Binocular rivalry of spiral and linear moving random dot patterns in human observers

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Binocular rivalry describes the alternating perception of two competing monocular images. It is hypothesized to arise at multiple levels of the visual pathway due to competition between neuronal populations representing the displayed images. We tested whether an enhanced neural representation of expanding motion yields a bias over other spiral motion (i.e., contraction and rotation) and linear motion stimuli during binocular rivalry. We presented random dot patterns of different motion types (i.e., linear and spiral), matched in contrast and speed, to human subjects through a mirror stereoscope. During spiral rivalry, expansion rivalry periods dominated over those of contraction and rotation, and contraction dominated over rotation. During linear motion rivalry, up, down, left, and right directions had similar rivalry periods. All spiral motions dominated over linear motions. Interestingly, when these motion types rivaled against each other, the rivalry periods of spiral motion slightly decreased while those of linear motion significantly increased. This rivalry also caused the bias for expansion relative to other spirals to disappear. Our results suggest a correlation between neuronal representations of different moving patterns and their perception during binocular motion rivalry and provide further evidence that rivalry periods are constrained by the ecologic relevance of stimuli.

Keywords: binocular rivalry, expansion, spiral, motion perception, linear motion, random dot patterns


Introduction

When the brain receives monocularly presented inputs from both eyes, it fails to provide a stable visual percept. Instead what ensues is a competition for dominance between the inputs, yielding random alternations between the independent images—a phenomenon termed binocular rivalry (Tong, Meng, & Blake, 2006). The potential sites of the neural competition and the integrative mechanisms that coordinate interactions between competing neuronal populations are still under debate. Three proposals for such mechanisms have been made: (1) rivalry occurs due to low-level interocular competitions between monocular neurons in the primary visual cortex (V1) or the lateral geniculate nucleus (LGN), (2) binocular rivalry transpires later in visual processing and reflects competition between different patterns (i.e., not interocular competitions), and (3) rivalry involves neural competition at multiple levels of the visual pathway (A. W. Freeman, 2005; Nguyen, Freeman, & Alais, 2003; Ooi & He, 2003; Wilson, 2003). Most recent studies have supported the latter view (Blake & Wilson, 2011; Sterzer, Kleinschmidt, & Rees, 2009).

One common finding in studies of binocular rivalry is that stimuli that are higher in contrast or contain motion have a tendency to be seen for longer periods (i.e., dominate the rivalry) than duller or stationary stimuli (de Weert & Wade, 1984; Blake, Yu, Lokey, & Norman, 1998; Levelt, 1965; Wade & de Weert, 1986; de Weert & Wade, 1984). Levelt (1965) suggested that this tendency is due to a reduction of the dominant stimulus's average suppression duration. However, in the specific case of motion stimuli this proposition has not been entirely confirmed (Bossink, Stalmeier, & de Weert, 1993; Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006). Motion stimuli are particularly well suited to study the neural basis of binocular rivalry since the selectivity of neuronal populations across the visual pathway for the different stimulus types (e.g., linear motion or spiral motion) is well documented.
For example, areas V1 and middle temporal (MT) contain units that are tuned for linear (i.e., translation-based) motion (Albright, 1984; Hubel & Wiesel, 1962; Livingstone & Hubel, 1988; Maunsell & Van Essen, 1983a, 1983b), while the dorsal medial superior temporal area (MSTd), located downstream from V1 and MT in the visual pathway, contains units selective for the processing of complex motion stimuli such as spirals (which are composed of a wide range of motion directions and contain speed gradients) as well as linear motion (Graziano, Andersen, & Snowden, 1994; Saito et al., 1986; Tanaka, Fukada, & Saito, 1989; Tanaka et al., 1986). In MT approximately 75% of neurons are tuned for linear motion with a preference for unidirectional motion away from the fovea rather than toward it (Albright, 1989; Tanaka et al., 1986); while in MSTd approximately 50% are similarly tuned (Tanaka et al., 1986). Besides a population of translation motion specific units, it has been reported that in MSTd expansion-tuned cells outnumber contraction cells by a ratio of 2:1 and rotation cells by a ratio of 3:1 (Duffy & Wurtz, 1991a, 1991b; Graziano et al., 1994; Saito et al., 1986; Tanaka et al., 1989). Magnetoencephalography (MEG) studies in humans, recorded over the homologue of MT/MST, also indicate a preference for expanding stimuli compared to other motions (Holliday & Meese, 2005). Holliday and Meese (2005) hypothesized that the relative numbers, or sensitivities, of differently tuned neuron groups are relative to the magnitude of their evoked magnetic responses; since expanding visual stimuli produced the greatest magnetic response and findings of the greater proportioned expansion-tuned units had been published, they suggested that the evoked magnetic responses are larger for motion stimuli that activate a larger pool of neurons. This bias may be related to the ecologic value of expansion relative to other spiral motions for primates, i.e., expanding patterns could indicate a potential collision (Franconeri & Simons, 2003; Gonzalez et al., 1988; Hassenstein & Hustert, 1999; Lee et al., 1976; Regan & Beverly, 1978; Regan & Hamstra, 1993; von Muhlenen & Lleras, 2007; Wang & Frost, 1992) and are common during forward locomotion since they are important in computing direction of heading (Crowell & Banks, 1993; T. C. Freeman, Harris, & Tyler, 1994; Gibson, 1950; Warren & Hannon, 1988). Moreover, evidence from motion transparency depth rivalry experiments has indicated that the relevance of a stimulus influences rivalry (Chopin & Mamassian, 2011; Maruya, Yang, & Blake, 2007). This suggests that the ecologically relevant expansion stimulus, which has influenced the perception of human observers during tasks such as visual search (Takeuchi, 1996) and speed illusions (Geesaman & Qian, 1996), may also influence dominance durations during binocular rivalry (Park & Alais, 2007; Wade et al., 1984).

Considering the physiologic data on the relative proportions of neurons selective for a given motion type in the primate brain and the magnitude of evoked MEG responses to spiral stimuli, it may be reasonable to assume that the signal strength of a given spiral motion mechanism depends on the proportion of cells tuned to that motion type; thus, if competition between neuronal populations underlies rivalry, the strongest represented motion should dominate rivalry periods.

