel, & Rubin, 2007). In models without any input asymmetries, the winner could be either one of the two competing populations, with no preference for one or the other across trials. However, subjects typically have a preferred eye (Mapp, Ono, & Barbeito, 2003), which almost always enjoys longer periods of dominance than the other in binocular rivalry (Coren & Kaplan, 1973; Lederer, 1961; Walls, 1951). Thus, one would expect that for low-contrast stimuli, the preferred eye will dominate more as the strength of the cross-inhibition increases, lapsing eventually into complete dominance of that eye. Conversely, this effect is expected to attenuate as a function of decreasing cross-inhibition strength until the system reaches the regime in which conflicting stimuli produce more balanced percept durations. Predictably, the other way to attenuate the effect of strong cross-inhibition would be to increase the strength of the visual input. Figure 1 illustrates these predictions by means of simulations with a simplified version of the adaptation reciprocal-inhibition model proposed by Noest et al. (2007).

Thus, as lateral inhibition effectively increases the strength of the cross-inhibition with decreasing interocular difference in motion direction, for weak inputs, decreasing the angle between the two motion directions should lead to larger predominance and longer dominance durations of the motion pattern presented to the preferred eye. Moreover, an attenuation of these effects should occur for strong inputs. If, on the other hand, the strength of the cross-inhibition changes due to opponent processing, the relationship between changes in eye dominance and motion–direction disparity should be opposite, i.e., the changes in eye dominance from Figure 1 should increase with increasing interocular differences in motion direction.

To test these different predictions, we manipulated the angle between the directions of motion in the two eyes as well as the contrast level of the stimuli. We report that decreasing the angle between the two monocular directions of motion increased the predominance and mean dominance durations of the motion pattern presented in the subjects’ preferred eye, and this effect was attenuated if the contrast of the two images was increased. Simulations with a neural network model showed that these results can be readily understood from lateral inhibition between populations of coarsely tuned motion sensitive units. Our findings thus contradict the hypothesis that binocular motion rivalry might rely on motion opponency, a conclusion which is consistent with earlier suggestions that motion opponency probably occurs at a monocular stage (Gorea, Conway, & Blake, 2001; Majaj, Tailby, & Movshon, 2007; Tailby, Majaj, & Movshon, 2010).
Interestingly, our subjects not only reported alternations between the two monocular directions of motion. If the motion directions differed less than 60°, they also reported dominance epochs of in-between motion percepts. This behavior could—in principle—be explained by extending our population model with positive feedback arising from adapting disinhibitory circuits, but other interactions are also considered.

Material and methods

Subjects and setup

Four human subjects with normal or corrected to normal visual acuity participated after giving informed consent. Subjects were seated in front of a computer screen (ViewSonic, VX1940w) in an otherwise dark room. Their head and chin was supported by a forehead rest and chin cup. Visual motion stimuli were generated by a personal computer equipped with an openGL graphics card and presented to the subjects’ left and right eye by means of a front-mirror stereoscope. The total viewing distance was 67 cm. The resolution of the screen was 1680 × 1050 pixels. The image refresh rate was 60 Hz. Subjects indicated the direction of perceived visual motion by pressing mouse buttons. Button presses were recorded by the stimulus program. Eye preference (e.g., ocular dominance) of each subject was determined with the hole-in-card test (Cheng, Yen, Lin, Hsia, & Hsu, 2004). The procedures were approved by the Radboud University Medical Centre.

Visual stimuli

The visual motion stimuli consisted of random dot kinematograms (RDKs) that were generated with Matlab (The MathWorks, Inc.) using the psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997). Each RDK consisted of 300 white dots (2 × 2 pixels, 0.04°) that moved coherently against a gray background (luminance: 5.2 cd/m²) within a 3° circular aperture. Every dot started at a random location within the aperture and then moved at 4.2°/s for a fixed duration of four frames. At the end of its 67 ms lifetime, a dot was replaced by a new dot at a new random location within the aperture. Life times of the individual dots were asynchronous. RDKs presented to the left and right eye were generated independently. The angle between the two motion directions (motion–direction disparity, ΔΦ) could be one of the six following: 0°, 30°, 40°, 60°, 90°, 150°, and 180°, where the motion directions with respect to the vertical meridian were always 0°, ±15°, ±20°, ±30°, ±45°, ±75°, and ±90°, respectively.

