Filling-in rivalry: Perceptual alternations in the absence of retinal image conflict

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During perceptual rivalry, an observer's perceptual experience alternates over time despite constant sensory stimulation. Perceptual alternations are thought to be driven by conflicting or ambiguous retinal image features at a particular spatial location and modulated by global context from surrounding locations. However, rivalry can also occur between two illusory stimuli—such as two filled-in stimuli within the retinal blind spot. In this "filling-in rivalry," what observers perceive in the blind spot changes in the absence of local stimulation. It remains unclear if filling-in rivalry shares common mechanisms with other types of rivalry. We measured the dynamics of rivalry between filled-in percepts in the blind spot, finding a high degree of exclusivity (perceptual dominance of one filled-in percept, rather than a perception of transparency), alternation rates that were highly consistent for individual observers, and dynamics that closely resembled other forms of perceptual rivalry. The results suggest that mechanisms common to a wide range of rivalry situations need not rely on conflicting retinal image signals.

Introduction

When observers view a visual stimulus that has multiple distinct interpretations, those interpretations alternate in visual consciousness. Multistable perceptual phenomena include bistable figures like the Necker cube (Necker, 1832) and Rubin's face-vase figure (Rubin, 1915), in which the image contours have conflicting perceptual interpretations. They also include binocular rivalry (Tong, Meng, & Blake, 2006; Wheatstone, 1838) and monocular rivalry (Breese, 1899), in which conflicting patterns at a given location perceptually alternate. In binocular rivalry, conflicting patterns are presented to different eyes, whereas in monocular rivalry, they are presented to the same eye. In both cases, the retinal image contains local conflicts, such as orthogonal image contours at the same spatial locations. These diverse types of rivalry have very similar temporal dynamics: The dominance durations of individual percepts often follow a gamma distribution or similar (Brascamp, van Ee, Pestman, & van den Berg, 2005; Mamassian & Goutcher, 2005; Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009) and have been reported to be sequentially independent for binocular rivalry (Fox & Herrmann, 1967; O'Shea, Parker, La Rooy, & Alais, 2009; but see Mamassian & Goutcher,

2005; van Ee, 2005, 2009 who reported small sequential dependencies), monocular rivalry (O'Shea et al., 2009), and dichoptic masking (van Boxtel, van Ee, & Erkelens, 2007). Such similarities have led to the suggestion that different types of perceptual rivalry are governed by a general underlying mechanism (Leopold & Logothetis, 1999; O'Shea et al., 2009; van Boxtel et al., 2007).

However, the nature of this proposed general mechanism remains unclear. In particular, it is debated to what degree perceptual alternations are governed by spatially localized conflicting signals versus global, high level information (Kornmeier, Hein, & Bach, 2009; Long & Moran, 2007; Long & Toppino, 2004; Maier, Logothetis, & Leopold, 2005; Meng & Tong, 2004). Bottom-up, local processes are implicated by studies showing that rivalry alternations are tied to eye movements (Jochen, Ralf, & Kliegl, 2008; van Dam & van Ee, 2005, 2006a), retinal image shifts (van Dam & van Ee, 2006b), adaptation (Blake, Sobel & Gilroy, 2003; Toppino & Long, 1987), and low-level stimulus properties (Babich & Standing, 1981; Levelt, 1965; Lynn, 1961). On the other hand, top-down stimulus factors from beyond the rivaling spatial location can also influence rivalry, including: center-surround interactions (Fukuda & Blake, 1992; Paffen, Alais, & Verstraten, 2005; Paffen, Tadin, te Pas, Blake, & Verstraten, 2006), grouping of common features (Alais & Blake, 1999; Kovács, Papathomas, Yang, & Fehér, 1996; Silver & Logothetis, 2004), and global stimulus configurations (Alais & Blake, 1998; Alais, O'Shea, Mesana-Alais, & Wilson, 2000). One study has found perceptual suppression in a conflict-free region of a monocular rivalry stimulus (Maier, Logothetis, & Leopold, 2005), suggesting that global competition can be sufficient to induce rivalry. However, whether rivalry that depends only on global image context has the same type of underlying process as other forms of rivalry is unknown.

Here we investigated rivalry between two illusory percepts, which were filled in across the retinal blind spot, thereby minimizing the influence of local, bottom-up input on rivalry dynamics. The blind spot refers to the area of the eye's optic disk where the optic nerve exits the orbit and no photoreceptors are present. Despite the absence of photoreceptors, monocular viewing does not lead to a perceived hole in visual space. Instead, the blind spot is perceptually filled in by information from the surrounding visual field (Mariotte, 1660, as cited in Andrews & Campbell, 1991). Filling-in occurs for uniform and textured backgrounds, as well as for objects reaching through the blind spot (Ramachandran, 1992). Neurophysiological and psychophysical studies have provided evidence that perceptual completion in the blind spot is due to active lateral or feedback propagation of neural activity from
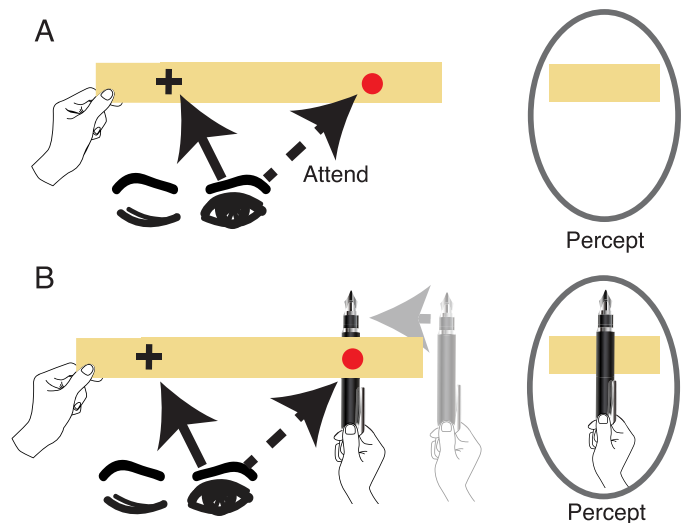

Figure 1. The jumping pen illusion, a demonstration of filling-in rivalry. (A) Step 1: Use a strip of paper with a fixation cross and a blind spot indicator (red circle) to find your blind spot. With the cross on the left, close your left eye, fixate the cross, and move the strip toward or away from you until the red circle disappears. (B) Step 2: While keeping the blind spot indicator in your blind spot, take a pen and hold it vertically behind the card. Slide the pen behind the card into your blind spot. The pen may appear to jump in front of the strip. When the pen and strip are held in fixed positions, the pen and strip can alternate as the object seen in front. Anecdotally, increasing the saliency of the pen using motion (e.g. wiggling the pen) or color (e.g. a red pen with a neutral-colored strip) tends to increase the perceptual dominance of the pen.

surrounding cortical regions (de Weerd, 2006; Komatsu, 2006; Maus & Whitney, 2016; Pessoa, Thompson, & Noë, 1998; Weil & Rees, 2011).

