

Equivalence of physical and perceived speed in binocular rivalry

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The relative dominance of gratings engaged in binocular rivalry can be influenced by their surroundings. One striking example occurs when surrounding motion is congruent with one but not the other grating (C. L. Paffen, S. F. te Pas, R. Kanai, M. J. van der Smagt, & F. A. Verstraten, 2004). However, such center-surround stimulus configurations can also modulate perceived speed, via a directionally tuned process (H. P. Norman, J. F. Norman, J. T. Todd, & D. T. Lindsey, 1996). We recorded rivalry for Gabor patches embedded in a drifting noise texture. Gratings whose directions opposed the background motion tended to dominate more, and vice versa, consistent with previous findings. Observers then matched the speed of a drifting noise-embedded Gabor to that of a Gabor surrounded by mean luminance. Surround motion produced substantial changes in perceived speed, by at least a factor of two for all observers. We then asked whether perceived speed could account for the contextual effects on dominance. We measured the effects of speed on rivalry dominance by changing the physical speeds of rivaling gratings, as determined by the matching data. We found the same pattern of dominance as for the context experiment, indicating that perceived and true speed influence rivalry in the same manner. We propose a Bayesian interpretation of the perceived speed illusion.

Keywords: binocular rivalry, motion, center-surround, context

Citation: Baker, D. H., & Graf, E. W. (2008). Equivalence of physical and perceived speed in binocular rivalry. *Journal of Vision*, 8(4):26, 1–12, <http://journalofvision.org/8/4/26/>, doi:10.1167/8.4.26.

Introduction

When the two eyes are shown different and incompatible images, an observer's percept alternates over time between the two possible interpretations. This phenomenon is known as binocular rivalry and has been extensively investigated over the past century (for a collection of recent work, see Alais & Blake, 2005). Because the stimulus remains constant, the changes in percept might provide insight into how the brain chooses between competing scene interpretations and may be of relevance to the study of consciousness (i.e., Crick & Koch, 1998).

The low-level properties of two rivaling images, such as spatial frequency, contrast, and motion, can greatly influence the relative levels of dominance. For example, stimuli of higher luminance contrast will dominate over stimuli of lower contrast (i.e., Levelt, 1965, 1966), and moving sinusoidal gratings are preferred to stationary ones (Wade, de Weert, & Swanston, 1984). The importance of low-level properties in binocular rivalry has led to the view (i.e., Blake, 1989) that rivalry occurs early in processing, perhaps between monocular channels in striate cortex (Sengpiel, Blakemore, & Harrad, 1995). However, more recent accounts favor a hierarchy of rivaling stages (Blake & Logothetis, 2002; Tong, 2001; Wilson, 2003) that may incorporate processing from extra-striate areas.

This distributed notion is supported by studies showing that the context in which rivaling stimuli are placed can also affect the dynamics of rivalry (Sobel & Blake, 2002). Placing the stimuli in a context that is congruent with one, but not the other, rivaling image can increase the dominance of the congruent image (Graf & Adams, 2008). This also occurs when one rivaling image contributes to a global percept, such as a globally coherent motion stimulus (Alais & Blake, 1998).

One particularly strong contextual effect in rivalry occurs when drifting rivaling gratings are surrounded by a larger (binocular) drifting grating (Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004). A rivaling grating moving in the same direction as the surround dominates less than one moving in the opposite direction. This is a surprising finding, as other studies have typically found that congruency with nearby stimuli confers increased dominance (i.e., Sobel & Blake, 2002, although see also, Fukuda & Blake, 1992). However, the effect is robust, affecting dominance with different surround diameters (Paffen, van der Smagt, te Pas, & Verstraten, 2005) and when one rivaling image is stationary (Paffen, Alais, & Verstraten, 2005), although the opposite effect has been shown at low contrasts (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006).

A possible neural substrate of this motion context effect is the direction-tuned center-surround interactions reported in area MT (Allman, Miezin, & McGuinness,

1985a, 1985b; Born, 2000; Eifuku & Wurtz, 1998; Pack, Hunter, & Born, 2005). Surrounding stimuli such as those used by Paffen et al. might reduce rivalry dominance via local suppressive interactions (i.e., Cannon & Fullenkamp, 1991; Tadin, Lapin, Gilroy, & Blake, 2003). Stimuli that cause increased dominance (i.e., Sobel & Blake, 2002) could be mediated by longer-range facilitatory connections, such as those thought to underlie contour integration (see Alais, Lorenceau, Arrighi, & Cass, 2006).

An important factor, so far overlooked in the discussion of surround motion in rivalry, concerns the influence of a surround on the perceived speed of a central stimulus. In general, the perceived speed of a central region is greatly increased when its surround moves in the opposite direction (Norman, Norman, Todd, & Lindsey, 1996) but is reduced by a surround moving in the same direction (Loomis & Nakayama, 1973; Walker & Powell, 1974). To some extent, this is dependent on the relative velocity of the surround (Loomis & Nakayama, 1973; Norman et al., 1996), but similar effects have been reported recently with static surrounds (Blakemore & Snowden, 2000; Nguyen-Tri & Faubert, 2007). Related effects of facilitation and inhibition also occur when the stimuli are arranged in adjacent rows (Bressan, 1991; Nawrot & Sekuler, 1990). For binocular rivalry between gratings, it has been shown that increasing the physical speed of one component confers greater dominance (Wade et al., 1984). We hypothesize that differences in *perceived speed* caused by the surround might be related to the substantial effects on predominance reported by Paffen et al. (2004, 2006), Paffen, Alais, et al. (2005), and Paffen, van der Smagt, et al. (2005).