In the low- and high-contrast conditions, luminance of the dots were set to 7.1 cd/m² and 124 cd/m², respectively, resulting in contrasts of C = 15% and C = 92% Michelson in both eyes.

Experimental procedure

Subjects fixated a 0.07° cross at the center of visual display for the duration of each trial. One second after the fixation cross appeared, RDKs with two different directions of motion were presented to the left and right eye for 1 min. The angle between the two directions of motion was manipulated from trial to trial and varied from either upward or downward vertical motion (ΔΦ = 0°) to either nasal or temporal horizontal (ΔΦ = 180°) motion. Figure 2 illustrates the ΔΦ = 180°, 90°, and 0° conditions.

Subjects were instructed to press and hold either the right or the left mouse buttons as long as either one of the two motion percepts (motion direction either to the top/bottom right or to the top/bottom left) was dominant. In case of piecemeal or transparent motion percepts (i.e., simultaneous perception of both motion directions), subjects were asked to press both buttons. If the direction of perceived motion was purely vertical, subjects were instructed to press a middle button. No button had to be pressed if no coherent visual motion pattern was perceived, e.g., if the pattern was perceived as dynamic noise.

Stimuli were presented in blocks of 24 trials in which all possible motion directions were presented in pseudo random order. To avoid fluctuations in light–dark adaptation of the retina, each block only included trials of the same contrast. High- and low-contrast blocks were presented in a random order. The time between two subsequent blocks was at least 24 hrs. On average, the duration of each block was 30 min. Each subject accomplished six blocks.

Data analysis

For each trial, we calculated the mean dominance duration of each motion percept as well as its predominance. Predominance was expressed either as a percentage of a total viewing time (percent total; Figure 3) or as a percentage of the viewing time during which either one of the oblique (i.e., leftward or rightward) percepts was dominant (percent oblique; Figure 4). The resulting values were sorted according to the eye of origin (i.e., preferred or non-preferred eye), averaged across trials and compared across conditions using multifactor analysis of variance (ANOVA). Post hoc
testing was done with linear regression analysis and Student’s t tests.

Results

For large interocular differences in motion direction (i.e., $\Delta \Phi \geq 60^\circ$) perception alternated almost exclusively between the two oblique/horizontal patterns of motion. Transparent motion or lack of a coherent motion percept was rarely indicated. However, as the two monocular directions of motion got closer (and more vertical), the subjects started to report pure vertical motion percepts. Since this behavior influenced the dominancy of the nonvertical motion percepts, especially at the smallest motion–direction disparities (where lateral inhibition predicts the biggest effects), we first present an analysis of the subjects’ vertical motion percepts in relation to the nonvertical motion percepts.

Predominance and mean dominance durations of the vertical percept

In line with previous reports by Blake, Zimba, and Williams (1985), the occurrence and durations of pure vertical, in-between motion percepts increased as the directions of motion got closer (and more vertical) thus reducing the overall predominance of the two non-vertical motion percepts. This behavior is illustrated in Figure 3, which shows the changes in predominance (Figure 3A) and mean dominance durations (Figure 3B) of the vertical motion percept (solid) and the oblique/horizontal motion percepts (dashed; both percepts taken together) as a function of motion–direction disparity. Note that the $\Delta \Phi = 180^\circ$ condition
corresponds with classic binocular rivalry whereas the \(\Delta \Phi = 0^\circ\) condition corresponds with unambiguous vertical motion (c.f., Figure 2). The unambiguous vertical stimuli were nearly always perceived as pure vertical motion, except by Subject S2. For these stimuli, this subject also reported oblique motion percepts for about 96\% of the total viewing time. All subjects, including S2, still reported vertical motion percepts if the two directions of motion differed by 30\° or 40\°. However, the predominance and mean durations of those in-between percepts decreased rapidly with increasing motion–direction disparity (and increasing deviations from vertical). The observed reductions were in fact contrast dependent; they were significantly larger in the high versus low-contrast condition (\(t\) tests, \(p < 0.01\), for all subjects).

In the following sections we quantify the respective changes in dominance of the two nonvertical motion percepts. All trials with motion–direction disparities of \(\Delta \Phi = 0^\circ\) and \(\Delta \Phi = 30^\circ\) were excluded from these analyses because of the strong bias towards in-between vertical motion percepts. We did, however, include the \(\Delta \Phi = 30^\circ\) condition in the graphs.