Rivalry between two filled-in percepts in the blind spot, which we call "filling-in rivalry," can occur when stimulation around the blind spot is compatible with multiple possible interpretations of what is present within the blind area. Filling-in rivalry can be readily experienced using real objects in a demonstration we developed called the "jumping pen illusion" (Figure 1). An ambiguous situation is created by holding an object (such as a pen held vertically) behind an occluder (such as a strip of paper held horizontally) with both objects viewed monocularly and crossing within the blind spot. At times, the pen appears to jump in front of the strip. This occurs even though other depth cues unambiguously provide information about the actual depth ordering of the two objects, such as proprioceptive cues from holding the objects in both hands (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997), and despite one's own knowledge about the true positions of the objects.

Filling-in rivalry has been reported previously, but it has not been well characterized, and its ongoing dynamics have not been investigated. Brown and

Thurmond (1993) observed that a vertical and horizontal bar that form a cross within the blind spot, but with their centers (at the crossing point) missing, create an ambiguous situation for filling-in. They reported that one of the bars could be filled in and seen "on top" and that which bar was filled in could alternate over time. However, they did not report the prevalence of exclusive dominance times or the time course of perceptual reversals. They noted that their observers experienced perceptual fading of the stimuli, which would have made these temporal properties difficult to assess.

We developed a method to measure perception during filling-in rivalry continuously over long viewing periods, in the absence of perceptual fading, allowing us to characterize its properties for the first time. We found robust rivalry between the two filled-in percepts, with a high prevalence of exclusive dominance, characteristic alternation rates for each observer, and temporal dynamics similar to other forms of rivalry (e.g. Fox & Herrmann, 1967; Leopold & Logothetis, 1999; Levelt, 1967; O'Shea et al., 2009), demonstrating that local retinal input is not critical for driving typical rivalry dynamics.

Methods

Participants

Five observers (one male, four female; mean age: 24.5; age range: 20–34 years), including two of the authors, participated in the experiment after giving informed consent. All observers had normal or corrected-to-normal visual acuity and were trained psychophysical observers with experience in maintaining fixation. The study was approved by institutional review at the University of California, Berkeley.

Apparatus

All stimuli were generated using Matlab (MathWorks) and Psychtoolbox 3 (Brainard, 1997; Pelli, 1997) running on an Apple Macintosh computer. Stimuli were displayed on two 21-inch CRT monitors (Sony Trinitron Multiscan G520) with a spatial resolution of 1280×1024 pixels and a frame rate of 75 Hz. Each eye of the observer viewed only one monitor at a viewing distance of 42 cm using a haploscopic setup. The two monitors were positioned to the left and right of the observer with their screens facing each other. Observers viewed the screens through two mirrors placed at 45° angles in front of the eyes. Head position was stabilized with a chin-and-forehead rest.
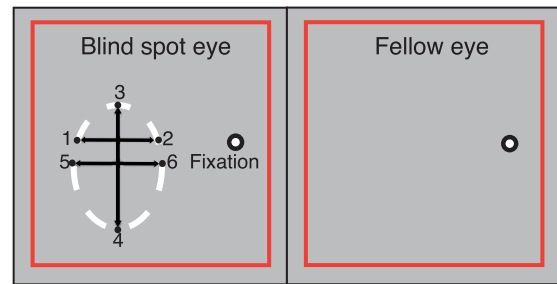

Figure 2. The blind spot measurement procedure. Observers moved a blinking mouse cursor into the blind spot at six locations and indicated with a mouse click where they could no longer see the blinking cursor.

Responses were recorded with mouse clicks and keyboard button presses.

Throughout all experimental procedures, the background of the screen was dark gray (14.6 cdm^{-2}). The fixation point was a black (1.11 cdm^{-2}) annulus with a white (103.5 cdm^{-2}) center with a diameter of 0.5° of visual angle and was placed vertically in the center of the screen and horizontally 7.7° left or right from the center of the screen. The fixation point was visible to both eyes. In addition, a centered red square frame (side length 25°) was presented to both eyes to help observers fuse the two screen's images.

Blind spot measurement

Before the experiment, we measured the center and the extent of each observer's blind spot for each eye using a procedure similar to previous studies (Baek, Cha, & Chong, 2012; Maus & Whitney, 2016; Figure 2). A square cursor (side length 0.4°) that flickered between black and white at a rate of 4 Hz was only visible to the blind spot eye. The observers were instructed to use the mouse to move the cursor slowly from different directions into the blind spot, and then move it back and forth to bring it to a position where it was just invisible (i.e. just inside the blind spot). They indicated this position by clicking the mouse. This method gives a conservative estimate for the blind spot area, because the target was relatively large and observers moved it to a position where it was completely invisible. This served the present purpose, which was mainly to ensure that the center of the stimulus cross (see below) always remained within the blind area. Six positions along the blind spot boundary were measured three times. The mean of the three measurements was used to define the blind spot boundary. First, the vertical position of the cursor was fixed in the center of the screen and the two boundaries of the blind spot on the horizontal meridian were measured. Next, the cursor moved vertically along a