In this study, observers viewed orthogonal gratings surrounded by a drifting noise texture. We report four experiments, in which we measure

- i. grating rivalry for eight directions of surround motion,
- ii. the perceived speed of a central grating for each surround direction,
- iii. grating rivalry with appropriate pairs of physical speeds, so as to simulate the perceived speeds of the first experiment, and
- iv. the summing and nulling effects of contrast and speed (perceived and physical) in the rivalry paradigm.

These experiments demonstrate that perceived and physical speeds have an equivalent influence on binocular rivalry.

Methods

Apparatus

All stimuli were displayed on a ViewSonic G90fB monitor (ViewSonic, California, USA), running at 75 Hz,

using an NVIDIA GeForce 7300 GT high performance graphics card (NVIDIA Corporation, California, USA) and an Apple Macintosh computer (Apple, California, USA). Stimuli were presented to different eyes by means of a mirror stereoscope (except in [Experiment 2](#)). The monitor was gamma corrected using standard techniques and had a mean luminance of 60 cd/m². Stimuli were generated and displayed using the Psychophysics Toolbox software (Brainard, 1997; Pelli, 1997) running under Matlab 7.4 (The Mathworks Inc., Massachusetts, USA).

Stimuli

Previous studies of surround motion effects have used sinusoidal grating stimuli (Paffen et al., 2004), moving dots (Loomis & Nakayama, 1973; Norman et al., 1996) or binary noise textures (Paffen et al., 2006). We chose to use orthogonal gratings for rivalry and a drifting noise texture as a surround. The noise texture is not subject to the motion aperture problem that occurs for periodic stimuli (i.e., Adelson & Movshon, 1982) and so has unambiguous direction and speed along any motion vector.

Rivaling stimuli were always 1 cpd Gabor patches, oriented obliquely ($\pm 45^\circ$), displayed at full (100%) contrast (except in [Experiment 4](#), where contrasts of 25% were also used). The Gaussian envelope had a standard deviation (σ) of 0.67 degrees of visual angle and a full width at half height of 1.57 degrees (i.e., ~ 1.5 grating cycles). In [Experiments 1, 2, and 4](#), the gratings were surrounded by a $7^\circ \times 7^\circ$ texture of smoothed Gaussian noise with an RMS contrast of $\sim 20\%$. A new noise image was generated for each trial, and the noise was always identical in both eyes. When the noise was present, both it and the Gabor patches moved at 0.5 degrees per second. When the noise was absent ([Experiments 2, 3, and 4](#)), the speed of the grating varied. In all cases, Gabor patches drifted beneath their Gaussian window orthogonal to their stripes and in the downward direction (see red arrows in [Figure 1](#)). The noise texture could move in one of eight directions (0° to 315° in steps of 45°). Static example stimuli are shown in [Figure 1](#).

In all experiments, a small black fixation cross (not shown) was displayed in the center of each image to aid fusion. When a surround texture was present, this also aided fusion. In conditions with no surround texture, a black square (thickness of 12 arcmin) was used to aid fusion, as shown in [Figure 1B](#).

Procedure

Observers were seated in a dark room, with their head stabilized by a chin rest and forehead bar at a viewing distance of 85.5 cm. In [Experiments 1, 3, and 4](#), a standard binocular rivalry paradigm was used. Each trial was initiated by a key press and preceded by three brief tones.

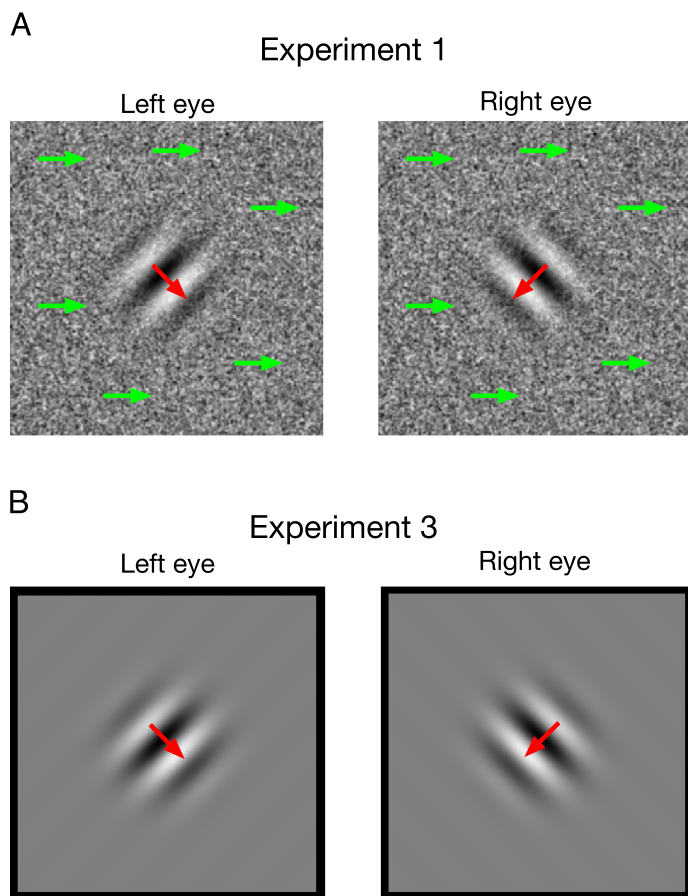


Figure 1. Diagram of stimuli. (A) Orthogonal Gabor patches, shown to the left and right eyes, surrounded by a noise texture. Here, the left eye's image is right tilted ($+45^\circ$), and the right eye's image is left tilted (-45°). This was counterbalanced in the experiments. The noise texture was identical in both eyes. (B) Orthogonal Gabor patches surrounded by mean luminance. The black square was intended to aid fusion in conditions with no surround. Coloured arrows indicate the direction of motion and were not present in the experiment.