If lateral inhibition causes the strength of the cross-inhibition to change with the interocular difference in motion direction, then for weak inputs, decreasing the angle between the two motion directions should lead to larger predominance and longer dominance durations of the motion pattern presented to the preferred eye as compared with the motion pattern presented to the non-preferred eye. Moreover, an attenuation of these effects should occur for strong inputs (c.f., Figure 1). If rivalry is instead mediated by opponent competition, changes in eye dominance as a function of motion–direction disparity should be opposite.

**Predominance**

We analyzed the changes in predominance of the two nonvertical motion percepts using multifactor ANOVA. Independent variables in this analysis were subject, motion–direction disparity, and stimulus contrast. Predominance of stimuli in the preferred and non-preferred eye was expressed as a percentage of the viewing time during which either one of the two oblique/horizontal stimuli was perceived as dominant.

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**Figure 3.** Predominance (A) and mean dominance durations (B) of the pure vertical motion percept (solid curves) and oblique percept (dashed curves in A) as a function of motion–direction disparity for the low-contrast (gray curves) and high-contrast (black curves) conditions. Predominance quantifies the percentage of total stimulus time during which a given percept was dominant. Data are averaged across subjects. Error bars indicate \(\pm 1\ SEM\). Subjects started to report pure vertical motion percepts as the monocular directions of motion approached the vertical meridian for small motion–direction disparities.
The results showed that predominance was significantly influenced by motion–direction disparity, main effect: $F(4, 569) = 15.54, p < 0.001$, and stimulus contrast, main effect: $F(1, 569) = 38.06, p < 0.001$, and that the effect of motion–direction disparity was contrast dependent, interaction effect: $F(4, 569) = 5.18, p < 0.001$. Figure 4 quantifies these effects by comparing the predominance of stimuli in the preferred (solid curves) and non-preferred (dashed curves) eye for the low- (gray) and high-contrast (black) condition. As predicted by our lateral-inhibition hypothesis, the mean predominance of the subjects’ preferred eye increased systematically with decreasing motion–direction disparity, especially in the low-contrast condition. Moreover, increasing the stimulus contrast in both eyes attenuated the dominancy of the preferred eye over the non-preferred eye. More specifically, for all subjects we found that the mean predominance of stimuli in the preferred eye was on average higher in high-contrast condition as compared with the low-contrast condition (paired $t$ tests, $p < 0.05$). In fact, increasing the stimulus contrast from 15% to 92% Michelson systematically attenuated the robust influence of motion–direction disparity in all subjects.

Figure 5 quantifies these interactions by plotting the difference in predominance of stimuli in the preferred versus non-preferred eye as a function of the motion–direction disparity for the two contrast conditions. Linear regression analysis indicated a systematic increase in predominance of the preferred versus non-preferred eye with decreasing motion–direction disparity. Although this effect was not statistically significant in two of the subjects, the slopes of the linear trend lines were always negative in both the low- (slope of average trend line: $a = -0.21 \pm 0.05\% \circ^{-1}$, $t$ test, $p < 0.01$) and high-contrast conditions (slope of average trend line: $a = -0.07 \pm 0.02 \% \circ^{-1}$, $t$ test, $p < 0.01$). Moreover, in the low-contrast condition, the slope of the trend line was on average about three times steeper than in the high-contrast condition. To better demon-
strate this dissociation between the low- and high-contrast conditions, the inset of Figure 5 plots their difference. In all subjects, the difference increased significantly with decreasing motion–direction disparity (slope of average trend line: \( a = -0.15 \pm 0.04^\circ/s, t \text{ test}, p < 0.01 \)).

Our findings thus indicate an increasing difference between binocular rivalry dynamics in the low- and high-contrast conditions if the angle between the two monocular directions of motion decreases.

### Mean dominance durations

We then analyzed the mean dominance durations of the non-vertical motion percepts. Independent variables in the initial ANOVA were subject, eye preference, motion–direction disparity, and stimulus contrast. The results indicated that also the mean dominance durations were significantly influenced by motion–direction disparity, main effect: \( F(4, 1128) = 27.42, p < 0.001 \) and stimulus contrast, main effect: \( F(1, 1128) = 55.09, p < 0.001 \). As predicted by our lateral-inhibition hypothesis, however, these effects were different for the preferred versus non-preferred eye. More specifically, the difference in mean dominance duration between the two eyes, main effect: \( F(1, 1128) = 107.83, p < 0.001 \) was significantly modulated by motion–direction disparity, first-order interaction: \( F(4, 1128) = 10.5, p < 0.001 \), and stimulus contrast, first-order interaction: \( F(1, 1128) = 10.5, p < 0.001 \). In fact, it appeared that the influence of motion–direction disparity on the dominance–duration difference between the two eyes was contrast dependent, second order interaction: \( F(4, 1128) = 3.16, p < 0.01 \).