A

Blind spot eye
upward tilted bar

Fixation

downward tilted bar

Fellow eye

Fixation

B

Blind spot eye

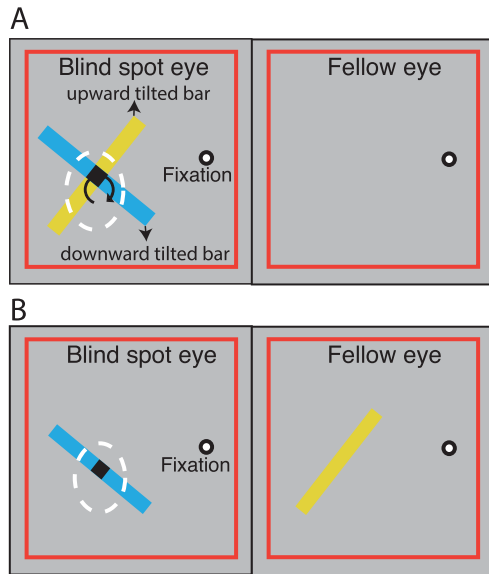Fixation

Fellow eye

Fixation

Figure 3. Stimuli. (A) Stimuli for the main experiment: A blue and yellow isoluminant cross was presented continuously for 60 s. The intersection of the cross was covered by a black square and centered within the blind spot area (white dashed ellipse). To prevent Troxler fading, the cross continuously moved along a circular trajectory (black arrow), keeping the intersection point well within the blind spot. (B) During unambiguous catch trial periods, one of the two bars of the cross was shown to the fellow eye.

line that went through the center between the two horizontal boundaries to find the upper and lower boundaries. Finally, the cursor was moved horizontally along a line passing through the vertical center to measure the horizontal diameter. The intersection between the horizontal and vertical diameters defined the center of the blind spot.

Stimuli and procedure

The visual stimulus was a cross, formed by two orthogonal bars centered on one eye's blind spot region (Figure 3A). The cross was presented monocularly to the blind spot eye. A black square (side length 1.6°) covered the center of the cross. The bars of the cross had the same size, luminance, and eccentricity to avoid biases in their predominance, as has been observed in previous displays (e.g. Brown & Thurmond, 1993; Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973). The bars were of different but isoluminant colors, yellow and blue (52.9 cdm^{-2}). Each bar had a length of 7.7° and a width of 1.6°. The cross was rotated from upright so that the proximal ends of the two bars were of equal distance to the fixation point. Because the blind spot is about 15° in the periphery, a static stimulus is likely to fade perceptually due to Troxler

fading (Troxler, 1804). To prevent fading, the stimulus was drifted continuously along a circular motion path within the blind spot, at a rate of 0.625 circles/s. The diameter of the circular path (mean 2.60°, SEM 0.30°) was fixed for each observer, so that the extreme positions of the center of the cross were at least 1/3 of the diameter of the blind spot (mean 1.53°, SEM 0.31°) away from the measured boundary.

Throughout the experiment, the observer was instructed always to maintain fixation while paying attention to the cross. We differentiated the two bars by their tilt directions, according to the ends of the bars that were closer to the fixation point (up or down). When one bar is filled-in as complete across the blind spot area, it appears to be in front of the other bar. The observers were instructed to press and hold the up arrow key whenever they perceived the upward tilted bar to be in front, and the down arrow key whenever they perceived the downward tilted bar to be in front. They were instructed to press no key if they were not sure which bar was in front. Observers were asked to refixate if the black square at the center of the cross (located in the blind spot) became visible at any point during the experiment.

To ensure that observers were correctly performing the task, unambiguous catch trial periods lasting 3 s were inserted into the 1-min experimental trials at random times (Figure 3B). During a catch trial period, one of the bars in the cross was presented to the fellow eye instead of the blind spot eye. We assumed that full presentation in the fellow eye would be dominant over presentation through the blind spot, and that the bar would therefore be more likely to be perceived in front. The luminance of the bar in the fellow eye was slightly reduced (to 31.1 cdm^{-2}) based on pilot observations in order to minimize observers' detection of a catch trial period based on an abrupt change of perceived brightness. Observers were not informed about the presence of catch trial periods.

The experiment consisted of 20 trials for each eye. Each trial lasted 60 s, and the stimulus was continuously presented throughout each trial. The colors of the up-tilted and down-tilted bars were randomized across trials. Half of the 1-min trials contained either one or two catch trial periods, adding up to 30 catch trial periods in total.

Data analysis

To investigate the characteristics of perceptual rivalry with filled-in stimuli, we quantified rivalry in several ways. First, we calculated "dominance prevalence," the percentage of time that either bar was reported unambiguously in front. Second, we obtained the rivalry alternation rate by counting the number of

times each observer reported a perceptual switch per minute. Third, we obtained dominance durations by measuring the durations of each individual key press for unambiguous percepts. Fourth, we compared the dominance prevalence for each bar orientation and color to assess whether observers had any biases in perceptual dominance linked to the stimulus features. The dominance prevalence for a bar orientation or color was calculated as the percentage of time that that orientation or color was seen in front out of the total time that observers reported unambiguous percepts. Data for each observer was combined across the two eyes. In all analyses, we excluded any truncated key presses at the end of each trial and any key presses that overlapped with a catch trial period.

Dominance durations of individual percepts for bistable stimuli generally follow a gamma distribution (Brascamp et al., 2005; Fox & Herrmann, 1967; Levelt, 1967; Logothetis, Leopold, & Sheinberg, 1996). Dominance durations were normalized by dividing the duration of each individual percept by the mean duration for that observer (Kovács et al., 1996; Maier et al., 2005; Meng & Tong, 2004). We plotted distributions of individual normalized dominance durations and assessed the fit of a gamma distribution. The probability density function is

$$f(x|\alpha, \beta) = \frac{1}{\beta^\alpha \Gamma(\alpha)} x^{\alpha-1} e^{-\frac{x}{\beta}}, \quad (1)$$

where x is the duration of a dominant percept, α is a "shape" parameter, β is a "scale" parameter, and $\Gamma(\cdot)$ is the gamma function. We compared fits to the data using the Kolmogorov-Smirnov goodness-of-fit test. The cumulative functions for this test were calculated without binning the data.