Observers viewed rivalrous orthogonal gratings (presented dichoptically) for trials of 1-min duration. They reported their percept continuously via a keyboard by pressing and holding the left arrow key when the left tilted (-45°) grating was dominant and the right arrow key when the right tilted ($+45^\circ$) grating dominated. When neither grating was clearly dominant, observers pressed either both keys or neither key, and these data were removed from further analysis. Such mixed percepts were reported $<6\%$ of the time across observers, experiments, and conditions (note that this includes the period between the start of each trial and the observer's first button press).

There were eight conditions of surround direction in Experiments 1, 2, and 3, which were counterbalanced across eye of presentation, grating orientation, and speed, where appropriate. Trials occurred in random order and

were usually completed in blocks of 10 or more. Observers repeated each condition 20 times. Rivalry data were analyzed by pooling over all sessions and by calculating the predominance of each grating. Predominance is defined as the proportion of time each percept was reported, relative to the total time a single percept was seen (i.e., after removing data where both or neither button was pressed). Thus, the sum of predominances for the two percepts always equalled one.

In Experiment 2, a spatial two-alternative forced-choice (2AFC) matching task was used to measure the perceived speed of gratings surrounded by a moving noise texture. The standard was always a Gabor patch moving at 0.5 deg/s , surrounded by the noise texture moving at the same speed, but in one of eight directions (see above). The matching stimulus was a Gabor with an orientation orthogonal to that of the standard, surrounded by mean luminance. Stimuli were horizontally separated by 4.2° . The speed of the matching stimulus was determined by 1-up, 1-down staircases, which always began at 1 deg/s and moved in steps of $0.025 \text{ log units of speed}$, terminating after 50 trials. For each background motion direction, four staircases were used (two standard orientations: $\pm 45^\circ$, two standard locations: left/right). Presentations were blocked by surround direction, such that the four interleaved staircases were run for a single direction, before moving on to the next. Stimulus inspection time was unlimited, and observers indicated which grating appeared to be moving fastest (left or right of screen) using the keyboard, at which point the trial terminated. This avoided any changes in perceived speed that might be caused by a short trial length.

We also performed two control versions of this experiment to rule out any influence of eye movements in determining perceived speed. In the first control, the stimuli were the same as above, but observers were instructed to fixate on a central cross, located in between the stimuli. The stimuli were therefore viewed simultaneously, rather than one at a time, to eliminate pursuit eye movements. In the second control, the stimuli were presented centrally in two 300 ms intervals (2IFC). This reduced the time available to make eye movements that could influence the perceived speed. Both of these control experiments produced equivalent results to the main experiment (data not shown), indicating that eye movements are not responsible for the perceived speed effect.

Data for Experiment 2 were pooled across all staircases and plotted as the proportion of trials in which the matching stimulus appeared faster. The psychometric function was fit using probit analysis (Finney, 1971) to estimate the point of subjective equality (PSE). DHB completed the PSE experiment twice (400 trials per condition, 3200 trials in total). As there was very little variation across repetition, the other observers completed one repetition of Experiment 2 (200 trials per condition, 1600 trials in total). The perceived speed estimates were then used to determine the physical speeds in Experiments 3 and 4.

Observers

Three observers completed all experiments, they were the two authors, DHB (25, male) and EWG (33, male), and a postgraduate student, KLG (23, female). All observers were emmetropic, with no abnormalities of binocular vision.

Results

Experiment 1—contextual motion

When drifting, rivaling gratings are surrounded by a binocular moving texture, it has a strong influence on the relative predominance of the two gratings. Figure 2 shows how predominance changes as a function of surround direction, relative to the +45° (right-tilted) grating. To a first approximation, dominance is increased when the surround moves in the opposite direction and reduced when it moves in the same direction. This extends the findings of Paffen et al. (2004, 2006), Paffen, Alais, et al. (2005), and Paffen, van der Smagt, et al. (2005) to other directions of surround motion and is apparent for each observer (Figure 2B). In some cases, these effects are substantial, producing an imbalance of dominance between the gratings of up to 40% (i.e., EWG at 315°). Statistical analysis (one sample *t* tests) performed across repetition indicated that predominance values for many

conditions were significantly different from the baseline (0.5) and are indicated by green asterisks in Figure 2B.

There are two points at which predominance is equal between the gratings. These are at 45° and 225° relative to the right oblique grating—in other words when surround motion is directly down, or directly up (respectively). Under these conditions, the relative context direction is equivalent for both gratings (assuming that motion effects are symmetrical for positive and negative relative directions—an assumption which we verify in Experiment 2). The blue and red functions shift horizontally about these points (Figure 2A), and not about the extremes of context direction (i.e., 0° and 180°). This occurs because of the combination of surround effects (suppression and facilitation) on the two orthogonal gratings, which produces the largest effects for horizontal (absolute) surround directions (relative directions of 135° and 315°).

