

# Individual differences point to two separate processes involved in the resolution of binocular rivalry

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Although binocular rivalry is different from other perceptually bistable phenomena in requiring interocular conflict, it also shares numerous features with those phenomena. This raises the question of whether, and to what extent, the neural bases of binocular rivalry and other bistable phenomena overlap. Here we examine this question using an individual-differences approach. In a first experiment, observers reported perception during four binocular rivalry tasks that differed in the features and retinal locations of the stimuli used. Perceptual dominance durations were highly correlated when compared between stimuli that differed in location only. Correlations were substantially weaker, however, when comparing stimuli comprised of different features. Thus, individual differences in binocular-rivalry perception partly reflect a feature-specific factor that is not shared among all variants of binocular rivalry. Our second experiment again included several binocular rivalry variants, but also a different form of bistability: moving plaid rivalry. Correlations in dominance durations between binocular rivalry variants that differed in feature content were again modest. Moreover, and surprisingly, correlations between binocular rivalry and moving plaid rivalry were of similar magnitude. This indicates a second, more general, factor underlying individual differences in binocular rivalry perception: one that is shared across binocular rivalry and moving plaid rivalry. We propose that the first, feature-specific factor corresponds to feature-tuned mechanisms involved in the treatment of interocular conflict, whereas the second, general factor corresponds to mechanisms involved in representing surfaces. These latter

mechanisms would operate at a binocular level and be central to both binocular rivalry and other forms of bistability.

## Introduction

When viewers are shown two incompatible images, one to each eye, their perception oscillates over time, with each monocular image being seen in turn (Figure 1A). Although this phenomenon, termed “binocular rivalry,” has been studied extensively (Wheatstone, 1838; Blake & Logothetis, 2002), many questions remain about the neural processes that underlie it. The present work centers on one recurring question in the literature, namely, whether or not binocular rivalry shares mechanisms with other forms of bistable perception that have a similar phenomenology but that involve no inter-ocular conflict (e.g., Necker cube perception). While it is common to think of binocular rivalry as critically dependent on inhibition between the left and right eyes’ monocular neurons early in the visual processing stream (Blake, 1989; Mueller, 1990; Wilson, 2005; Baker & Graf, 2009; Klink, Brascamp, Blake, & van Wezel, 2010; Brascamp, Sohn, Lee, & Blake, 2013), binocular rivalry likely also depends on higher level processes that might well be shared with other forms of perceptual bistability (Leopold & Logothetis, 1996; Blake & Logothetis, 2002; Nguyen, Freeman, & Alais, 2003; Wilson, 2003; Tong, Meng, & Blake, 2006; Alais & Melcher, 2007). Indeed, numerous authors have pointed to similarities between binocular

Citation: Brascamp, J. W., Qian, C. S., Hambrick, D. Z., & Becker, M. W. (2019). Individual differences point to two separate processes involved in the resolution of binocular rivalry. *Journal of Vision*, 19(12):15, 1–17, <https://doi.org/10.1167/19.12.15>.

<https://doi.org/10.1167/19.12.15>

Received March 26, 2019; published October 17, 2019

ISSN 1534-7362 Copyright 2019 The Authors



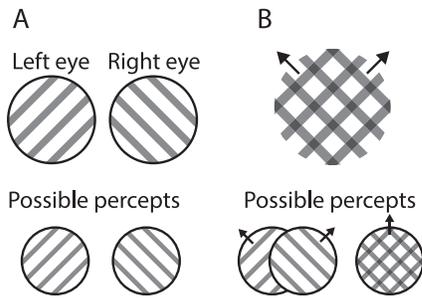


Figure 1. Schematic illustration of the bistable stimuli used in this study. (A) In binocular rivalry two incompatible images are shown to the two eyes and observers alternately perceive the left eye’s image or the right eye’s image. (B) In moving plaid rivalry two drifting gratings are shown superimposed (to both eyes) and observers alternately perceive the two gratings sliding over each other, or a rigid plaid moving in an intermediate direction.

rivalry and other forms of bistable perception in terms of aspects such as the statistics of the perceptual time course and its dependence on stimulus manipulations (Leopold & Logothetis, 1996; Andrews & Purves, 1997; Rubin & Hupé, 2005; O’Shea, Parker, La Rooy, & Alais, 2009; Moreno-Bote, Shpiro, Rinzel, & Rubin, 2010; Bonneh, Donner, Cooperman, Heeger, & Sagi, 2014; Brascamp, Klink, & Levelt, 2015).