To test for sequential dependencies in filling-in rivalry dominance durations, we computed autocorrelations between the recorded sequence of dominance durations in each trial and the same sequence offset by various lags in the sequence of dominance durations (Fox & Herrmann, 1967; Levelt, 1967; O'Shea et al., 2009; van Boxtel et al., 2007). Lags of 1–7 durations were analyzed, because all observers had sequences of at least eight dominance durations during the 1-min trials. Dominance durations were first centered on zero for each observer by subtracting the mean dominance duration across all trials. Autocorrelations were calculated such that they had a value of 1 at zero lag. For each observer, autocorrelations were calculated for each trial, Fisher Z-transformed, averaged across trials, and the mean was then transformed back to Pearson's r.

The expected autocorrelation for short random sequences can be biased away from zero (Arnau & Bono, 2001). This bias is not negligible for our sequences of dominance durations from single trials,

which could be as short as $N = 8$. We simulated gamma-distributed random number sequences (of the same length and sample size, and with similar gamma parameters as our data) and confirmed a positive bias for autocorrelations. Therefore, we opted not to test the measured autocorrelations against a null hypothesis of zero. Instead, we used a permutation test to determine whether the measured mean autocorrelations for each observer were significantly different from the values expected from randomly ordered sequences. We shuffled the order of the sequence of dominance durations in each trial and calculated autocorrelations for lags 0 through 7 for each shuffled sequence. We then computed the mean autocorrelation for the shuffled trials in the same way as for the original data. A null distribution of the mean autocorrelations was generated for each observer by repeating this procedure 5,000 times. Two-tailed p values were calculated by computing the proportion of permuted autocorrelations in each observer's null distribution with an absolute value larger than or equal to the absolute value of the observed autocorrelation.

We also calculated the Lathrop statistic (Lathrop, 1966), the mean absolute slope of successive dominance durations, which has been used as a measure of first-order sequential dependencies in perceptual rivalry (Fox & Herrmann, 1967; Logothetis, Leopold, & Sheinberg, 1996; Walker, 1975). The Lathrop statistic, L, was computed for the sequence of dominance durations obtained in each trial as follows:

$$L = \sqrt{\sum_{i=1}^{N-1} \frac{|X_{i+1} - X_i|}{(N-1)\sigma}}, \quad (2)$$

where X_i and X_{i+1} are successive dominance durations, N is the total number of durations, and σ is the standard deviation of the durations in the sequence. A permutation test analogous to that described for the autocorrelation analysis was used to determine whether the measured L values were significantly different from expected values generated from shuffled sequences. A lower-than-expected L value would reflect a stable and flat sequence, whereas a higher-than-expected value would reflect a fluctuating and potentially alternating sequence.

We further excluded trials with catch trial periods (20 trials per observer) from the autocorrelation analysis and calculation of the Lathrop statistic, because these analyses characterize sequential dependencies that could have been interrupted by catch trial periods.

We determined whether observers were attending to the task and performing accurately by analyzing catch trial periods. Catch trial accuracy was calculated as the percentage of time that observers reported the "cor-
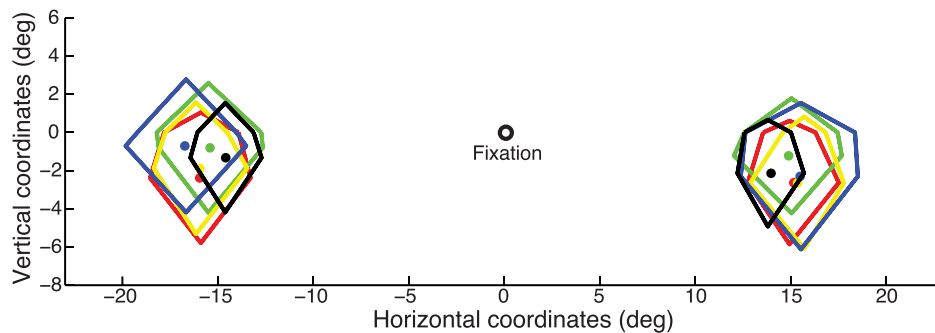
Figure 4. Blind spot centers and boundaries for five observers (both eyes) in degrees of visual angle. Different colors represent different observers.

rect" percept (the bar in the fellow eye) out of the total time they were pressing either button during catch trial periods:

$$\frac{\sum Correct\ percept}{\sum Correct\ percept + \sum Wrong\ percept} \times 100\%. \tag{3}$$

We excluded key presses that started before the catch trial period, as these were likely responses to the previous percept.

Results

The measured blind spots for all five individual observers are shown in Figure 4. On average, the blind spot center was at 15.40° (SD 0.77°) in the periphery and 1.80° (SD 0.74°) below the horizontal meridian. The horizontal diameter was on average 5.43° (SD 1.01°), and the vertical diameter was 6.57° (SD 0.67°). Note that these are conservative estimates for the blind spot area, consistent with previous reports using similar
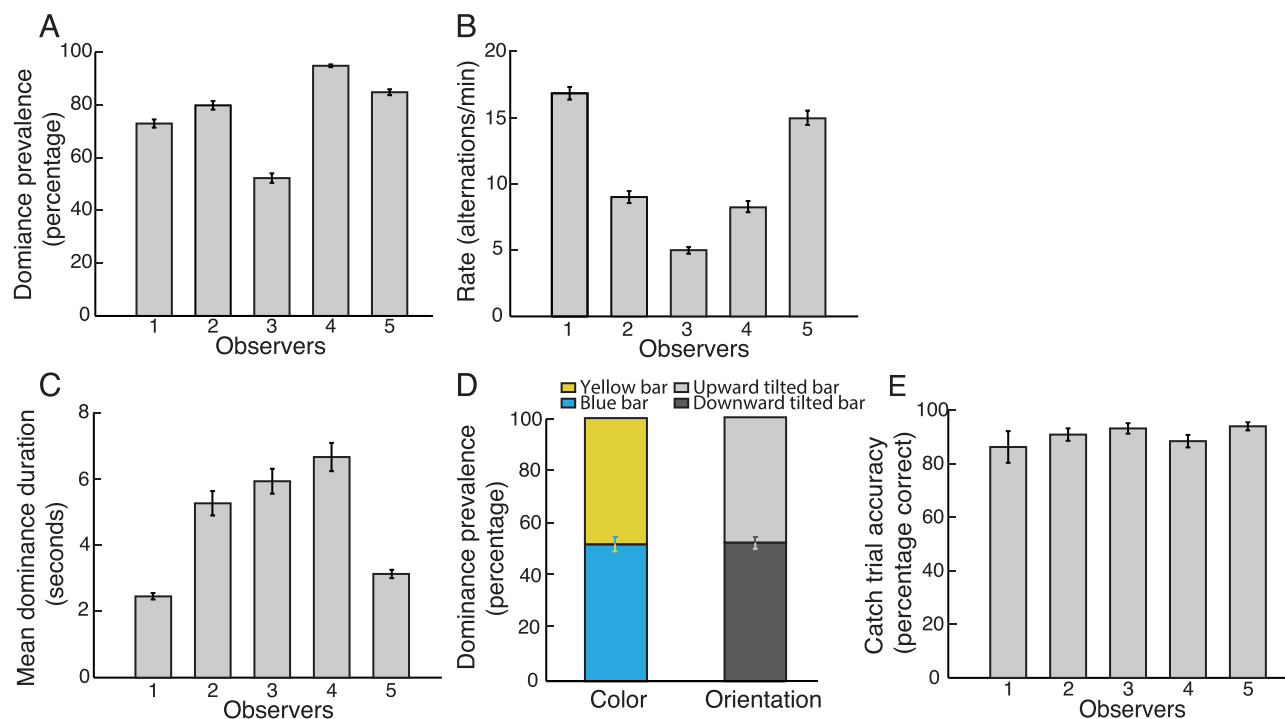