In order to investigate this issue, we designed a series of binocular rivalry experiments using motion stimuli to: (a) quantify the periods of binocular rivalry corresponding to each spiral motion type when competing with one another, (b) determine whether such periods are altered when they compete against linear motion stimuli, and c) test whether removing the speed gradient that naturally characterizes these complex motion types has an effect on their rivalry periods. Finally, we interpret our findings according to our current knowledge of the motion processing hierarchy and the selectivity of neurons for the various motion types in different areas of the primate dorsal pathway.

### General methods

#### Stimuli

The stimuli were generated using MATLAB® (R2007b, The MathWorks, Inc., Natick, MA) software and the Psychophysics Toolbox (Brainard, 1997). They were presented on a CRT monitor (LaCie Electron2blueIV, 40 × 30.5 cm [15.75 × 12 inches], resolution: 1280 × 1024 pixels, screen refresh rate: 75 Hz; Portland, OR). Observers viewed the stimuli through a mirror stereoscope, with the left eye seeing only the left half of the screen and the right eye seeing only the right half of the screen. The viewing distance was 35.6 cm (or 14 inches) and each dot was a square pixel that extended over a visual angle of 0.043°.

The stimuli were random dot patterns (RDPs) moving behind a circular aperture with a diameter of 300 pixels. A black circle with diameter of five pixels was added to the center for all stimuli; previous studies have indicated that the addition of such a circular field does not influence global results (de Weert & Wade, 1984), and it was necessary in order to avoid the accumulation of dots at the center of the contracting stimuli. Each stimulus consisted of 300 white dots (luminance: 39.75 cd/m², 1 × 1 pixels) displayed on a black background (luminance: < 0.001 cd/m²).
Ten stimuli motion types were created and are categorized here in two groups: linear (left [270°], right [90°], up [0°], down [180°]) and spiral (expansion with speed gradient, expansion without speed gradient, contraction with speed gradient, contraction without speed gradient, clockwise rotation with speed gradient, and counterclockwise rotation with speed gradient). Spiral stimuli programmed to move with a speed gradient had dot movements calculated by the following equations:

For expansion and contraction:

\[\Delta r_f = \omega \times r_{f-1}\]  
\[\Delta x_f = \Delta r_f \cos \theta_{initial}\]  
\[\Delta y_f = \Delta r_f \sin \theta_{initial}\]

For clockwise and counterclockwise rotation:

\[\Delta \theta_f = \frac{\omega}{\theta_{f-1}}\]  
\[\Delta x_f = r_{initial} \cos \Delta \theta_f\]  
\[\Delta y_f = r_{initial} \sin \Delta \theta_f\]

\(\Delta r_f\) is the change in distance of a dot from the stimulus center for frame \(f\) in expanding and contracting spirals. The contraction stimulus’ \(\Delta r_f\) was multiplied by \(-1\) so that the dots would travel inwards. For rotating stimuli \(\Delta \theta_f\) is a dot’s change in angle for frame \(f\). The counterclockwise \(\Delta \theta_f\) was multiplied by \(-1\) so that the dots would move counterclockwise. \(\Delta x\) is the change in the \(x\)-direction which is added to the \(x\) variable of the prior frame, \(\Delta y\) is the change in the \(y\)-direction which is added to the \(y\) variable of the prior frame, and \(\omega\) is a constant we selected to be equivalent to 0.02/frame so that, in the case of expansion for example, dots that are further from the center appear to be moving faster than dots closer to the center thus giving the impression that the dots are looming.

To determine the appropriate speed to apply to translation stimuli and the expansion/contraction stimuli without speed gradient, we followed the method described by Geesaman and Qian (1996). The speed was calculated for dots 106 pixels from the center of the circle and was equivalent to \(4.7°/s\) (0.082 rad/sec, Geesaman & Qian, 1996). Using this speed and the equations mentioned above for expansion and contraction, the \(\Delta r_f\) was no longer a function of the distance from the center but rather a constant equal to \(0.063°/frame\), or \(0.001\) rad/frame. An image of each stimulus is illustrated in Figure 1A.

Dots were initially assigned random positions and trajectories. Once their radii exceeded the radius of the RDP, the dots were reassigned new positions and trajectories consistent with the specified motion pattern.

For each of the three experiments performed, a different set of conditions was made from different combinations of these stimuli. Each experiment’s conditions are tabulated in panel A of the figure associated with each experiment.

**Procedure**

Experiments were performed in a dark room. At the beginning of a session two white circles were presented, one on each side of the screen, so that the mirror stereoscope was adjusted for each subject to achieve fusion of the images presented to each eye. Subjects were also instructed to maintain fixation at the center of the stimuli as best they could. An indication as to how well fixation was achieved is addressed in the General discussion under Additional Factors: Optokinetic nystagmus and in the Supplementary Information (Supplementary Figure 5 and Supplementary Table 1). A chin rest was used to keep a subject’s head still during the experiments. Each trial lasted 70 seconds, but only responses during the last 60 seconds were considered for the analysis. During the first 10 seconds, subjects were told to close their right eye while keeping their left eye open so they could see the left stimulus and then close their left eye and open their right eye to determine what the right stimulus was. They were also informed of what the stimuli were before starting each trial in order to avoid confusion about which stimulus was presented to which eye. During the experiment, subjects pressed the number “1” key of a keyboard whenever they perceived the left stimulus, the number “3” whenever they perceived the right stimulus, and the number “2” when both stimuli were perceived as either fused or piecemeal. Each key press prompted MATLAB to record the time at which the key was pushed starting 10 seconds into the trial (therefore during the 70-second trial, times recorded must be between 0 and 60 seconds). During the analysis, the difference between consecutive times was calculated in order to obtain the duration of each key press.

Depending on the length of the experiment, subjects were asked to come in for two to three days to complete each experiment. During a session, subjects were allowed to take breaks whenever they became tired. All procedures were pre-approved by the McGill University Faculty of Medicine Ethics Review Board.