Experiment 2—PSE for grating speed

As described in the Introduction, the perceived speed of a central stimulus can be influenced by motion in the surround. We quantified this for our stimuli by measuring the point of subjective equality (PSE) for speed at each surround motion direction. Figure 3 shows the results for three observers, plotted in polar coordinates. The axis labels give the direction of surround motion relative to that of the central grating, and the data points represent observer settings of the speed of a Gabor patch surrounded by mean luminance. The physical speed of surround and center was always 0.5 deg/s; however, the perceived speed

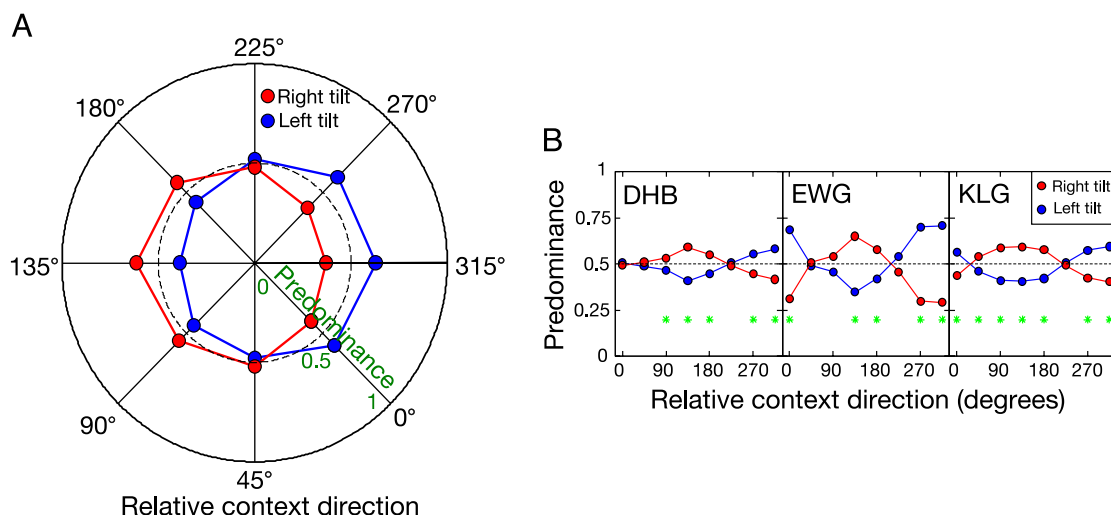


Figure 2. Predominance ratios for drifting orthogonal Gabor patches, surrounded by a drifting noise texture. Panel A gives values averaged across three observers plotted in polar form. The absolute radial direction corresponds to the true direction of the surround motion (see Figure 1A), and axis labels give the direction relative to that of the right oblique grating (red function). Panel B shows data from individual observers, plotted on standard axes. Dashed lines indicate predominance of 0.5, where the gratings are perceived for equal amounts of time. Green asterisks indicate conditions which were significantly different ($p < 0.05$, two tailed) from 0.5 (one sample *t* test).

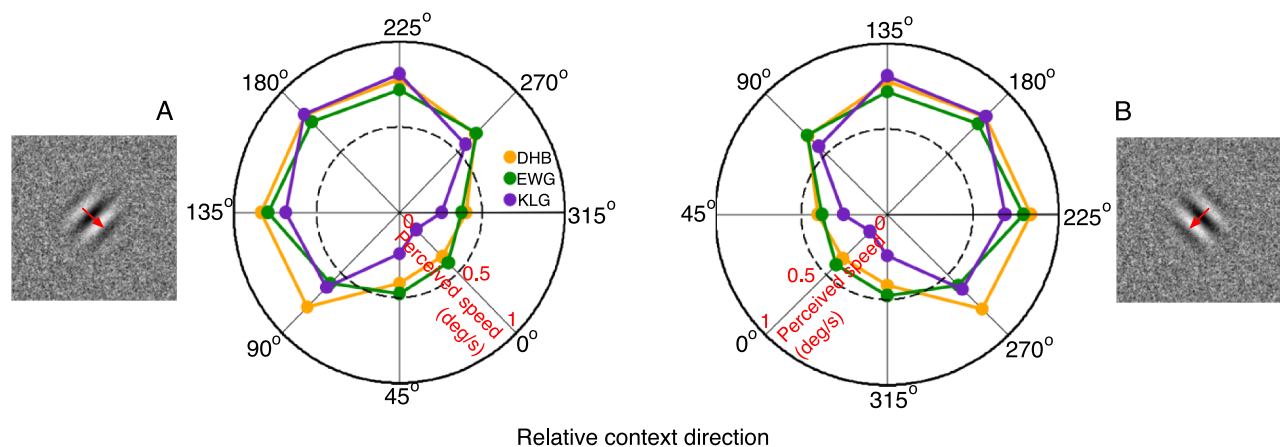


Figure 3. Results of [Experiment 2](#). Data indicate perceived speed of a central Gabor, as a function of surround motion direction. Data are shown relative to the right tilted grating (A) and mirror reversed about the vertical axis for the left tilted grating (B) to elucidate later procedures. The standard Gabor and the surrounding texture always had a physical speed of 0.5 deg/s, given by the black dashed lines. When surround motion and grating motion directions were similar (around 0°), the grating appeared to move slower. When surround motion opposed grating motion (around 180°), the grating appeared to move faster. The standard error of the probit fit was always smaller than the symbols and is not shown.

of the center was strongly influenced by surround direction. When center and surround moved in a similar direction, PSE settings indicated that observers perceived the center as moving slower than its physical speed. When center and surround motions opposed, the center appeared to move faster than its true speed. The difference between the slowest and the fastest perceived speeds was at least a factor of two for all observers and substantially greater for observer KLG. The functions are approximately symmetrical about the 0°–180° axis, indicating that *relative* context direction is the key variable for the illusion. This justifies the assumption of symmetry made in the previous section.

Observers also completed a control version of the PSE experiment with no surround. All observers produced thresholds to within $\pm 1\%$ of the true speed (0.5 deg/s), indicating the high precision of both our methods and observers.

These data extend previous findings with dot motion (Loomis & Nakayama, 1973; Norman et al., 1996) to our current grating stimuli. The relationship between this effect and the binocular rivalry results of [Experiment 1](#) is explored in [Experiment 3](#). Interested readers are directed to [Movie 1](#), which demonstrates the perceived speed illusion.