Here we take an individual-differences approach to examining rivalry’s unique and shared mechanisms. Individuals differ widely in the rate at which perception oscillates during binocular rivalry: One observer may experience a perceptual switch almost every second, whereas another may regularly see the same image for 5 s without interruption (Carter & Pettigrew, 2003; Gallagher & Arnold, 2014; Chen et al., 2018). By examining the extent to which such differences are correlated across various forms of bistability, one can gain insight into the overlap between the mechanisms of binocular rivalry and of other bistable phenomena. Recent work along these lines indicates that all tested forms of visual bistability do not necessarily correlate with each other (Gallagher & Arnold, 2014; Brascamp, Becker, & Hambrick, 2018; Cao et al., 2018), but that binocular rivalry does belong to a cluster of correlated phenomena (Cao, Wang, Sun, Engel, & He, 2018) that also includes, among others, the perception of bistable moving plaids (Figure 1B; described in detail below). This demonstration of a relatively global factor—one that affects all phenomena in that cluster—is in line with the idea that some of the mechanisms responsible for binocular rivalry transpire at a higher processing level that is also involved in other forms of perceptual bistability.

To better understand the nature of mechanisms that are unique to binocular rivalry and of ones that are not, our first experiment aimed to establish across-observer

correlations in switch rate between different versions of binocular rivalry that differed in the feature content and retinal location of the stimuli used. The extent to which such differences impact the correlation is informative as to the selectivity, or tuning, of the neural mechanisms that determine binocular rivalry switch rate. Indeed, if any interobserver variance in switch rate is shared across all forms of binocular rivalry irrespective of stimulus properties, then this constitutes a “binocular rivalry factor,” suggestive of a neural process that affects binocular rivalry generally. In a second experiment, we added a different bistable stimulus to our battery, namely a bistable moving plaid (Figure 1B). When viewed continuously, this stimulus is perceived alternately as two gratings sliding transparently over each other (Figure 1B, bottom left), or a single plaid that moves rigidly in an intermediate direction (Figure 1B, top right; Hupé & Rubin, 2003; Moreno-Bote et al., 2010; Kondo et al., 2012). This allowed us to extend our inquiry to correlations that included a bistable stimulus other than binocular rivalry, in search of a factor that operates across multiple bistable phenomena, i.e., a factor that is even more general than a putative binocular rivalry factor.

## Methods

### Observers

For Experiment 1, we recruited 137 healthy participants (122 females) from the psychology subject pool at Michigan State University. Of these participants, 118 indicated they fell in the 18–20-year age range; the remaining 19 indicated they were 21–25 years old. For Experiment 2, we recruited 115 different healthy participants (75 females) in the same way. The age range distribution was: 98 between 18 and 20 years, 16 between 21 and 25 years, and one between 26 and 30 years. The study protocol was approved by the Michigan State University institutional review board, and written informed consent was obtained from all participants prior to testing. Participants fulfilled course requirements through their participation.

### Stimuli and tasks

All experiments were performed using a mirror setup (Qian & Brascamp, 2017) that allowed each eye to view a separate computer monitor (for practical reasons we also used this setup for the plaid motion experiment, even though the stimulus did not require it). All stimuli in both Experiments 1 and 2 were presented within the same pattern for aiding fusion. This pattern consisted

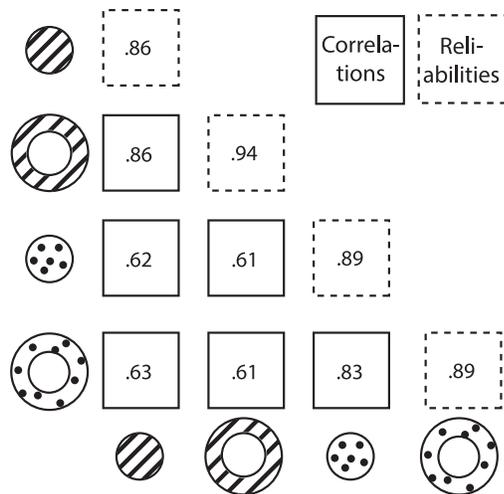


Figure 2. Correlation matrix of average percept durations for the four binocular rivalry stimuli of Experiment 1, indicated schematically along the sides of the matrix. Cells on the diagonal show reliabilities; off-diagonal cells show Pearson correlation coefficients.

of a set of two nested square frames, each filled with a black and white pattern (Michelson contrast of 1): a coarse square wave grating for the outer frame (0.2 cycles/degrees of visual angle [c/dva]) and a finer square wave grating for the inner frame (1.3 c/dva). The outer frame ranged from 5.6 to 7.3 degrees of visual angle (dva) in eccentricity; the inner frame from 4.2 to 5.3 dva. Finally, for both experiments observers were instructed to fixate their gaze on a round fixation mark (radius 0.12 dva) shown in the center of each stimulus.