Figure 5. Results for the rivalry experiment: (A) Dominance prevalence, the percentage of time that either bar was reported unambiguously in front. (B) Rivalry alternation rate, the number of times each observer perceived a perceptual switch per minute. (C) Mean dominance durations, the duration of each individual key press for an unambiguous percept. (D) Dominance prevalence for bar color and orientation. (E) Catch trial accuracy. Error bars show ±1 SEM.
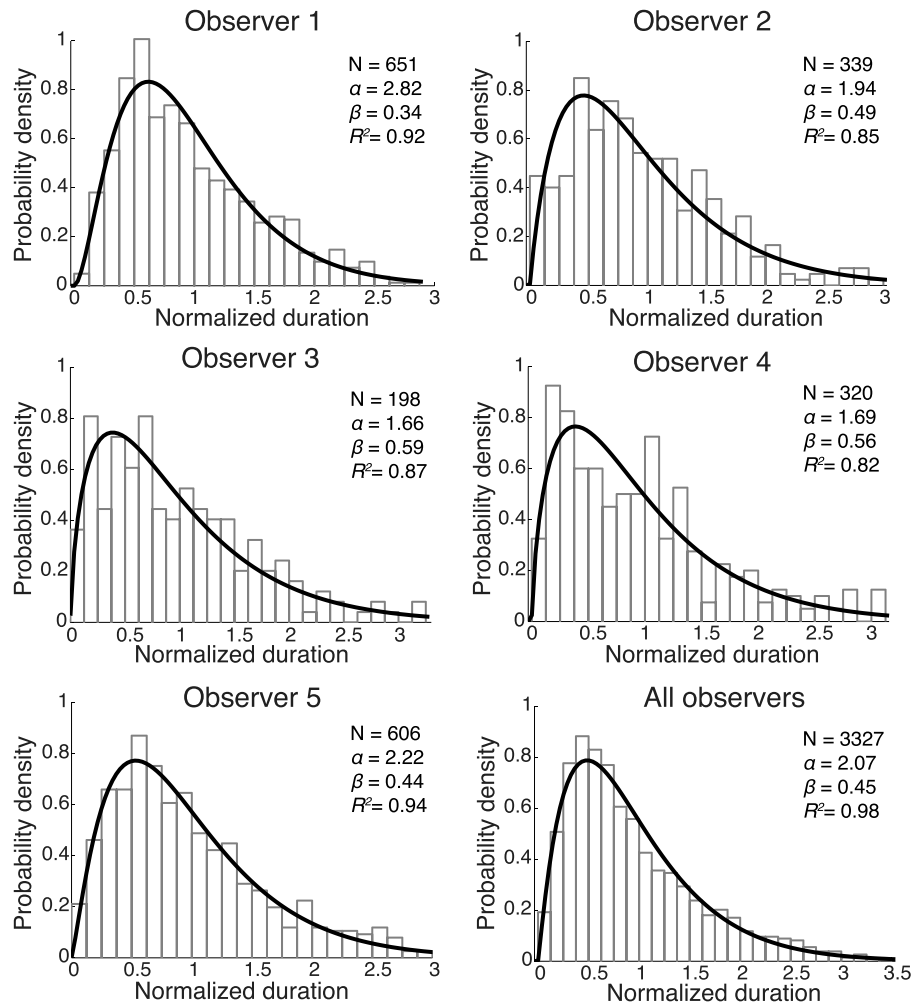
Figure 6. Distributions of normalized dominance durations for individual observers and combined across observers. The durations were binned into 125-ms intervals for plotting and calculating R^2. Black curves show the best-fitting gamma distributions. N is the number of dominance durations that were used to estimate a distribution; α and β are the estimated shape and scale parameters of the fitted distribution.

measurements (Baek et al., 2012; Maus & Nijhawan, 2008; Maus & Whitney, 2016).

High dominance prevalence indicated that observers mostly perceived an unambiguous depth ordering (Figure 5A). Mean dominance prevalence was 76.92% (*SEM* 7.13%). Dominance prevalence varied across observers, ranging from 52.25% to 94.82%, but was consistent within an observer across eyes. The Pearson correlation coefficient between mean dominance prevalence of the left and right eyes across observers was 0.86.

Perceptual alternations during filling-in rivalry occurred with a mean rate of 10.74 alternations/min (*SEM* 2.23; Figure 5B). Alternation rates also varied considerably across observers, ranging from 5.00 to 16.55 alternations per minute, and were highly correlated between eyes across observers (Pearson's $r =$ 0.92).