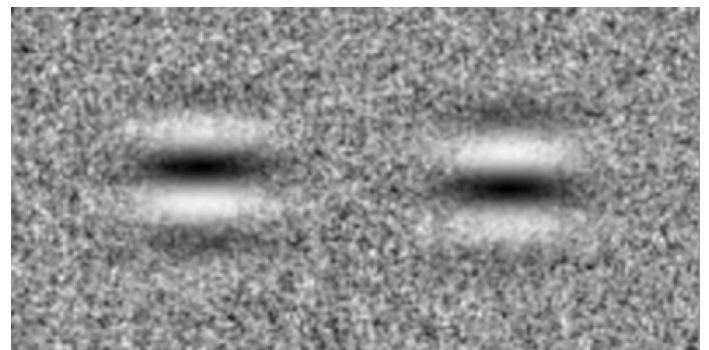
Experiment 3—physical speed

Given the effect a moving background has on perceived speed, it is important to ask how the perceived speed of a grating influences rivalry. To investigate this, we rivaled physical speeds determined by the estimated (perceived) grating speeds from [Experiment 2](#). Thus, in [Experiment 3](#) we simulate the perceived grating motions from [Experiment 1](#) by manipulating physical grating speed rather than

surround direction. Rivalry stimuli in this experiment consisted of Gabor patches surrounded by mean luminance.

For each observer, eight pairs of speeds were calculated, corresponding to the eight surround directions from [Experiment 1](#). In other words, the physical speed of each grating was determined by the perceived speed for the appropriate relative context direction (pairwise combination across [Figures 3A](#) and [3B](#) of points lying on each radial line). Rivalry was measured for each of these speed pairs under the same conditions as [Experiment 1](#), and the predominance for each pair is shown in [Figure 4](#).

It is clear that the results shown in [Figures 2](#) and [4](#) are very similar in form. Both sets of average data depart from the dashed midline (predominance of 0.5, indicating equal dominance) maximally at the 135° and 315° points. With context direction (true or simulated) of 45° and 225°,



Movie 1. Demonstration of perceived speed illusion. Two gratings, moving at equal speeds but in opposite directions, are embedded in a noise background moving in the same direction as one of the gratings. There is a strong illusory percept of differing speeds.

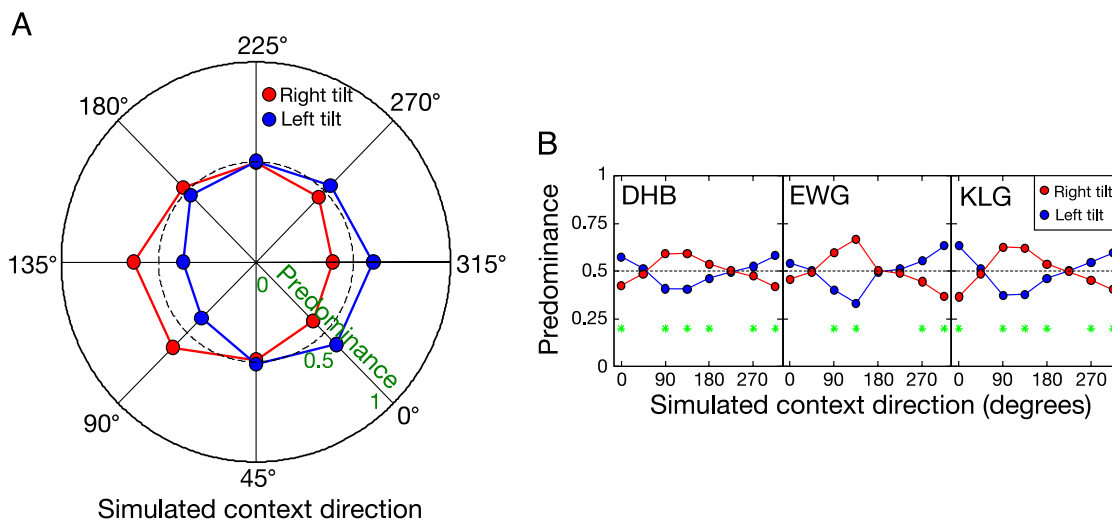


Figure 4. Grating rivalry in the absence of a surround, where the different grating speeds induced by the surround are substituted for physical speeds. The pattern of results strongly resembles those of [Experiment 1](#), indicating that perceived and physical speed affect rivalry in an equivalent manner. The panel arrangement is the same as that of [Figure 2](#). Green asterisks again denote statistical significance at the 0.05 level (one sample t test, two tailed).

both data sets show no difference in dominance between the gratings. This is unsurprising, as the relative context direction is the same for both gratings at these points, so their speeds (both perceived and physical) are equal.

The data of [Experiment 3](#) are highly correlated with the results of [Experiment 1](#) ($r = 0.91$, $p < 0.01$; average data for right tilted grating; r values were >0.8 for the individual data of all subjects). It appears that the changes in perceived speed induced by a moving surround have an equivalent effect on binocular rivalry to changes of physical speed. This has important implications for our understanding of the motion context effect in rivalry, which we consider in the [Discussion](#).

Experiment 4—interactions with grating contrast

In the final experiment, we explore how stimulus speed (both physical and perceived) interacts with grating contrast in rivalry. Both faster and higher contrast stimuli exhibit increased dominance, and here we determine if changing component contrast can enhance the effect of speed (summing) or reverse it (nulling). This provides a further comparison between physical and perceived speed.

Since the predominance scores always sum to one, taking their difference gives an indication of the extent to which one grating is favored over the other during rivalry (this was calculated as *right oblique grating*–*left oblique grating*, so for predominances of 0.6 and 0.4, the difference would be 0.2). [Figure 5A](#) shows predominance difference data averaged across the three observers for baseline conditions, and [Figure 5B](#) shows data for summing and nulling.