**Experiment 1: Rivalry between spiral motions**

The goal of this experiment was to quantify rivalry periods corresponding to each type of spiral stimulus.
for different combinations of spirals. Under the assumptions that: (1) rivalry is based on the competition between neurons tuned for the different stimuli (Blake, 1989; Blake & Logothetis, 2002; Logothetis & Schall, 1989; Logothetis, Leopold, & Sheinberg, 1996), (2) the strength of neural activation determines the dominance during rivalry, and (3) expansion neurons relatively outnumber contraction-tuned neurons, the latter relatively outnumber rotation-tuned neurons, and expanding stimuli evoke greater MEG responses (Duffy & Wurtz, 1991a, 1991b; Graziano et al., 1994; Holliday & Meese, 2005; Saito et al., 1986; Tanaka et al., 1989), we hypothesized that during rivalry: (1) expanding stimuli would be perceived over a longer mean duration (i.e., dominate) relative to contracting and rotating stimuli, (2) the contracting stimuli would dominate over the rotating stimuli, and (3) clockwise and counterclockwise rotating stimuli would have similar rivalry periods.

As a control we examined rivalry between linear motion stimuli (left [= 270°], right [= 90°], up [= 0°], and down [= 180°]). Because neurons tuned for these cardinal directions of linear motion are found in relatively equal proportions within area MT (Xu, Collins, Khaytin, Kaas, & Casagrande, 2006), we hypothesize that rivalry periods for all linear motions would be similar.

**Subjects and stimuli**

Seven subjects participated in Experiment 1; six were naïve to the purpose of the experiment. All subjects had
normal or corrected-to-normal vision. Five subjects were right-eye dominant, while two were left-eye dominant. Eye dominance was determined, prior to starting the experiment, by asking each subject to perform a standard Dominant Eye Test. During this ‘screening’ test, subjects would extend their arm straight out and, with both eyes open, align their thumb with a mark on a wall; staring at their thumbs, subjects closed each of their eyes separately to determine which eye’s occlusion would lead to the thumb and target misalignment—this eye is the dominant eye. Subjects were then trained for a minimum of 30 trials until they reported they were comfortable with the task.

The four linear motion stimuli and the four spiral motion stimuli with speed gradient were used to produce 24 conditions, 12 consisted of linear motion types rivaling against one another and 12 consisted of...
spirals rivaling against one another (Figure 2A). Each condition was presented 10 times for a total of 240 trials. The different combinations were presented in random order.

Results and discussion

Upon measuring the rivalry periods for each stimulus during each trial (see General methods), we first analyzed the total time dominant (TTD) for each stimulus (Figure 2B)—regardless to which eye it was presented—when rivaling against a specific stimulus. In other words, the rivalry periods of a stimulus obtained for a subject’s trials were added and then pooled across the trials for conditions that displayed the pair of stimuli. The TTD was then averaged across subjects.

Since one trial is 60 seconds long, 10 trials existed per condition, and a combination of stimuli would comprise of two conditions (so that both stimuli are viewed by both eyes), the sum of the two dominance totals for each combination should be less than 1,200 seconds and the difference between the sum and this total observation period represents the total piecemeal duration. Using paired t-tests to compare TTD, only expanding motion predominated significantly longer when presented against another spiral stimulus (against contraction [CONT]: $t[6] = 4.014, p = 0.007$; against clockwise [CW] rotation: $t[6] = 2.515, p = 0.013$; against counterclockwise [CCW] rotation: $t[6] = 2.560, p = 0.042$, paired t-test). Contracting and rotating motions showed no significant differences among their rivalry periods (CONT against CW: $t[6] = 0.128, p = 0.902$; CONT against CCW: $t[6] = 0.370, p = 0.724$; CW against CCW: $t[6] = 0.925, p = 0.390$, paired t-test). We also tested whether the TTD was significantly different under the three different presentation conditions for each stimulus using Bonferroni’s Multiple Comparison test; no significant differences resulted in a stimulus’ rivalry period when presenting it against the different spiral stimuli (EXP: $t[12] = 1.101, p = 0.085$; CONT: $t[12] = 1.120, p = 0.385$; CW: $t[12] = 0.643, p = 0.554$; CCW: $t[12] = 0.588, p = 0.576$, Bonferroni’s Multiple Comparison test). For linear motion, the stimuli’s TTDs were very similar ($t[6], 1.831, p > 0.1$, paired t-test) and, not surprisingly, each stimulus showed no significant difference in rivalry periods even if presented against different linear stimuli ($t[12] < 1.401, p > 0.05$, Bonferroni’s Multiple Comparison test).

The cumulative fits (obtained from the same parameters as the probability density fit to the gamma distributions included in Supplementary Figure 1) of the dominance durations are plotted in Figure 2C and 2D. These distributions indicate the probability of perceiving a stimulus for a certain period of time or less. In other words, a distribution shifted to the right represents a stimulus that has a larger probability of being observed for greater durations; this can be clearly

![Figure 3](image-url)
seen in the case of the expanding motion when presented against the contraction and clockwise rotation stimuli. By testing whether the distances between two cumulative distributions are significant, via the non-parametric Kolmogorov-Smirnov statistic, we are able to obtain an even finer distinction between rivalry periods because this statistical test is sensitive to both location and shape of the samples’ cumulative forms.

Unlike the results of the paired t-test on TTD, expansion only showed a prominent difference in dominance duration when rivaling contraction \((d = 0.28, p = 0.00059, \text{Kolmogorov-Smirnov})\) and clockwise rotation \((d = 0.29, p = 0.00054, \text{Kolmogorov-Smirnov})\). When presented against counterclockwise rotation, expansion remained to be reported for longer times however it breaches the significance level \((d = 0.049, p = \ldots\).
0.069, Kolmogorov-Smirnov). We speculate that this is due to discrepancies between subjects’ perceptions (Kanai, Bahrami, & Rees, 2010) because, as pointed out beforehand, there is a significant difference between the cumulative distributions for expansion and clockwise rotation, whilst the distributions for clockwise and counterclockwise rotations are not significantly different (\(d = 0.043, \ p = 0.145\), Kolmogorov-Smirnov). Competition among contraction and rotating motion stimuli and among translating motion stimuli show no significant differences between the dominance duration cumulative distributions (\(d < 0.085, \ p > 0.09\), Kolmogorov-Smirnov), therefore providing the same verdict determined from TTD.