To demonstrate these interaction effects, Figure 6 plots the mean dominance durations of the subjects’ preferred (solid curves) and non-preferred (dashed curves) eye in the low-contrast (gray) and high-contrast (black) conditions. Note that the mean dominance durations increased systematically as a function of decreasing motion–direction disparity, especially in the preferred eye. Moreover, for each eye the mean dominance durations were typically shorter in the high-contrast condition compared with the low-contrast condition. This truncating effect of increasing the stimulus contrast was statistically significant for dominance durations of both the preferred (paired \( t \text{ tests} \ p < 0.01 \)) and the non-preferred (paired \( t \text{ tests} \ p < 0.05 \)) eye in all four subjects.

In addition, there was a robust difference between mean dominance durations of the preferred and non-preferred eye, which increased with decreasing motion–direction disparity. To further quantify these effects, Figure 7 plots the difference between the mean dominance durations of the preferred and non-preferred eye (positive values indicate larger predominance of the preferred eye) as a function of motion–direction disparity. Linear regression analysis of these data showed that the difference in the eyes’ dominance durations was significantly boosted by decreasing the motion–direction disparity, both in the low-contrast condition (slope of average trend line: \( a = -0.04 \pm 0.01^\circ/s, t \text{ test}, p < 0.05 \)) and high-contrast condition (slope of average trend line: \( a = -0.01 \pm 0.002^\circ/s, t \text{ test}, p < 0.01 \)). Although this boosting effect was consistent across all four subjects, it was not always significant in the high-contrast condition (two subjects, \( t \text{- tests}, p > \).
Indeed, in the low-contrast condition, the slope of the regression line was on average about four times steeper than in the high-contrast conditions. The inset of Figure 7 demonstrates this dissociation between the low- and high-contrast conditions by plotting the difference. In all our subjects, the difference increased significantly with decreasing motion–direction disparity (slope of average trend line: $a = -0.02 \pm 0.008 \text{s}^\circ$, $t$ test, $p < 0.05$) for motion–direction disparities down to $\Delta \Phi = 40^\circ$. For smaller angles, the oblique motion percepts gave way to pure vertical motion percepts (c.f. Figure 3).

Model simulations

Our experimental findings are consistent with the notion that decreases in motion–direction disparity effectively increase the strength of the mutual inhibition between neural populations that represent the two monocular directions of motion. Here, we explore the possibility that these changes in cross-inhibition strength could be an emergent property of weighted lateral inhibition between populations of coarsely tuned visual motion cells. Towards that end, we extended the adaptation reciprocal-inhibition model from Figure 1 by incorporating two layers of 36 adapting cells (Figure 8A), each coarsely tuned to a different direction of motion (Figure 8B). The preferred directions of the cells were uniformly distributed, and cells within each layer received visual input only from one eye. Moreover, each unit inhibited cells in the other layer via an interneuron which had long-range inhibitory connections (gray connections). The fixed strength of these feedback connections decreased as a function of the cells' tuning distance so that cells having the same preferred direction inhibited each other strongest (Figure 8C). As in the model of Figure 1, the inhibitory interneurons had no dynamics, and also the properties of the adapting cells were kept the same. Figure 8D illustrates the spatial–temporal pattern of activity within each of the two percept-encoding layers in response to opponent horizontal motion stimuli (i.e., classic rivalry). Note the reciprocal activation pattern of the two populations. Mean dominance durations of the two states scale with the adaptation time constant, here set to one for simplicity.

To further analyze the response properties of the network, we expressed the instantaneous activity in each layer as a population vector (for simplicity computed from a classic, weighted vector-summation scheme; e.g., Georgopoulos, Schwartz, & Kettner,
with decreasing motion–direction disparity which was strongest for stimuli in the preferred eye, and these effects were attenuated by increasing the strength of the inputs to both layers. For symmetry reasons, a population model with opponent interactions (not shown) produced results opposite to the ones shown in Figure 8, which is clearly inconsistent with our data.