For this experiment, the condition which produced the largest effect in [Experiment 1](#) was used—a surround direction of 135°. For the physical speed settings, the appropriate pair of speeds (based on the matching data) was selected for comparison. We used contrasts of 100% and 25%, which pilot experiments indicated gave an approximately equal size of effect to the speed conditions.

As might be expected, there was no difference between the predominance scores of gratings of the same speed and contrast, in the absence of the moving context (“identical” condition). However, when one grating had higher contrast (100% vs. 25%), it was perceived for longer (“contrast” condition). The contrast effect can be compared to the remaining bars of [Figure 5A](#), which represent predominance differences from single conditions of [Experiment 1](#) (135° relative background motion) and [Experiment 3](#) (speed difference factor >2), averaged across observers. Both of these manipulations produce a similar size of effect to changing contrast by a factor of 4.

In the summing condition ([Figure 5B](#), left), the grating with the lower speed (perceived or physical) was also given lower contrast (25%), while the faster grating remained at full contrast (100%). This led to an increase in predominance for the faster grating, as the two stimulus attributes combined to confer greater dominance. In the nulling condition, the speed–contrast relationship was reversed so that faster gratings had lower contrast (25%). This manipulation greatly reduced the predominance difference between the gratings, as the stimulus attributes were brought into conflict ([Figure 5B](#), right).

The magnitudes of both the summing and nulling effects were the same for both perceived and physical speed, suggesting that they interact with contrast in a similar manner. This supports our conclusion from the previous

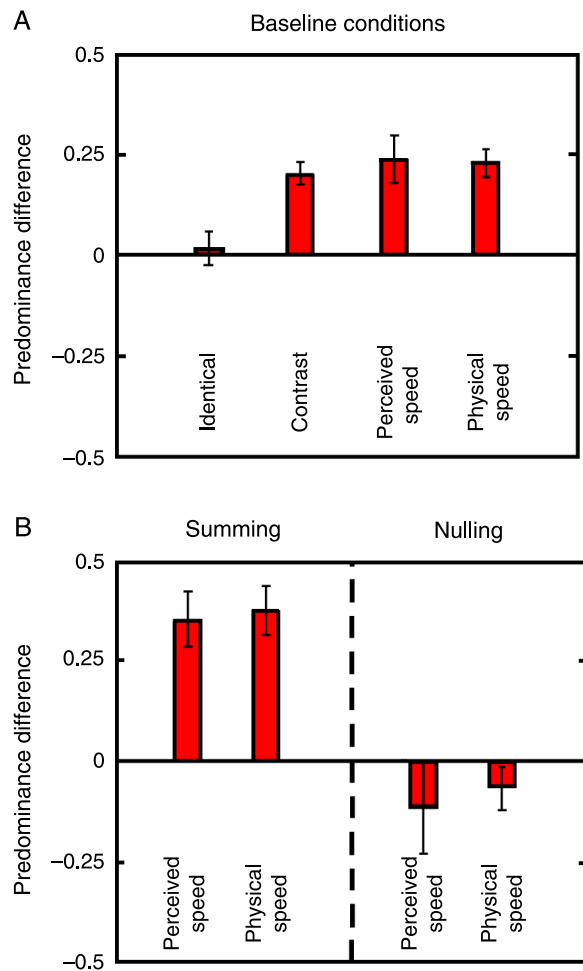


Figure 5. Combination of speed and contrast. Panel A shows the difference in predominance for gratings with equal speed and contrast (“identical”), differing contrast (“contrast”) and differing perceived or physical speed. Panel B shows summing and nulling data. In the summing condition (left), the slower grating had a lower contrast and in the nulling condition (right), the faster grating had a lower contrast. Red bars are empirical data, averaged across three observers. Error bars give the standard error of the mean.

section that perceived and physical speed are equivalent in rivalry, and that perceived speed and the motion context effect may be underpinned by the same mechanism.

Discussion

We explored the effect of a moving background on binocular rivalry between two drifting gratings. The pattern of dominance was determined by the relative direction of surround motion, such that the member of the rivalry pair moving opposite to the background had greater dominance. Since moving surrounds can affect

the perceived speed of a central region, we used a speed matching experiment to quantify this illusion for our stimuli. Consistent with previous findings, when center and surround had the same direction of motion, the perceived speed of the central grating was reduced, and when motion directions were opposite, it was increased. The rivalry-context experiment was simulated using appropriate pairs of physical speeds, based on the matching results. This simulation produced the same pattern of results, indicating that perceived and physical speeds are equivalent for binocular rivalry. This was further confirmed in a final experiment, in which speed and contrast were combined either concurrently or in opposition. Changing contrast produced the same effect on grating dominance for both physical and perceived speed.

In addition to analyzing the predominance of one stimulus over another, it is often informative to consider differences in dominance durations across rivalry conditions. When a moving stimulus rivals with a static one, it has previously been shown that a surround with the same motion direction serves to increase the mean duration of the static component (Paffen et al., 2004). Such a comparison is less straightforward for our stimuli, as the surround would be expected to influence both moving components. This was confirmed by inspection of the mean durations from Experiments 1 and 3 (not shown). The moving surround altered dominance durations by equal and opposite amounts for the two components, following the same pattern as shown for predominance in Figures 2 and 4.