In Experiment 1, we used four different binocular rivalry stimuli; each stimulus had one of two retinal locations and was made up of one of two visual patterns (see icons in Figure 2 for illustration). In addition, we used a type of “mimic” condition (Blake & Fox, 1974) where the two images that were shown monocularly in one of the rivalry conditions were instead shown binocularly and in alternation, in an attempt to emulate the binocular rivalry experience without any stimulus conflict. The reason for this is that correlations in switch rate across bistability paradigms in part reflect individual differences in nonperceptual factors related to response criterion and/or motor control; a mimic condition like this allows one to isolate those factors in order to focus further analyses on the perceptual differences of interest (Gallagher & Arnold, 2014; Brascamp et al., 2018). All stimuli in Experiment 1 were presented on the same uniform background (luminance of 31.8 cd/m<sup>2</sup>, formed by blending equal luminances from the monitor’s red and green channels).

### Small grating stimulus of Experiment 1

This stimulus was a variant of a very similar one we used in a previous study (Brascamp et al., 2018). Each monitor displayed a sinusoidal grating (2.0 c/dva, Michelson contrast 0.5, mean luminance same as background luminance) presented within an annular aperture (inner radius 0.37 dva, outer radius of 0.85 dva). Grating orientation (−45 and +45 degrees from vertical) and color (using either only the monitor’s red channel or only the monitor’s green channel) differed between eyes, resulting in interocular conflict. The phase of the gratings continually shifted slowly to counteract the formation of negative afterimages: Each grating drifted diagonally upward or downward, orthogonal in the two eyes, at 0.24 dva/s (direction was balanced between trials).

### Large grating stimulus of Experiment 1

This stimulus consisted of the same drifting gratings as the previous stimulus, but now they filled a different, nonoverlapping, retinal area: an annular region that spanned from 0.91 dva to 1.82 dva in eccentricity.

### Small dot stimulus of Experiment 1

This stimulus filled the same retinal area as the small grating stimulus, but it consisted of a different pattern. Each eye viewed a pattern of randomly placed dots (average density 27.3 dots/dva<sup>2</sup>; dot diameter 0.12°) that expanded from the center in one eye, and contracted toward the center in the other (speed 1.5°/s; eye configuration of expansion/contraction was balanced between trials). In each eye, half the dots had twice the background luminance and the other half had half the background luminance, but in one eye they were red (using only the monitor’s red channel) and in the other they were green (using only the green channel).

### Large dot stimulus of Experiment 1

This stimulus was like the small dot stimulus except that it filled the same, nonoverlapping, retinal area as the large grating stimulus, and that its average dot density was slightly lower (21.8 dots/dva<sup>2</sup>).

### Mimic condition

The mimic condition involved the same gratings that also formed the monocular images of the small grating stimulus, but now shown binocularly and dynamically alternating on the screen over time. In other words, these were animations that emulated the perceptual experience of viewing the small grating stimulus, but without any binocular rivalry. The animations behaved

the same as a mimic condition we used in a previous study (Brascamp et al., 2018), with minor modifications specified here. In brief, animations consisted of alternating periods of exclusive visibility of either grating (of random duration, uniform distribution between 1 and 5 s) as well as periods of mixed perception during which the animations displayed patchworks consisting of parts of one grating and parts of the other. Such mixed perception also occurs during binocular rivalry (Brascamp, Van Ee, Noest, Jacobs, & van den Berg, 2006). In the animations these mixed periods also had a degree of randomness to them, both in terms of duration and in terms of the spatial layout of the patchwork (for details see Brascamp et al., 2018).

During all conditions of Experiment 1 the observers had the task of reporting, using three keyboard keys, the onsets of periods where the red pattern was visible, periods where the green pattern was visible, and periods where both were partly visible (i.e., mixed perception). Individual trials lasted 45 s and were separated by a forced break of 10 s (observers could wait longer if they wanted). Each observer ran a single experiment session that included six trials of each binocular rivalry condition and four trials of the mimic condition, and all trials were randomly interleaved within the session. Before the experiment observers were informally familiarized with the stimulus layout and task, until they were comfortable to start the experiment.

Experiment 2 included Experiment 1's small grating stimulus, small dot stimulus, and mimic condition. In each case we used the same trial numbers and durations as in Experiment 1. Experiment 2 also included two additional conditions.