Dominance durations during filling-in rivalry lasted for an average of 4.70 s (*SEM* 0.81; Figure 5C), ranging from 2.48–6.68 s across observers. The Pearson correlation coefficient between the mean dominance durations of the left and right eyes across observers was 0.75.

Dominance prevalence did not depend on the color or orientation of the bars (Figure 5D), indicating no stimulus-related biases in perceptual dominance. Dominance prevalence was analyzed using a within-subjects ANOVA with two-factors (color and orientation). There were no significant main effects of color, $F(1, 4) = 0.22$, $p = 0.66$, or orientation, $F(1, 4) = 0.004$, $p = 0.95$, and no significant interaction between the two factors, $F(1, 4) = 0.29$, $p = 0.62$.

Catch trial performance confirmed that observers were accurately performing the task. The mean catch trial accuracy across observers was 91.08% (*SEM*
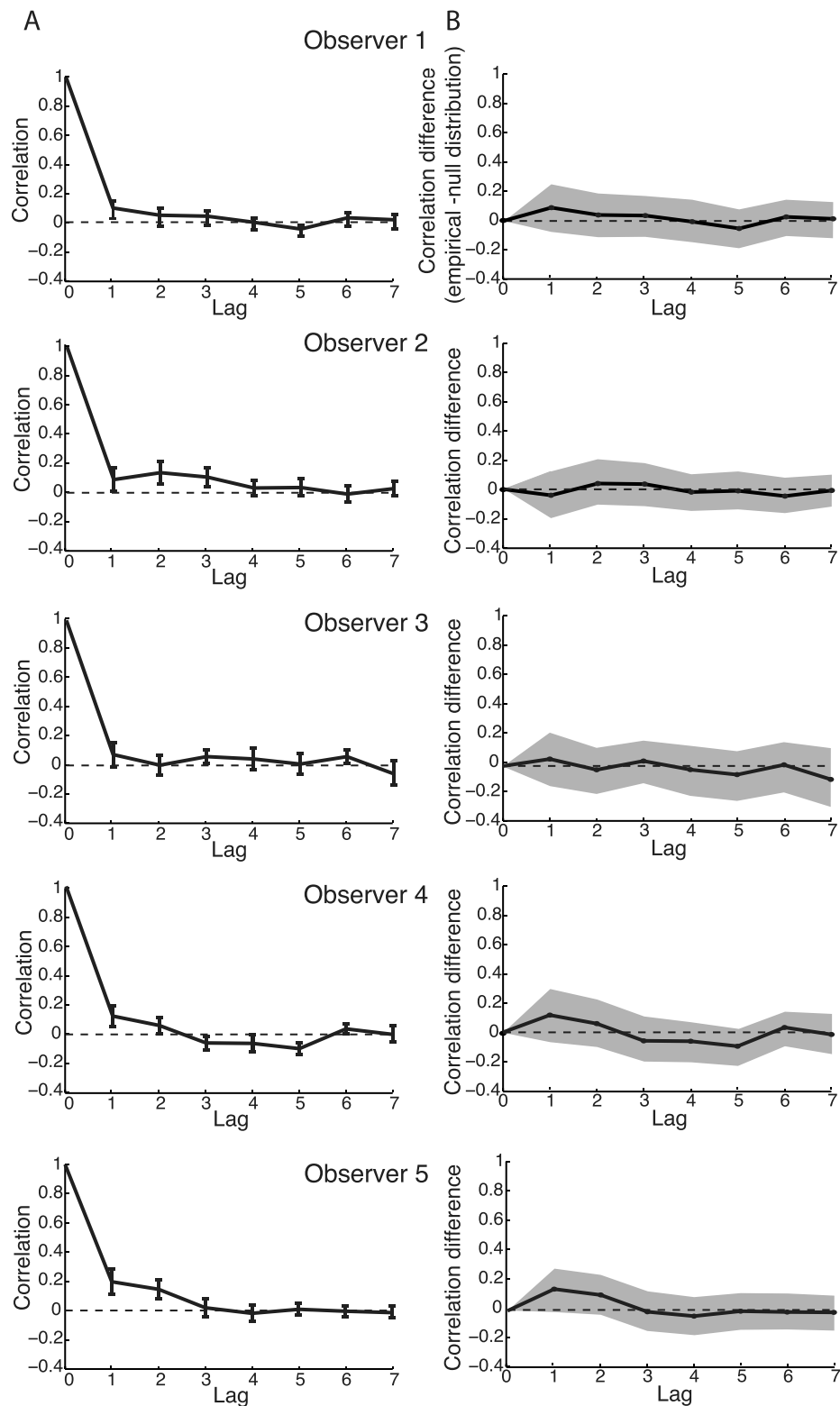
Figure 7. Autocorrelation analysis. (A) Mean autocorrelation of the sequence of dominance durations for individual observers. Error bars show ±1 *SEM*. (B) Mean difference between empirical autocorrelations and expected autocorrelations calculated from a permutation analysis (5,000 shuffled sequences to form a null distribution, see Methods) across trials for each observer. 95% confidence intervals (shaded regions) for the difference between empirical and shuffled data all include zero, which indicates non-significant results from the permutation analysis.
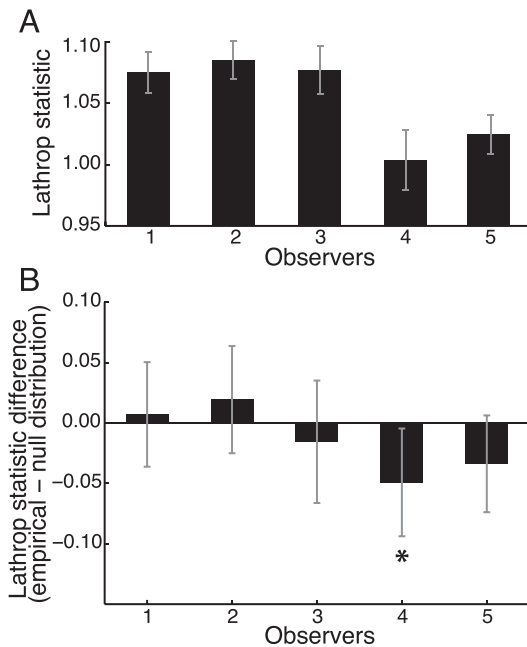
Figure 8. Lathrop statistic for first-order sequential dependence. (A) Mean Lathrop statistic across trials for each observer. Error bars show ± 1 *SEM*. (B) Mean difference between empirical Lathrop values and expected Lathrop values calculated from shuffled sequences (null distribution) across trials for each observer. Error bars show 95% confidence intervals. * $p < 0.05/5 = 0.01$ (Bonferroni correction).