Note, however, that for $\Delta \Phi$’s below $60^\circ$ the lateral inhibition model from Figure 8A did not produce epochs with in-between motion percepts (Figure 9A), which we did observe in the experiments (c.f., Figure 3). Moreover, for unambiguous ($\Delta \Phi = 0^\circ$) upward motion, the activity continued to alternate between the two layers (thin magnitude curves in Figure 9A). The net motion percept (thick curves in Figure 9A) nonetheless stabilized on the actual upward motion stimulus since both populations only voted strongly for the $90^\circ$ upward motion direction.

The inability of the model to generate in-between motion percepts for $\Delta \Phi < 60^\circ$ is due to the fact that it cannot disengage the feedback cross-inhibition between cells having the same preferred direction even if the two monocular directions of motion are the same. Following the conceptual scheme proposed by Buckthought, Kim, and Wilson (2008), we speculated that the occurrence of in-between motion percepts might be explained by positive feedback arising from disinhibitory circuits. To explore this possibility, we augmented the model from Figure 9A with a third layer of inhibitory cells, which allowed the network to switch between fusion and rivalry through inhibition and disinhibition of the cross-inhibition feedback path (see Supplemental materials). Simulations showed that this extended population model was indeed able to account for the observed alternations between the two oblique motion percepts and the in-between vertical-motion percept.

**Discussion**

In the present study, we report new evidence that binocular motion rivalry involves mutual inhibition between monocular motion patterns, and that this inhibition arises from lateral inhibition between populations of coarsely tuned motion-sensitive cells, rather than from opponent type cross-inhibition.

Reciprocal inhibition between monocular input representations is widely used to account for suppression and dominance of competing monocular stimuli in binocular rivalry. To quantify suppression, previous studies have compared thresholds for detecting brief probe stimuli presented to one eye in its suppressed and dominant state (Fox & Check, 1968). These studies showed that the sensitivity for detecting probes in the...
Suppression was long thought to be a nonselective process in which sensitivity is reduced to all kinds of visual stimulation (Blake, 1989). More recently, however, it has been suggested that the suppression might be selective for both high- and low-level stimulus features (Alais & Parker, 2006; Apthorp, Wenderoth, & Alais, 2009; O'Shea & Crassini, 1981). Stuit et al. (2009) tested this theory by presenting probe gratings with a range of spatial frequencies and orientations. They found that the thresholds were elevated for probe frequencies and orientations close to those of the suppressed grating. However, the inherent nonlinear nature of the rivalrous flip-flop and its stochastic behavior makes it difficult to disentangle the contribution of adaptation and inhibition. To study the

Figure 8. Parsimonious population model for binocular motion rivalry. (A) The network consisted of two layers of adapting cells (white, \( n = 36 \)) with uniformly distributed preferred directions of motion \( \theta \in [0^\circ, 10^\circ, \ldots, 350^\circ] \). Units in each layer received monocular visual inputs \( \{X_i, X_j\} \) and inhibited cells in the other layer via an inhibitory interneuron (gray). For clarity, the graph only shows the connections for two of those interneurons. The fixed strength of these inhibitory feedback connections decreased as a function of tuning distance, so that cells having the same preferred direction inhibited each other strongest. Black arrows: excitatory connections. Gray bullets: inhibitory connections (two units only). (B) Input pattern for opponent horizontal motion in the two eyes (i.e., \( \Delta \Phi = 180^\circ - 0^\circ = 180^\circ \)), illustrating the cells’ coarse Gaussian tuning for motion direction, \( \Phi \): \( X_i = A_i \exp[\kappa_\Phi \cos(\theta_i-\Phi)] \); tuning width, \( \kappa_\Phi = 1.0 \); stimulus strength, \( A_i = 1.0/\exp[\kappa_\Phi] \). (C) Weights of the inhibitory feedback connections \( \gamma_{ij} \) illustrated for four different units with preferred directions \( \theta = [0^\circ, 90^\circ, 180^\circ, 270^\circ] \). Weights were defined by the Gaussian weighting function: \( \gamma_{ij} = w_\gamma \exp[\kappa_\gamma \cos(\theta_i-\theta_j)] \); \( \kappa_\gamma = 0.25 \); \( w_\gamma = 0.30/\exp[\kappa_\gamma] \). D) Spatial-temporal activity patterns \( \{Y_i, Y_j\} \) of the two populations in response to the two monocular input patterns shown in B. Gray values represent the activity level of each cell (identified by its preferred direction on the ordinate) at each moment in time.

suppressed state is reduced by about 0.3–0.5 log units.
Dynamic interactions between mutual inhibition and adaptation Lankheet (2006) correlated perceptual switches in a binocular motion rivalry task with dynamic changes in motion coherence. He found that changes in stimulus strength at different moments during rivalry affect the dynamics of perceptual switches in different ways, an effect that is consistent with mutual inhibition at a short time scale and slow self-adaptation at longer time scales.