To further verify the findings of the preceding analysis, we also calculated the mean dominance duration for each stimulus after pooling across all stimulus combinations for each eye and across subjects (Figure 3). The mean durations allow us to look at potential differences when the stimuli are presented to either eye. There were non-significant differences between the rivalry periods for motion in the cardinal directions (\(p > 0.2\), Wilcoxon signed-rank test), as illustrated in Figure 3A, regardless of whether the stimuli were presented to the left (LE) or the right eye (RE). Once again, the direction of the linear motion is shown not to influence rivalry periods. On the other hand, for spiral motion (Figure 3B), expansion was perceived for longer periods than contraction (\(p = 0.0156\), to RE: \(p = 0.0782\), Wilcoxon signed-rank test) and either rotating motions (LE and RE: \(p = 0.0235\), Wilcoxon signed-rank test).

When examining the plots of mean duration, a trend appears that was not made obvious by the TTD and cumulative distributions: expansion is perceived longer than contraction and rotation for both eyes, and contraction longer than rotation mainly for the right eye. Although contraction appeared to dominate over both rotating motion types, the difference in durations reached significance only for the right eye but not for the left (CONT presented to RE: \(p = 0.0469\), LE: \(p = 0.258\), Wilcoxon signed-rank test). This difference between the left eye and the right eye for contracting and rotating stimuli may be due to the right-eye dominance of most subjects. Rivalry periods for the clockwise and counterclockwise rotating stimuli were not significantly different for either eye (CW presented to LE: \(p = 0.938\), to RE: \(p = 0.688\), Wilcoxon signed-rank test). In general, competing clockwise and counterclockwise motion types and competing linear motions have dominant periods that do not significantly differ from one another. Our findings potentially indicate a correlation between proportions of neurons tuned for moving stimuli in area MSTd and the durations over which the stimuli are perceived during motion binocular rivalry.

An unexpected observation from the results in Experiment 1 is shown in Figure 3C. The mean dominance durations for rivaling linear motions were shorter than that for spiral motion stimuli (spiral motion presented to LE: \(p = 0.0000376\), to RE: \(p = 0.00000423\), Wilcoxon signed-rank test). This result prompted Experiment 2, which we felt could provide further insight on the integrative mechanisms that take place during binocular rivalry.

A comparison with an earlier study

A previous study, conducted by Parker and Alais (2007), also investigated the predominance of expanding and contracting motion and reported that looming concentric sine wave gratings do predominate over receding ones. However, when Parker and Alais utilized random dot patterns as stimuli, the bias for expansion did not occur. They suggested that the random dots create percepts of surfaces undergoing expansion within a fronto-parallel plane and therefore lacked an approaching sensation.

However, in our experience random dot patterns are a more appropriate stimulus than concentric rings to explore motion processing in the dorsal processing pathway since the latter contain spatial frequency information and, at a more local level, orientation information that can activate neurons selective for these features in areas of the ventral pathway, such as V4 (Desimone & Schein, 1987). Another important reason to use random dot patterns is to remove a noise component that may be found in other types of stimuli; a noise component would possibly render a subject to perceive an expansion, contraction, or translation stimulus with the same sensitivity (Braddick & Holliday, 1991; Takeuchi, 1997). To enhance the distinction between the signal-to-noise ratios of spiral and linear motion stimuli, de Bruyn and Orban (1990) proposed using more signal dots. As such, while Alais and Parker (2007) utilized random dot patterns with 150 dots, we used random dot patterns with 300 dots—this may help to partly account for the discrepancies between their results and ours. Moreover, random dot patterns have been the most commonly used stimuli to explore the properties of neurons in motion sensitive areas of macaques (Braddick, 1974; Nakayama, 1985; Siegal, 2004). Thus, we re-examined this issue using random dot patterns and found that expansion does indeed predominate over contraction and over other spiral types. This follows the findings of Tanaka and Saito (Tanaka et al., 1989) and Geesaman and Andersen (1996), which show that the selectivity for radial, rotation, and translation motion of MSTd neurons does not depend on the carrier of the motion, i.e., random dots, windmills, rings, or Glass patterns.
Another advantage of using random dot patterns instead of concentric rings is that one can explore the entire spiral space. By using concentric rings, Alais and Parker could only explore two of the four cardinal directions of the spiral space because they could not produce clockwise and counterclockwise rotating stimuli. Moreover, the use of random dot patterns allows interpretation of our results in relationship to physiology studies in macaques that first isolated the bias in the representation of the different spiral types (Graziano et al., 1994; Saito et al., 1986; Tanaka et al., 1989) and in humans that determined the magnitude of MEG responses evoked by different spiral and linear motions (Holliday & Meese, 2005)—all of which also used random dot pattern stimuli.

**Experiment 2: Rivalry between spiral and linear motions**

While in Experiment 1, similar proportioned neuron populations may account for the non-significant differences between clockwise and counterclockwise rotation and between translational motion rivalry periods, it does not explain why rotating motion, or why the other spiral stimuli, are perceived significantly longer than the linear motion in the cardinal directions. One possibility is that rivalry periods may have been influenced by variables such as the subject’s level of awareness that could vary across sessions. However, the longer rivalry periods of spiral motion stimuli in Experiment 1 are supported by the findings of an earlier study, which found an augmented predominance for spiral motion stimuli after it was transitioned to from a local target in a multiple-aperture stimulus (Alais & Blake, 1998). In addition, MEG studies have indicated that the evoked magnetic responses to linear motions are always lower than responses to spiral motions (Holliday & Meese, 2005). In Experiment 2, we programmed linear motion stimuli to rival against spiral stimuli in order to establish whether the rivalry periods for each stimulus type would be affected or remain the same as in Experiment 1.

**Subjects and stimuli**

Twelve subjects volunteered to participate in Experiment 2. All subjects were naïve to the purpose of the experiment, except for one, and had normal or corrected-to-normal vision. Eight subjects were right-eye dominant and four subjects were left-eye dominant. All subjects were trained prior to the experiment until they felt comfortable with the task.