### ***Moving plaid stimulus of Experiment 2***

The plaid stimulus filled the same retinal area as the small grating and dot stimuli. It consisted of two overlapping grayscale square wave gratings ( $\pm 26.6^\circ$  relative to vertical, 0.5 Michelson contrast, 2.0 c/dva). They were presented on a uniform gray background (35.2 cd/m<sup>2</sup>; same as average grating luminance). The gratings translated diagonally upward at a speed of 0.48 dva/s, and observers used two keyboard keys to indicate the onsets of periods during which they perceived either a solid, vertically shifting plaid, or two transparently superimposed gratings (there was no third key for reporting mixture perception, given that such perception is not typically observed for this stimulus). At locations where the bright bands of the two gratings overlapped, their intersection luminance was computed as follows. First we computed the difference between the logarithm of the luminance of the gratings' bright bands and the logarithm of the luminance of the gratings' dark bands. Then the intersection luminance was set such that the same

difference was obtained between the logarithm of the intersection luminance and that of the luminance of the gratings' bright bands. In other words, in log space the luminance difference between the intersections and the gratings' bright bands equaled the difference between the gratings' bright bands and dark bands. This choice of intersection luminance has been shown to invite the perception of transparency (Van den Berg & Noest, 1993), which was desirable because in pilot work observers tended to have a preference for the perception of a solid, nontransparent, plaid. Observers completed six trials of 60 s each, separated by forced breaks of 10 s and any additional time they required. We chose this slightly longer trial duration (60 s, compared to 45 s for all binocular rivalry conditions) because pilot work indicated switch rates to be relatively lower for the moving plaid stimulus, and we wanted to ensure sufficient data for this condition.

### ***Plaid-derived grating stimulus of Experiment 2***

This was a binocular rivalry grating stimulus made up of the same gratings as made up the moving plaid stimulus, drifting at the same speed, shown at the same orientations and on the same background, but now shown dichoptically (i.e., one to each eye). Observers used three keys to report periods of exclusive dominance as well as periods of perceptual mixture. Observers completed six trials of 45 s each, separated by the same breaks as described above. Movement direction (either upward or downward) was randomized between trials.

In contrast to Experiment 1, conditions in Experiment 2 were not randomly interleaved within the same experiment session. The reason for this was that we could not use the same observer instruction (i.e., "report which color you see") across all conditions, and asking observers to memorize multiple instructions in parallel was deemed too demanding for this type of project involving large numbers of untrained participants. So, instead, each condition's trials were presented in a block-wise fashion, and the conditions were randomly ordered. Prior to each block of a given condition, observers received an informal introduction to the upcoming stimulus and task. This introduction was more extensive for the moving plaid condition, because observers sometimes had trouble identifying any percept other than that of a rigid, upward moving plaid. Accordingly, prior to the block of moving plaid trials an observer was shown the same stimulus continuously for up to several minutes, as the experimenter explained the various perceptions. This introduction was deemed complete when the observer acknowledged the presence of both perceptual interpretations.

## Data analysis

For all conditions except the moving plaid condition and the mimic condition, we excluded observers whose perception was strongly imbalanced toward one percept. In particular, we excluded observers if the total amount of time perceiving one color or motion direction was less than 75% that of perceiving the other color or motion direction. Our reason not to take such a measure for the moving plaid condition was that that condition is inherently asymmetrical in its percepts (the two percepts are not interchangeable), making it difficult to design a stimulus that achieves a near-balanced dominance cycle for a large proportion of the observers. We also excluded observers who, during a binocular rivalry condition, reported mixed perception more than 60% of the viewing time and ones for whom “return transitions” constituted more than 50% of their perceptual switches. Return transitions (Mueller & Blake, 1989) are defined as occasions where an observer reports a transition from an exclusive percept to a mixture, and then back to the same exclusive percept again instead of to the other one. All these situations (strong perceptual imbalance, extensive mixture perception, abundant return transitions) were deemed to preclude a meaningful estimate of an observer’s average percept duration. For all conditions except the mimic condition we also excluded observers who reported fewer than two perceptual dominance episodes. These criteria left us with between 84 and 120 observers for the various conditions of Experiment 1. In the treatment of Experiment 1 below we will report results only for the 79 observers who produced valid data for each condition individually. For Experiment 2 the number of observers who passed the inclusion criteria ranged from 85 to 110 for the various conditions, and we will report results only for the 71 observers who produced valid data for each condition. For both experiments, we have also performed the same analyses after excluding only the specific conditions for a given observer where that observer did not pass inclusion criteria. This less stringent approach, which allows different observer numbers for different comparisons, leads to the same conclusions as our reported approach, which equates observer numbers across all comparisons.