1.44%). All observers performed with at least 86.22% accuracy (Figure 5E).

The distributions of dominance durations were well fit by a gamma distribution for every observer, as well as for data from all observers combined (mean $R^2 = 0.88$, $SD = 0.050$; K-S test, $p > 0.1$; mean K-S statistic = 0.043). The parameters of the fitted gamma distributions were similar across observers (Figure 6).

Autocorrelation analysis was used to test whether a given dominance duration was systematically related to a previous dominance duration for 1 to 7 lags. Mean autocorrelation coefficients tended to be small in magnitude and slightly positive at shorter lags, as were the null distributions generated from shuffled sequences (Figure 7; see Methods). None of the 35 autocorrelation coefficients (7 lags × 5 observers) differed significantly from the empirical null distribution, as assessed using permutation tests with Bonferroni correction for multiple comparisons ($p > 0.018$; $\alpha_{Bonferroni} = 0.05/35 = 0.0014$).

First-order sequential dependencies (between successive dominance durations) were also not found reliably across observers when assessed with a Lathrop statistic (Lathrop, 1966). The measured L values (Figure 8) differed significantly from the expected L values computed from shuffled sequences for only one observer, as tested using permutation tests with

Bonferroni correction for multiple comparisons ($p_{observer4} = 0.0006$; otherwise, $p > 0.14$; $\alpha_{Bonferroni} = 0.05/5 = 0.01$). For this observer, the empirical L value was lower than the null distribution would predict; successive dominance durations tended to be more similar to each other than expected for shuffled sequences with no first-order sequential dependencies.

Discussion

We found that when the visual stimulation surrounding the blind spot is ambiguous, consistent with two equally likely physical situations, the visual system resolves the ambiguity via a rivalry process that determines what is seen in the blind spot. We term this process "filling-in rivalry." The stimulus we developed enabled continuous measurements of perceptual dominance in the blind spot, with no bias toward either of the rivaling percepts, allowing us to characterize the prevalence and dynamics of filling-in rivalry. We found that filling-in rivalry displays a prevalence of unambiguous percepts (~80%), shows characteristic alternation rates for each observer, and has dominance durations that follow a gamma distribution with sequential dependencies that are small in magnitude and similar to random sequences. These properties are shared by other forms of perceptual rivalry, including binocular (Blake, Fox, McIntyre, 1971; Fox & Hermann, 1967; Levelt, 1967; Walker, 1975) and monocular rivalry (Brascamp et al., 2005; O'Shea et al., 2009) and dichoptic masking (van Boxtel et al., 2007).

Distributions of dominance durations have been shown to be well-approximated by gamma distributions for many types of perceptual alternations, including figure-ground reversals (Parkkonen, Andersson, Hämäläinen, & Hari, 2008), ambiguous structure-from-motion rotation (Klink, van Ee, & van Wezel, 2008), rivalry between filled-in and real images (Baek et al., 2012), rivalry between afterimages (Wade, 1975), and motion-induced blindness (Carter & Pettigrew, 2003), suggesting that they are governed by a common type of stochastic process. We found small positive autocorrelation coefficients in sequences of dominance durations, consistent with some earlier observations (van Ee, 2005, 2009). However, these autocorrelations did not differ from permuted null distributions. They may be due to a bias in the autocorrelation coefficient arising from the relatively short sequence lengths and skewed distributions of our data (Arnau & Bono, 2001). Other researchers have attributed these small positive autocorrelations to neural adaptation (Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009; van Ee, 2009).

Perceptual alternation rates during filling-in rivalry varied considerably across individuals, a common

finding in binocular rivalry (Aafjes, Hueting, & Visser, 1966; Hancock, Gareze, Findlay, & Andrews, 2012; Patel, Stuit, & Blake, 2015), rivalry between illusory and real contours (Fahle & Palm, 1991), and other types of perceptual rivalry (Carter & Pettigrew, 2003; Patel et al., 2015). Individual differences in bistable perception have been associated with a variety of factors, including genotype and brain structure (Kanai, Bahrami, & Rees, 2010; Kondo et al., 2012; Scocchia, Valsecchi, & Triesch, 2014). The range of alternation rates for filling-in rivalry (5–17 alternations/min) can be compared to previous detailed reports of rivalry alternation rates. For example, binocular rivalry between gratings was reported to alternate more quickly, 9–36 times/min (Hancock et al., 2012), while monocular rivalry between face and house images alternated more slowly, 4–8 times/min (O'Shea et al., 2009). Rivalry between illusory and real contours was reported to have 3–13 reversals/min (Fahle & Palm, 1991), comparable to the rate we observed. The mean alternation rate of filling-in rivalry (10.7 switches/min) was twice the rate of perceptual disappearance of a monocular rivalry stimulus in a conflict-free region reported by Maier et al. (2005), which, like filling-in rivalry, was driven by surrounding context. We present these previous results as points of reference, but note that rates of rivalry alternation strongly depend on stimulus and other factors (Hancock et al., 2012; Kornmeier et al., 2009; Leopold & Logothetis, 1999; Levelt, 1966).

Individual differences have been found to be stable across some types of rivalry: temporal characteristics of binocular rivalry (e.g. dominance durations and alternation rates) correlate with those of "flicker/swap rivalry" (Patel et al., 2015) and motion-induced blindness (Carter & Pettigrew, 2003) across observers. Future studies that examine the correlation of temporal dynamics between filling-in rivalry and other types of rivalry measured in the same observers may further support the existence of a common, underlying neural mechanism.