The eight stimuli presented in Experiment 1 were again used in Experiment 2 but in different combinations to create 32 conditions (Figure 4A). Each condition was presented twice, in a random fashion, to generate a session with a total of 64 trials.

**Results and discussion**

Experiment 2 was analyzed using the same methods and statistical tests as Experiment 1. Whether using TTD or cumulative distributions, we found that spiral stimuli are perceived for significantly longer durations than linear stimuli. From paired t tests on TTD durations, certain combinations such as contraction versus upward motion (t[11] = 1.363, p = 0.200, paired t test) and contraction versus downward motion (t[11] = 1.893, p = 0.085, paired t test) have insignificantly different total rivalry periods, while the remaining combinations exhibit significant spiral dominance (t[11] > 1.936, p < 0.033, paired t test, Figure 4B). Using the more sensitive Kolmogorov-Smirnov statistic from the cumulative distributions, each spiral stimulus has significantly greater dominance durations than every linear stimulus (d > 0.053, p < 0.047, Kolmogorov-Smirnov, Figure 4C; refer to Supplementary Figure 2 for the probability density fits of the gamma distributions).

Using the Bonferroni multiple comparison test to compare the durations for each stimulus when presented as different combinations, we find that the periods over which a stimulus was perceived did not significantly differ when rivaling against different stimuli (t[33] < 1.168, p > 0.1, Bonferroni multiple comparison test). Knowing this, we pooled the TTD for each stimulus across conditions to discern whether the same trend among spiral stimuli found in Experiment 1 remained. Contrary to Experiment 1, the trend (expansion rivalry periods > contraction periods > rotation periods) disappeared and showed insignificant differences among the dominance durations of most spiral stimuli (t[47] < 4.108, p > 0.1, paired sample t test). The contracting stimulus, however, was perceived for significantly shorter periods of time as compared to how long expanding and rotating stimuli were observed (t[47] > 2.717, p < 0.009, paired sample t test). A better visualization of the trend’s disappearance can be observed from the mean dominance durations (Figure 5).

From pooling rivalry periods across stimulus combinations and across subjects, for each stimulus and for each eye, we find that (as in Experiment 1) the mean rivalry periods in Experiment 2 for motion in the cardinal directions were not significantly different from one another (p > 0.3, Wilcoxon signed-rank test), no matter which eye the stimulus was presented to (Figure
5B). On the other hand, rivaling spirals and translational stimuli rendered the average dominance durations of expansion stimulus as significantly longer than the duration of contraction in the LE only (EXP presented to RE: \( p = 0.0122 \), Wilcoxon signed-rank test). The rivalry periods for expansion were non-significantly different from the periods over which contraction in the RE (EXP presented to LE: \( p = 0.850 \), Wilcoxon signed-rank test) or either rotation stimulus (EXP presented to LE: \( p = 0.499 \), to RE \( p = 0.144 \), Wilcoxon signed-rank test) were perceived. The differences observed for expansion stimuli when presented to the right eye could be due to the greater number of right-eye dominant subjects. No differences between mean rivalry periods were obtained for the contraction stimulus versus rotation stimuli (CONT presented to LE: \( p = 0.523 \), to RE: \( p = 0.245 \), Wilcoxon signed-rank test) and for clockwise versus counterclockwise rotation (CW presented to LE & RE: \( p > 0.2 \), Wilcoxon signed-rank test).

A hypothesis as to why the trend observed in Experiment 1 is absent in Experiment 2 may be due to differing dynamics between competing neuronal populations when spiral stimuli rival against themselves relative to when they rival against linear motion. For example, neurons selective for spiral space stimuli may have stronger inhibitory connections among each other as compared to neurons selective for linear motion. This connectivity pattern may result in a stronger competition between spiral motions and thus explain the dominant effect of expansion seen in Experiment 1 relative to other spirals. When rivaling against linear motion these interactions may be absent or much weaker.

To further investigate this issue, we looked at rivalry periods for linear motion in the cardinal directions, as well as for expansion and rotation. The mean dominance durations, pooled across eyes, were recalculated without pooling across stimulus combinations. The rivalry periods for clockwise rotation when presented against counterclockwise rotation are compared to (a) the pooled clockwise rotation periods when presented against all linear motions and (b) the clockwise rotation periods when presented against expansion. The dominance durations for clockwise rotation are not significantly affected by rivaling against linear motions (\( p = 0.408 \), Wilcoxon signed-rank test) but are significantly reduced during the presentation against expanding spiral stimulus (\( p = 0.0131 \), Wilcoxon signed-rank test). This suggests stronger interactions between spiral stimuli when rivaling against each other than when rivaling against linear motion.

Furthermore, unlike the perceived durations of rivaling linear motions in Experiment 1, the rivalry periods for motion in the cardinal directions in Experiment 2 are significantly pulled toward those of spiral motion stimuli despite which eye the stimulus was presented, so that linear motion stimuli were seen for significantly longer durations in Experiment 2 than in Experiment 1 (EXP 1 vs. EXP 2 LE & RE: \( p = 0.0078 \), Wilcoxon signed-rank test). The spirals still had mean dominance durations significantly greater than mean dominance durations of linear motion stimuli.
(spiral motion presented to LE: \( p = 0.000142 \), to RE: \( p = 0.00000553 \), Wilcoxon signed-rank test). This further suggests a different neuronal interaction dynamic when spiral and linear motion rival relative to the rivaling of spiral motions or linear motions.

**A comparison to Experiment 1**

To better conceptualize the different effect of presenting a spiral stimulus against another spiral versus presenting it against a linear stimulus, Figure 6A graphs the cumulative distributions for every stimulus comparing its dominance durations in Experiment 1 to Experiment 2 (refer to Supplementary Figure 3 for the associated probability density functions of the gamma distributions). A significant change occurs for each spiral stimulus: expansion dominance durations decrease from Experiment 1 to 2 (\( d = 0.064, p = 1.0 \times 10^{-5} \), Kolmogorov-Smirnov Test), while an increase is observed in contraction (\( d = 0.072, p = 4.5 \times 10^{-7} \), Kolmogorov-Smirnov Test), clockwise (\( d = 0.078, p = 1.6 \times 10^{-7} \), Kolmogorov-Smirnov Test), and counterclockwise rotation (\( d = 0.083, p = 7.7 \times 10^{-9} \), Kolmogorov-Smirnov Test) durations. Figure 6C compares the mean dominance durations for linear and spiral stimuli during Experiment 1 and Experiment 2, after pooling across conditions, subjects, and eyes.