In this study we manipulated the angle between two monocular directions motion. Based on the notion that the strength of the lateral inhibition between populations of coarsely tuned motion-sensitive cells probably increases systematically with decreasing differences in their preferred directions, we assumed that this manipulation directly influences the gain of the feedback cross-inhibition without altering the adaptation dynamics (i.e., gain and time constant). We therefore predicted that for low-contrast motion stimuli, decreasing the angle between the directions of motion in two eyes should lead to larger predominance and longer dominance durations of the motion pattern in the ocular dominant eye. This prediction is in line with earlier findings showing that the mean dominance durations of competing gratings increased with decreasing orientation disparity (Buckthought et al., 2008; Kitterle & Thomas, 1980; O’Shea, 1997; Schor, 1977) and that dichoptic gratings exhibit the greatest amount of interocular masking when the orientations are similar compared to orthogonal (Baker & Graf, 2009; Baker & Meese, 2007). Moreover, we predicted that an attenuation of this effect should occur for stronger inputs as previously observed with competing gratings (Buckthought et al., 2008). Our experiments confirmed both predictions.

Figure 9. Response of the network for decreasing motion–direction disparity and contrast. (A) Response to \( \Delta \Phi = 120^\circ - 60^\circ = 60^\circ, \Delta \Phi = 105^\circ - 75^\circ = 30^\circ \) and \( \Delta \Phi = 90^\circ - 90^\circ = 0^\circ \) motion–direction disparities, expressed in terms of the magnitudes (top) and directions (bottom) of three dynamic population vectors: one for activity in the layer receiving inputs from the dominant eye (light gray lines), one for activity in the layer receiving the slightly weaker (3%) inputs from the other eye (dark gray lines), and one for the net activity in both populations (thick black lines). We assumed that the latter population vector determined the motion percept. (B) Mean dominance duration of the stimulus in the preferred (solid curves) and non-preferred (dashed curves) eye in the low-contrast (gray curves) and high-contrast (black curves) conditions. (C) Predominance of each stimulus for the same conditions.
Our results therefore strongly support the notion that the strength of the cross-inhibition in binocular rivalry increases with decreasing distances in visual feature space. Although intuitively one might perhaps expect that monocular images compete stronger if more dissimilar, this proposition is fully in line with the general principles of information processing in the brain where lateral inhibition between similarly tuned populations of neurons is known to play an important role in enhancing the performance of different sensory systems. Although our findings thus argue against the hypothesis that binocular motion rivalry might rely on motion opponency, it is important to emphasize that they do not provide evidence against the existence of opponent motion processing per se. Previous studies have indicated that motion opponency is probably monocular (Gorea et al., 2001; Majaj et al., 2007; Tailby et al., 2010), which indeed reconciles our findings under dichoptic viewing conditions with those of other studies that have reported opponent motion interactions under binocular viewing conditions (e.g., Heeger et al., 1999). For example, it is not difficult to see that our simulation results (Figures 8 and 9) would be the same if one were to assume that the monocular inputs to each unit in the model actually consisted of excitatory and inhibitory inputs from monocular cells with opposite preferred directions (as proposed, e.g., by Kalisvaart, Klaver, & Goossens, 2011).