Our finding that filling-in rivalry has temporal dynamics similar to other forms of perceptual rivalry shows that driving retinal input is necessary neither to initiate rivalry nor for typical rivalry dynamics. Surrounding context is sufficient. Because the blind spot receives no retinal input, the local patch that rivals within the blind spot is internally generated, demonstrating rivalry between two illusory percepts. Such rivalry has previously been reported for two bars crossing in the blind spot (Brown & Thurmond, 1993) and for rivalry between the figure-ground assignments of shapes generated from illusory contours (Harris & Gregory, 1973), but the dominance prevalence and dynamics had not been characterized. Rivalry between illusory percepts also occurs in binocular rivalry

between afterimages (Bartels, Vázquez, Schindler, & Logothetis, 2011; Wade, 1975), though in this case past retinal input is responsible for the conflicting perceptual interpretations.

Three main neural processes are thought to drive perceptual rivalry: mutual inhibition (for a review, see Shpiro, Curtu, Rinzel, & Rubin, 2007), adaptation (Alais, Cass, O'Shea, & Blake, 2010; van Ee, 2011) and neuronal noise (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Moreno-Bote, Rinzel, & Ruben, 2007). These processes (in various combinations) can explain the characteristic dynamics of rivalry (Seely & Chow, 2011; Shpiro et al., 2009; van Ee, 2009) and so are good candidates for the circuit-level mechanisms underlying filling-in rivalry, as evidenced by the similar temporal dynamics we observed. For example, both adaptation and noise are necessary for a mutual inhibition model to produce a gamma distribution of dominance durations (Shpiro et al., 2009). The continuous movement of our stimuli prevented retinal and other spatially precise adaptation, consistent with the possibility that higher-level representations are competing during filling-in rivalry.

We consider two possible systems-level neural mechanisms for filling-in rivalry in the blind spot. The first is that the two bars rival globally, which then determines which bar is perceptually filled-in. Such global rivalry might be related to the rivalry that has been observed for figure-ground assignments in ambiguous border ownership situations (Fahle & Palm, 1991; Harris & Gregory, 1973; Kogo, Hermans, Stuer, van Ee & Wagemans, 2015; Sobel & Blake, 2003). In our stimulus, determining which bar is in front involves interpreting one of the bars as the "figure" and the other as relatively in the background. Rivalry between overlapping shapes defined by illusory contours (Harris & Gregory, 1973) could reflect a similar figure-ground assignment process. Rivalry between global patterns also seems to be at play in monocular rivalry when one pattern suppresses another, even in regions of the stimulus that are free of local conflict (Maier et al. 2005). These examples are consistent with rivalry between higher-level representations that extend over a fairly large region of space. This account suggests that higher-order areas play a critical role in filling-in in the blind spot. Neurophysiological studies have suggested a role for feedback from V2 to V1 neurons in blind spot filling-in (Matsumoto & Komatsu, 2005) and top-down influences from higher levels to early visual cortex in figure-ground perception (Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006; Parkkonen et al., 2008). Models of rivalry with interacting hierarchical levels (Freeman, 2005; Wilson, 2003) may be good candidates for filling-in rivalry in their general structure, though the details of existing models would need to be adjusted

to accommodate the lack of retinal input at the location where rivalry is perceived in filling-in rivalry.

The second possibility for the resolution of filling-in rivalry is that both bars are filled in locally within the blind spot representation and these local representations compete at this early stage. Whichever representation dominates determines the bar that is seen as in front. Physiological studies have shown that a retinotopic representation of the blind spot exists as early as V1 (Awater, Kerlin, Evans, & Tong, 2005; Azzi, Gattass, Lima, Soares, & Fiorani, 2015; Fiorani, Rosa, Gattass, & Rocha-Miranda, 1992; Komatsu, Kinoshita, & Murakami, 2000, 2002; Matsumoto & Komatsu, 2005). Neurons within the blind spot representation have relatively large receptive fields that extend beyond the borders of the blind spot (Azzi et al., 2015) and can exhibit color (Komatsu et al., 2000; Komatsu et al., 2002) and orientation (Fiorani et al., 1992; Komatsu et al., 2000) selectivity. Thus one might imagine rivalry arising from competition between neurons within the blind spot representation tuned to the orthogonal orientations and conflicting colors of the bars. However, in this case, it is not clear why observers would see rivalry instead of a plaid or transparent overlay of the two bars (Said & Heeger, 2013).

Filling-in rivalry should be distinguished from binocular rivalry between filled-in information in the blind spot, or a blank region, and a physical image in the corresponding area of the fellow eye (Baek et al., 2012; He & Davis, 2001; Meng, Remus, & Tong, 2005; Tong & Engel, 2001). Unlike binocular rivalry, filling-in rivalry occurs only within a monocular region within the blind spot and so does not involve interocular suppression. However, activity in lower-level cortical areas (V1 and V2) is coupled with the appearance and disappearance of the filled-in percept during binocular rivalry (Meng et al., 2005; Tong & Engel, 2001), which could support the involvement of these regions in filling-in rivalry as well.

The robustness of filling-in rivalry may indicate a bias in the visual system for filling in opaque rather than transparent surfaces within the blind spot. For example, T-junctions are more common than X-junctions in natural scenes (Changzi, Zhang, Ye, & Shimojo, 2006; Stoner, 2001). If there were a corresponding bias, or a stronger prior for representing T-junctions over X-junctions, it might predict rivalry of apparently opaque surfaces, as we find, rather than fusion or the appearance of transparency. Transparent percepts do arise in other situations of conflicting depth and occlusion information, suggesting that the visual system is capable of creating a subjective perception of transparency in such circumstances (Howard, 2012; Kersten, 1991; Nakayama, Shimojo, & Ramachandran, 1990; Watanabe & Cavanagh, 1993). However, given the lack of retinal input at the blind spot, perhaps the

visual system's prior toward opaque surfaces is more effective.

Conclusions

In summary, our study establishes filling-in rivalry as a robust rivalry process, sharing common characteristics with other types of perceptual rivalry, in the absence of local image conflict. Retinal conflict is therefore not needed to drive perceptual alternations; the same types of rivalry mechanisms are also triggered for internally generated conflicts that depend entirely on global context. Our findings suggest that information in the blind spot is actively filled in based on a higher level stochastic sampling process that determines the contents of visual awareness.

Keywords: filling-in, blind spot, rivalry, ambiguous stimuli, jumping pen illusion

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