To better see the diminished relationship between spiral stimuli during Experiment 2, the lines of best fit were plotted for each trend (Figure 6D) so that the slopes could be compared to 0, i.e., a horizontal line showing no major trend. The best-fit lines for the linear motion stimuli in Experiment 1 and Experiment 2 have slopes with 95% confidence intervals that include 0 (Experiment 1: lower confidence level \([\text{LCL}] = -5.08\) and upper confidence level \([\text{UCL}] = 7.72\); Experiment 2: \( \text{LCL} = -6.30\) and \( \text{UCL} = 11.12\) ), therefore do not show significant trends. The spiral motion stimuli of Experiment 1 show a slope that is significantly different from 0 (\( \text{LCL} = -211.88\) and \( \text{UCL} = -125.52\) ); while in Experiment 2, the spiral motion stimuli’s slope also shows a significant difference, however it is far less prominent (\( \text{LCL} = -69.16\) and \( \text{UCL} = -6.86\) ). From the cumulative distributions and, more so, from the best fit lines, it almost appears as though in Experiment 2 the spiral stimuli rivalry periods are pulled or pushed towards a midline of the observed trend from Experiment 1.

In addition, the cumulative distributions in Figure 6A strongly indicate the increased dominance durations of linear motion in Experiment 2 as compared to in Experiment 1 (\( d > 0.22, p < 3.1 \times 10^{-63} \), Kolmogorov-Smirnov Test), and from Figure 6C it can be seen that spiral motion stimuli have greater mean durations than linear motion stimuli whether as presented in Experiment 1 or Experiment 2.

### Experiment 3: Rivalry between stimuli with and without speed gradient

To determine whether the disappearance of the expanding motion bias in Experiment 2 was due to the difference in stimuli combinations presented or due to the participation of different subjects, Experiment 3 re-examines the rivalry between expanding and contracting stimuli. As an extension to Experiment 1, we also chose to determine whether the speed gradient affected perception periods during rivalry.

A previous study reported that the speed gradient contributes little to the looming or receding illusion observed in expanding and contracting spirals and likely to the tuning of MST neurons for spiral motion (Geesaman & Qian, 1996). Based on these results, we anticipate that mean durations of rivaling spirals without speed gradients will be similar to those found for spiral motion stimuli during Experiment 1 and Experiment 2 (which were relatively equivalent: Experiment 1 \( \approx 1837.95\) ms and Experiment 2 \( \approx 1973.35\) ms). We would also assume that they would show the same bias for expansion as in Experiment 1, which advocates that the experiment would reflect, as per our hypothesis, the activation of the outnumbering units encoding expansion.

### Subjects and stimuli

The subjects were the same as in Experiment 2. The stimuli were combinations of four spiral motion stimuli—expansion with speed gradient (EXP G), expansion without speed gradient (EXP NG), contraction with speed gradient (CONT G), and contraction without speed gradient (CONT NG)—producing 12 different conditions (Figure 7A). Each condition was presented five times for a total of 60 trials per session.

### Results and discussion

The TTD (Figure 7B)—calculated as described under the Results and discussion section of Experiment 1—demonstrated a similar trend as in Experiment 1. A bias for EXP G was observed when presented against CONT G (\( t[11] = 3.524, p = 0.0048, \text{paired}\ t\text{test} \)) and when presented against CONT NG (\( t[11] = 2.420, p = 0.0034, \text{paired}\ t\text{test} \)). More importantly, periods were longer for EXP G relative to EXP NG when these two types of stimuli competed (\( t[11] = 2.567, p = 0.0262, \text{paired}\ t\text{test} \)), yet the difference between these rivalry periods was not as prominent as those between EXP G and either contracting stimulus. Therefore, even
without the speed gradient there remains a bias for expansion. So while, CONT G rivalry periods did not show significant differences from CONT NG ($t_{11} = 1.467, p = 0.1703$, paired $t$ test), EXP NG had rivalry periods that were longer than those of CONT G ($t_{11} = 3.428, p = 0.0056$, paired $t$ test)—providing a further indication that the stimuli deprived of the speed gradient still activated a substantial proportion of expansion-tuned neurons. Support for this result can be lent from Holliday and Meese’s (2005) MEG study that found expansion still evokes greater magnetic responses even without the speed gradient. Thus, the arrangement of velocity vectors probably had a greater influence on the isolated biases than the speed gradient.

Moreover, when removing the speed gradient and comparing EXP NG versus CONT NG rivalry periods, they were also significantly different from each other ($t_{11} = 3.273, p = 0.0074$, paired $t$ test). The dominance of EXP NG over CONT NG promotes the hypothesis put forth in Experiment 1 that rivalry periods mirror the proportion of neuron populations tuned for the specific motion in area MSTd; however, since EXP G was seen significantly as the longest of the four stimuli, this also suggests that the radial speed gradient
increased the dominance of the expanding stimuli, possibly because the gradient produced a stronger activation of expansion-tuned neurons than the expansion stimulus without the gradient.

The cumulative form (Figure 7C) of Experiment 3’s gamma distributions (Supplementary Figure 4) reveal the same results as described through the TTD. An exception was that the Kolmogorov-Smirnov test yielded CONT NG as having longer rivalry periods than CONT G ($d = 0.071$, $p = 0.019$, Kolmogorov-Smirnov test). This may indicate an effect of the speed gradient. Nevertheless, our results, in general, advocate that people’s perceptions are swayed by ecologically relevant stimuli. In this case, a person might show more interest in an unfamiliar object that appears to be sinking at a center or receding slowly than in an unfamiliar object moving away from them very quickly.