The outcomes of our study thus suggest that the essential part of suppression in binocular rivalry is based on the mechanism of lateral inhibition between adjacent feature-tuned neuronal populations. This mechanism is one of the basic organizational principles of the visual system and was demonstrated on a large variety of different perceptual phenomena such as Mach bands (Ratliff, 1965), illusory expansions of acute angles (Blakemore et al., 1970; Mather & Moulden, 1980; Qian & Geesaman, 1995; Wilson & Kim, 1994), and motion repulsion (Marshak & Sekuler, 1979). The latter phenomenon is of specific interest for our study, since it not only supports the notion of lateral inhibition between two motion–direction channels, it was also explicitly tested under dichoptic viewing conditions (Buckthought et al., 2008; Chen, Matthews, & Qian, 2001; Grunewald, 2004; Marshak & Sekuler, 1979). Marshak and Sekuler (1979) indicated that their subjects did not experience binocular rivalry under dichoptic viewing conditions, but Chen et al. (2001) pointed out that this could be due to the fact that Marshak and Sekuler only used very short stimulus durations (1 s). After controlling for reference repulsion no motion repulsion was observed in dichoptically presented motion stimuli (Chen et al., 2001; Grunewald, 2004). Interestingly, our model also predicts no motion repulsion in binocular rivalry. Instead, the lateral inhibition in our model supported competition between veridical motion percepts. Unfortunately, none of the authors tested for the presence of in-between motion percepts or changes in binocular rivalry dynamics arising as a result of manipulating the angle between two competing motion directions. Our results fill this gap. Note also that the effect sizes observed in our study fit well with the 20°–40° range reported for the biggest motion repulsion effects (Kim & Wilson, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Qian & Geesaman, 1995; Snowden, 1989).

The idea that lateral inhibition between feature-tuned channels could be an essential part of the mechanism responsible for binocular rivalry competition was proposed earlier for explaining propagation of rivalry dominance waves (Knapen et al., 2007; Wilson et al., 2001). It was modeled with two layers of cortical neurons receiving separate inputs from the two eyes. Neurons in either layer sway negative interactions to the retinotopically nearby cells in an opposite layer via inhibitory interneurons and collinearly facilitate neighboring cells in their own layers. The architecture of our model in Figure 9A is conceptually similar to these schemes, except that our model did not include local excitation between neighboring cells in their own layers. This feature could not explain the occurrence of in-between percepts, nor was it otherwise necessary to account for the influence of motion–direction disparity. To limit the complexity of the model it was therefore omitted. The fact that the in-between motion percepts occurred at motion–direction disparities far exceeding the psychometric threshold of ~3° for motion–direction discrimination along the cardinal axes (Ball & Sekuler, 1987) indicates that these perceptual states did result from neural interactions between the competing inputs, rather than from an inability of subjects to accurately discern the oblique directions of motion from pure vertical motion.

We considered the possibility that these in-between percepts arise from local excitation between similarly tuned cells across the two percept-encoding layers of our model, but such a facilitatory component could not explain this behavior either. In fact, opposite to our findings, it merely predicted decreases in mean dominance durations for the smaller motion–direction disparities because it effectively reduced the strength of the cross-inhibition for those smaller angles. Following the conceptual scheme proposed by (Buckthought et al., 2008), we therefore conjectured that the positive feedback between two similar patterns of motion might instead arise from disinhibition. Simulations showed that this principle can indeed account for the observed alternations between the oblique and vertical motion percepts, provided that the inhibitory circuits also exhibit some form of adaptation.
We should note, however, that our results do not specify the exact nature of the observed in-between percept. One might expect that an in-between percept results from binocular fusion or from superposition of the two images. Although we did not ask our subjects to judge a possible increase in the amount of dots or motion in depth, their subjective reports after the experiments (as well as our own judgment of the stimuli) indicated that they did not perceive motion in depth or increases in the amount of dots. The lack of a change in the number of elements in the scene suggests that the images did fuse even though the subjects did not perceive motion in depth. This lack of motion in depth is not too surprising because our motion stimuli were such that the correspondence information between the left and right eye changed randomly with every frame (Methods). Thus, it is possible that our results reflect the competition between units representing stereopsis and rivalry, with adaptation to the current state of fusion (Buckthought et al., 2008; Julesz & Tyler, 1976; Tyler & Julesz, 1976). Indeed, it is known that subjects can still perceive motion when presented with stimuli that contain binocular motion signals but no monocular motion signals (Meng & Tong, 2004), indicating the presence of binocular motion detectors, which have not been included in our model. Another (perhaps complementary) possibility is that the in-between percept arises from intersection of constraints, which has been proposed as a mechanism to extract the true global motion from the inherently ambiguous information of local motion detectors (Adelson & Movshon, 1982).

In summary, our study provides a new experimental approach to manipulate the inhibitory link between two rivalry percepts. Moreover, our findings provide strong evidence for the important role that lateral feedback inhibition plays in binocular rivalry and support adaptation mutual-inhibition models.

Keywords: binocular rivalry, lateral inhibition, adaptation, motion–direction disparity, visual awareness, computational modeling

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