A linear relationship between predominance and speed difference

Although there are several studies in which moving stimuli rival with static stimuli (Blake, Yu, Lokey, & Norman, 1998; Paffen, Alais, et al., 2005; Paffen, van der Smagt, et al., 2005; Wade et al., 1984; Wiesenfelder & Blake, 1990), we are unaware of any rivalry studies reporting how dominance changes when both components are drifting gratings moving at different speeds. This means that the effect of *relative* speed (or speed difference) is not known for grating stimuli. In Figure 6, we replot the data of Experiments 1 and 3 as predominance difference (see above) against the speed difference of the components (for the context condition, this was the difference in perceived speed, based on the results of Experiment 2). Both conditions show a strong correlation between speed difference and predominance difference. The best-fitting regression lines pass through the origin and have a slope of ~ 0.5 . The similarity across the two panels of Figure 6 further confirms the equivalence of perceived and physical speed.

We note, however, that when component speeds differ greatly, rivalry breaks down (van de Grind, van Hof, van der Smagt, & Verstraten, 2001), so a linear relationship

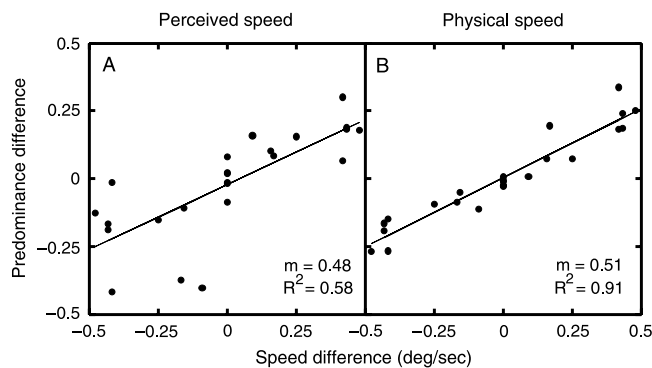


Figure 6. Predominance difference vs. speed difference. For both perceived and physical speed, there is an increase in predominance difference with increasing speed difference. Data points are taken from Experiments 1 and 3, for three observers, with speed difference being calculated relative to the right tilted grating. Lines are best-fitting linear regressions, which have a slope (m) of ~ 0.5 for both conditions. This provides further evidence that perceived and physical speed influence rivalry in the same manner.

would only be expected to hold over a limited range of relative speeds. This is also apparent in the data of Blake et al. (1998) for rivaling dot stimuli. At low speeds (<1 deg/s), dominance increases with speed as found here. This reaches a plateau at intermediate speeds before decreasing again at faster speeds (>2 deg/s).

Relation to previous work

The equivalence of perceived and physical speed in rivalry sheds light on the results of several previous studies (Paffen et al., 2004, 2006; Paffen, Alais, et al., 2005; Paffen, van der Smagt, et al., 2005), which can now be more closely linked to the broader domain of motion in rivalry (i.e., Blake et al., 1998; Wade et al., 1984; Wiesenfelder & Blake, 1990). This means that key findings from context–motion experiments should be expected to generalize to rivalry between gratings moving at different speeds. For example, sensitivity to a test probe shown to the suppressed eye is reduced by context-enhanced rivalry (Paffen, Alais, et al., 2005) when compared to standard rivalry. This should be expected to occur for rivalry between gratings of different speeds, such that a faster grating will produce deeper suppression of a slower grating.

A possible alternative explanation of our effect is that the surround could alter the perceived contrast of the center (i.e., Cannon & Fullenkamp, 1991). Since lower contrast stimuli appear to move slower than high contrast stimuli (Thompson, 1982), this could account for our effect. However, the change in perceived contrast would have to be substantial (even a standard–test contrast ratio of 7:1 at 2 cpd produces a smaller effect on perceived speed than our moving surround, see Thompson, Brooks,

& Hammett, 2006), and visual inspection of our stimuli reveals no perceptible change in contrast (presumably due to saturation at the high contrasts used here). We therefore consider this to be an unlikely explanation.

Neural underpinnings of speed in rivalry

Our findings suggest that physical and perceived speed influence rivalry at the same stage of processing, presumably via the same neural circuitry. Given the general preference of the medial temporal area (MT/V5) for moving stimuli (i.e., Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Maunsell & van Essen, 1983; Mikami, Newsome, & Wurtz, 1986), this brain area would seem a likely contender for mediating speed in binocular rivalry. Indeed, a recent fMRI study has reported strong activation in area MT for coherent dot motion engaged in binocular rivalry (Moutoussis, Keliris, Kourtzi, & Logothetis, 2005). There is also much neurophysiological evidence for center-surround interactions in area MT (Allman et al., 1985a, 1985b; Born, 2000; Eifuku & Wurtz, 1998; Pack et al., 2005). Some of these are direction tuned and, crucially (for the perceived speed illusion), include suppression and facilitation of same and opposite motion directions, respectively (Born, 2000; Eifuku & Wurtz, 1998).

An alternative explanation is that the surround effects occur in V1 itself. Neurons in V1 are also responsive to motion and show strong center-surround interactions (Bair, Cavanaugh, & Movshon, 2003; Born & Tootell, 1991; Levitt & Lund, 1997; Sillito & Jones, 1996), some of which are also direction specific (Gulyás, Orban, Duysens, & Maes, 1987; Jones, Grieve, Wang, & Sillito, 2001). We find this explanation unlikely; Paffen et al. (2004) have found that context effects increase with surround diameter, up to at least 6° . The inhibitory surrounds in V1 typically saturate by 4° in diameter (Sengpiel, Sen, & Blakemore, 1997), making them too small to fully account for the rivalry effects. MT neurons have much larger receptive fields for both center and surround (Eifuku & Wurtz, 1998), making them more plausible candidates for our present effects. However, this does not rule out the possibility that both areas contribute, as has been suggested previously (Paffen et al., 2004), or that MT modulates rivalry in V1 via feedback connections.