**General discussion**

The initial goal of this study was to investigate the relationship between expanding, contracting, and rotating stimuli during binocular rivalry—as was done in Experiment 1. We found that there is a bias (i.e., perceived for longer durations) for expansion over contraction and rotation stimuli, and a bias for contraction over rotation stimuli. We attributed this finding to the greater activation of expansion-tuned neurons, the ecologic importance of the expansion stimulus, and the relative proportions of spiral-tuned neurons found in primate MSTd—a 2:1 ratio of expansion-tuned neurons to contraction-tuned neurons and a 3:1 ratio of expansion-tuned neurons to rotation-tuned neurons (Crowell & Banks, 1993; Duffy & Wurtz, 1991a, 1991b; Franconeri & Simons, 2003; T. C. Freeman et al., 1994; Gibson, 1950; Gonzalez et al., 1988; Graziano et al., 1994; Hassenstein & Hustert, 1999; Holliday & Meese, 2005; Lee et al., 1976; Regan & Beverly, 1978; Regan & Hamstra, 1993; Saito et al., 1986; Tanaka et al., 1990; von Mühlenen & Lleras, 2007; Wang & Frost, 1992; Warren & Hannon, 1988).

On the other hand, when linear moving patterns in the cardinal directions rivaled against each other we did not find any bias in favor of any direction. This is probably due to the lack of bias in the representation of these motion types at the level of areas such as MT.

A finding of Experiment 1 was that spiral stimuli had a consistently greater mean duration than linear motion stimuli. Interestingly, during Experiment 2, where the spiral stimuli rivaled against linear motion, the strong
bias for expansion disappeared, and instead all spirals exhibited mean dominance durations that were not significantly different from each other. Additionally, in Experiment 2 the rivalry periods for linear motion increased in duration relative to Experiment 1, however, remained shorter than spiral motion durations.

In Experiment 3, when we examined the role of a speed gradient on rivalry periods, the bias returned. The expansion stimulus was more strongly dominant when it contained a speed gradient. Nevertheless, when the speed gradient was removed, the expansion stimulus was still observed for longer dominant periods than the contracting stimulus either with or without the gradient. The return bias in favor of expansion confirms the results of Experiment 1 and further suggests that the speed gradient influences dominance durations. One possible explanation is that the MSTd neurons tuned for spiral motions do not calculate derivatives of flow, but rather signal how well the flow presented on the retina matches their preferred flow component or mixture of components (Orban, 2008). Therefore, it is possible that the expanding stimulus containing the gradient better represented the flow component encoded in the MSTd expansion-tuned neurons causing stronger activation of these units (Orban et al., 1992).

Stimulus representation in the visual pathway

We speculate that rivalry between simple translational motions (Experiment 1) activate the first stage of cortical processing (V1) as well as areas downstream in the motion hierarchy such as MT and MST (Maunsell & Van Essen, 1983a; Saito, et al., 1986). The rivalry of spiral motions (Experiment 1 and Experiment 3), on the other hand, requires a stimulus selectivity that is not present until reaching area MSTd, which combines the local unidirectional motion inputs from previous stages—most likely MT, which is not only selective for radial and rotational motion but also contains representation of optic flow (Bex & Makous, 1997; Bex, Metha, & Makous, 1998; T. C. Freeman & Harris, 1992; Lappe & Rauschecker, 1994). This hypothesis, that outputs of local sensors are combined in a higher-order detector, is supported by the findings of studies, which have shown that the speed discrimination threshold of expansion can be predicted from the simple linear combination of local translations (Morone, Burr, & Vaina, 1995; Sekular, 1992). These unidirectional motion inputs from MT may also reach units tuned for linear motion in MSTd. Previous studies have proposed that separate pathways exist for the detection of spiral and linear motions (Regan & Beverly, 1978; Steiner, Blake, & Rose, 1994). Our findings may agree with this hypothesis since we document decreased interactions (i.e., bias in favor of expansion disappears) between spiral representations when spiral stimuli rival against linear motion. In addition, our results suggest that the proportion of neurons tuned for a specific motion correlates with how long it is perceived. This inference can also be drawn from other findings that show how the perception of motion during rivalry cannot be fully represented by the responses of individual neurons, at least not in MT (Tailby, Majaj, & Movshon, 2010). The partiality for expanding motion reflects its high ecological value and how expansion is the most highly represented spiral motion in area MSTd and other higher cortical areas (Anderson & Siegel, 1999; Duffy & Wurtz, 1991a, 1991b; Franconeri & Simons, 2003; Gonzalez et al., 1988; Graziano et al., 1994; Hassenstein & Hustert, 1999; Lee et al., 1976; Merchant, Battaglia-Mayer, & Georgopoulos, 2003; Regan & Beverley, 1978; Regan & Hamstra, 1993; Saito et al., 1986; Steinmetz, Motter, Duffy, & Mountcastle, 1987; Tanaka et al., 1989; von Muhlenen & Lleras, 2007; Wang & Frost, 1992; Zhang & Britten, 2004).

Additional factors

Our study concentrates on the role of ecologic relevance and the possible role of the proportion of neurons tuned for spiral and linear motion on binocular rivalry periods. However, we cannot rule out that during our experiments other factors, such as attention, adaptation, saliency retention, further processing in higher cortical areas, and optokinetic nystagmus, may have contributed to the observed bias favoring expansion over other spiral stimuli, and spiral motion over linear motion.

Adaptation

Kang and Blake (2010, 2011) have confirmed that adaptation is involved in triggering switches in perception during binocular rivalry. Adaptation-based models of binocular rivalry suggest that the neural representation of a dominant stimulus weakens over time owing to slow adaptation, thereby reducing its inhibitory impact on the weaker non-dominant representation (Kalarickal & Marshall, 2000; Laing & Chow, 2002; Lanksheet, 2006; Lehky, 1988; Wilson, 2003). Rivaling stimuli that are of equal energy (i.e., having equivalent properties) such as rivaling linear motions or rivaling rotating motions are quickly and similarly adapted to and therefore have short dominant durations highly similar to one another (Kang & Blake, 2011). On the other hand, dissimilar stimuli, such as spiral and linear motion or motions within the spiral
space, likely produce different rates of adaptation and, consequently, different dominant durations when rivaling against each other.

In agreement with this hypothesis, enhanced motion after-effects (MAE) are normally associated with slower adaptations (i.e., for stimuli that are perceived over prolonged periods) and it has been found that spiral motions have a greater MAE than linear motions and that durations of MAE for translational motions are approximately the same (Bex, Metha, & Makous, 1999; Hershenson, 1993; Steiner et al., 1994). This means that spiral motions are more slowly adapted to than linear motions, and, therefore, their neural activation may remain relatively strong during the stimulus presentation, as compared to linear motions, resulting in the spiral motions’ longer mean durations.

In spite of this, while adaptation may play a role in the similar rivalry periods between linear motions, the equivalent durations of rotating motions, and the greater dominance durations of spiral motion compared to linear motion, it fails to explain the bias for expansion over contraction. Several studies have reported that MAE following adaptation to contraction are longer than those following adaptation to expansion (Bakan & Mizusawa, 1963; Reinhardt-Rutland, 1994; Scott, Lavender, McWhirt, & Powell, 1966), which would mean that contraction should have been perceived for longer periods than either expansion or rotation. This was not observed in our experiments.

**Attention**

During the study, many subjects expressed that the expansion stimulus with speed gradient seemed much more salient compared to the remaining stimuli. As such, it is possible that exogenous attention played a role during the rivalry. Attention has been described as having similar competitive selection mechanisms as binocular rivalry and is known to increase the response of neurons in the early part of the visual system that is tuned for the attended feature, including motion (Alais & Blake, 1999; Somers, Dale, Seiffert, & Tootell, 1999; Stoner, Mitchell, Fallah, & Reynolds, 2005; Treue & Martinez Trujillo, 1999). Moreover, based on previous studies and the behavioral urgency hypothesis, looming motion captures attention to a far greater extent than receding and translating motion because it signals an event that requires urgent action and hence has processing priority (Franconeri & Simons, 2003; von Muhlenen & Lleras, 2007). The processing priority of expansion over contraction has also been confirmed in a human functional magnetic resonance imaging (fMRI) study (Yang, Chao, & Lin, 2011). But again, this hypothesis may explain only part of the bias for the expanding stimulus, because the preference for expansion decreased in Experiment 2, while it should have been equally salient regardless of whether compared against a spiral or against a linear motion.

**Salient stimuli retention**

Expanding stimuli may maintain a certain degree of saliency even when it is suppressed—as was reported using fearful faces and contrast changes during binocular rivalry (Ling, Hubert-Wallander, & Blake, 2010; Pasley, Mayes, & Schultz, 2004). Parker and Alais (2007) suggested the looming stimulus could be retained during suppression through neurons that respond in the superior colliculus and feed to processes responsible for suppression during binocular rivalry. The retention of expansion information may increase the likelihood for its bias.

**Motion processing in higher cortical areas**

It is important to also keep in mind that while MSTd is the first area that contains neurons selective for spiral motion, it is not the only. This may be critical because higher-level neurons have been reported to be directly responsible in causing the elements of our perception (Barlow, 1972). MSTd neurons project to other extrastriate areas, including anterior superior temporal polysensory (STPa) in the upper bank of anterior superior temporal sulcus (STS), ventral intraparietal (VIP) of intraparietal sulcus, and 7a in the posterior part of inferior parietal lobule (IPL; Orban, 2008). Few of the neurons contained in these areas are selective to translational motion, while a substantial fraction of these neurons are tuned for spiral motions, especially expansion (STPa: Anderson & Siegel, 1999; VIP: Zhang & Britten, 2004; 7a: Merchant et al., 2003; Steinmetz et al., 1987). Therefore the activation of these large populations of expansion-tuned neurons in these higher cortical areas may also prompt the bias for expansion.

**Optokinetic nystagmus**

Fox, Todd, and Bettinger (1975) demonstrated that when two very strikingly different stimuli are presented during binocular rivalry, a subject would move their eyes without realizing; this type of eye movement is termed optokinetic nystagmus (OKN). More importantly, they discovered a high correlation between eye movements and the reported alternations between the presented stimuli. These findings are of particular interest for our study since no border, point, or cross was provided for subjects to maintain fixation.
In order to test for the effect of OKN on our results, we measured eye movements in three subjects using video-based eye tracking (DiScenna et al., 1995) during all experimental conditions (refer to Supplementary Materials: Additional Experiment: Testing for Optokinetic Nystagmus for more detailed information). We found that only one of the three subjects showed a measurable OKN (in only 7 out of 66 trials). Thus, we consider it unlikely that the pattern of dominance observed during rivalry was due to eye movements.

**Eye dominance**

The contribution of eye dominance to rivalry periods has been reported by previous studies using contrast and color stimuli (Bartels, Vazquez, Schindler, & Logothetis, 2011; Stanley, Carter, & Forte, 2011). In our experiments, rivalry periods were significantly different between left and right eyes in some right-eye dominant subjects during Experiment 1 and Experiment 2 (Experiment 1, \( n = 3 \); Experiment 2, \( n = 5 \); \( p < 0.0391 \); Wilcoxon signed-rank test). This may partially explain why the mean durations for certain stimuli had a more prominent significance when presented to the right eye. In addition, it follows the effect of eye dominance demonstrated in prior studies that use contrast and color stimuli but instead with motion stimuli.

**Conclusion**

In sum, our study is not inconsistent with the following claim: motion perception, during motion binocular rivalry, relies—among other factors—on how strongly the rivaling stimuli are represented in the motion processing system and on how these representations interact. We confirmed that expanding stimuli, probably the most ecologically relevant motion pattern for human and other species, have a strong tendency to predominate over other types of spiral stimuli and that spiral stimuli tend to be predominant as compared to linear stimuli. This tendency becomes weaker when removing the speed gradient of the expanding patterns. Our results suggest that rivalry can occur between stimuli processed at different levels in the motion hierarchy. Nevertheless, the dynamic of this process changes when stimuli within and between levels are confronted with each other. This suggests that binocular rivalry is a multistage processing that involves several brain areas that can display complex interactions depending on the specific situation.

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