A Bayesian interpretation of the perceived speed effect

Although the changes in firing caused by surround suppression and facilitation provide a plausible mechanism for influencing rivalry, the link between these and the perceived speed illusion (see Movie 1) is less clear. Born (2000) reports that surround motion changes the mean firing rate of neurons stimulated at their optimal

speed and direction but does not change their speed tuning. Since MT neurons encode a specific velocity range (Perrone & Thiele, 2001), a change in firing will not necessarily lead to a change in apparent speed, at either the single cell or population level. To reconcile the surround inhibition account with the perceived speed illusion, we offer an explanation that draws on recent developments in the application of the Bayesian framework to human motion perception.

Several recent studies have used Bayesian models to successfully account for a number of motion perception phenomena and illusions (Ascher & Grzywacz, 2000; Weiss & Adelson, 1998; Weiss, Simoncelli, & Adelson, 2002). A key component of some of these models is a prior for slow and smooth motion (Weiss & Adelson, 1998), reflecting the relative absence of fast motion in most visual scenes. We suggest that such a prior might also account for our perceived speed illusion with a moving background (see [Movie 1](#)), when considered in combination with surround suppression and facilitation.

Consider a prior for “slowness,” centered at speed zero (depicted by the blue Gaussian in [Figure 7A](#)). Viewing a

moving stimulus generates a likelihood function (which could correspond to activity in a neural population, i.e., Jazayeri & Movshon, 2006; Knill & Pouget, 2004), shown in red in [Figure 7A](#). Optimal combination of these components yields a posterior estimate of perceived speed located between the distributions, as shown by the green Gaussian in [Figure 7A](#). When the surround suppresses activity in the neural population ([Figure 7B](#)), this reduces the signal-to-noise ratio, increasing the variance of the likelihood function. In the Bayesian framework, this reduces the contribution of the sensory data and shifts the posterior distribution toward the prior, reducing perceived speed. If the surround enhances (facilitates) the signal, it will increase the signal-to-noise ratio of the sensory data, reducing its variance. The posterior will then shift to the right ([Figure 7C](#)), increasing the perceived speed.

This interpretation provides a plausible link between the center-surround processes known to occur in cortex and the perceived speed illusion. We suggest that the resulting neural representation of speed, which is now equivalent for equal physical and illusory speeds, might subsequently influence dominance in rivalry.

Architectures for binocular rivalry

Recent computational models of binocular rivalry have featured a hierarchy of suppressive stages (Freeman, 2005; Wilson, 2003). The earliest stage of rivalry suppression is believed to occur between monocular channels in V1 (i.e., Blake, 1989). This is probably too early in the visual pathway to be directly affected by the center-surround effects discussed above, which might indicate that a later stage is responsible, perhaps through modulation by feedback signals from later areas (i.e., MT). This prevents any clear prediction based on our results of where a “speed unit” might be introduced into existing models.

In any potential modeling scheme, it is important to note that the neural representation of speed (as discussed above) is not necessarily affected by rivalry suppression (when the stimulus is not perceived). There is evidence from several studies to indicate that many features of a stimulus are still processed during rivalry suppression (i.e., Alais & Parker, 2006; Carlson & He, 2000; Fang & He, 2005), and in principle this might apply to speed also. Such an arrangement would mean that a moving context can influence rivalry during both the suppressed and dominant phases for each component.

Summary

We have shown that the effect of a moving surround on binocular rivalry is consistent with the change in perceived

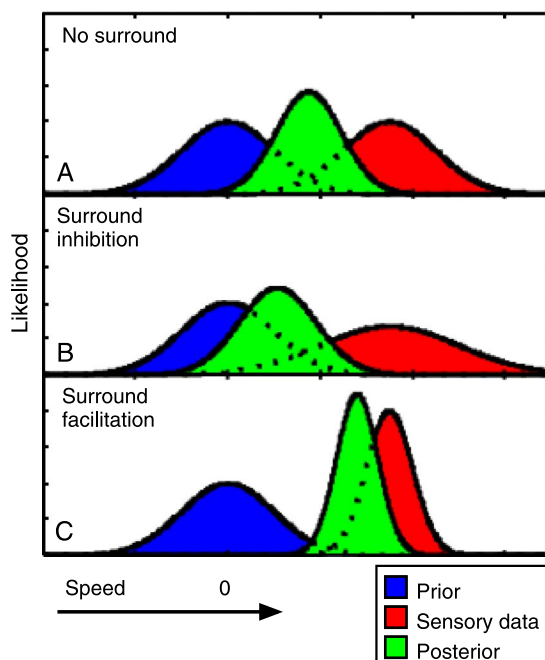


Figure 7. Illustration of a Bayesian interpretation of the perceived speed illusion. A “slowness” prior centered around zero is depicted in blue. Red functions are sensory observations (“likelihoods”) of motion speed, and green functions are posterior distribution functions, which determine the resulting perceived speed following a decision rule (e.g., maximum a posteriori (MAP)). Surround inhibition (B) decreases firing and reduces the signal-to-noise ratio. This is shown by the increased variance of the likelihood function (broadening of the red distribution). The reduced signal increases the effect of the prior, reducing the perceived speed. A similar effect occurs in the opposite direction for facilitation (C).

speed of the rivaling gratings caused by the surround. We first measured the pattern of dominance in binocular rivalry for different directions of surround motion. We then quantified the substantial perceived speed illusion that occurs for drifting gratings surrounded by a moving noise texture. The perceived speed values were used to simulate the context experiment and produced the same pattern of dominance as a moving surround. Perceived and physical speed are therefore equivalent in determining dominance during binocular rivalry.

Acknowledgments

This research was supported by BBSRC grant number BB/E012698/1. We thank Wendy Adams for valuable comments on the manuscript and for first suggesting the Bayesian interpretation of the perceived speed illusion.

Commercial relationships: none.

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