It has been reported that interobserver variability in the ability to faithfully report the on-screen perceptual sequence of a mimic condition explains some of the individual differences in reported perceptual dominance durations during bistable perception (Gallagher & Arnold, 2014). It has also been shown (Brascamp et al., 2018) that this is particularly true if one defines a perceptual dominance episode as the period between the onset of an exclusive percept and the end of that exclusive percept (i.e., a “start-to-end” measure that

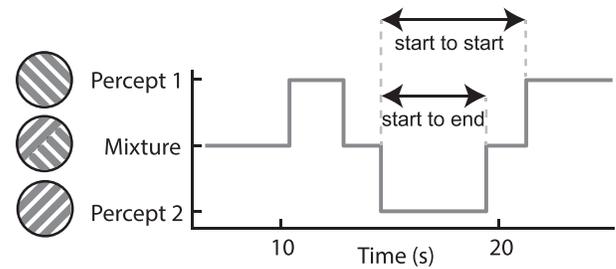


Figure 3. Schematic illustration of a perceptual sequence during binocular rivalry, which includes both periods of exclusive dominance and periods of mixed perception. We used a start-to-start measure of percept durations, which is relatively less affected by across-observer variance in nonperceptual factors than a start-to-end measure.

excludes mixture percepts; cf. Figure 3), rather than defining it as the period between the onset of an exclusive percept and the onset of the opposite exclusive percept (i.e., a “start-to-start” measure that includes mixture percepts; cf. Figure 3). Therefore, in our correlation analyses below we will not focus on periods of dominance as such, but instead use a derived measure that arguably is more closely tied to individual differences in perception rather than in motor behavior. In particular, and following the same approach as we have used before (Brascamp et al., 2018), for all conditions except the mimic conditions we first computed the logarithm of each individual’s average start-to-start dominance duration (taking the logarithm ensures a distribution that is closer to normal). We then computed an index of motor-related factors by taking, for each observer, the average reported start-to-start dominance duration during the mimic condition and dividing it by the average start-to-start dominance duration of the on-screen animation that the observer was actually watching. Perfectly faithful motor report should result in a ratio of 1, and smaller and larger ratios indicate a tendency to under- or overreport perceived dominance durations, respectively. In agreement with our earlier work, across the population of observers this ratio, which is indicative of motor behavior rather than perception, showed a small-to-medium correlation with reported start-to-start dominance durations during genuine bistability (correlation coefficients ranged from 0.11 to 0.34 across the various conditions of Experiment 1 and Experiment 2 and averaged at 0.24; the corresponding correlations were higher when using the start-to-end measure). The quantity that we will use in the results reported below is the  $y$ -axis residual of these correlations. In other words, it is the logarithm of the start-to-start dominance duration, corrected to the best of our ability for inaccuracies in motor report. Below we will often simply refer to this corrected measure as “dominance duration” or equivalent for brevity. Note that results

were qualitatively equivalent if we did not correct for motor factors in this fashion, and also if we used the start-to-end measure for dominance durations. This indicates that neither individual variability in motor factors nor individual variability in the occurrence of mixed perception underlies our conclusions.

To compute the reliability of our measures we calculated the correlation between two halves of the data for a given condition, obtained by splitting the six trials that an observer performed for that condition into three odd trials and three even trials. This correlation was then boosted using the Spearman-Brown prediction formula so that we could meaningfully compare the correlation to the between-condition correlations, which are based on twice the amount of data. For examining differences between correlation coefficients we used a web tool (I. A. Lee & Preacher, 2013) that implements Steiger's test for the equality of two dependent correlations (Steiger, 1980; Keith, 2006).

Akin to existing work in this field (Kondo et al., 2012; Cao et al., 2018) we applied factor analysis to more closely examine the components underlying individual variability in rivalry perception. As part of the analysis of both experiments, we performed exploratory factor analysis (maximum likelihood) with an oblique rotation (oblimin) to allow the factors to correlate. We also performed confirmatory factor analysis to examine the overall appropriateness of measurement models that were suggested by our initial correlation analyses and exploratory factor analyses. Because, for confirmatory factor analysis, no single index of model fit is decisive as to a factor model's fit quality, we report several fit statistics in the Results section, and we will discuss their interpretation and limitations here. A chi-square test examines whether the difference between the model and the data is significant; thus, a nonsignificant  $p$  value indicates a good fit of the model. The root-mean-square error of approximation (RMSEA) divides the estimated model error by the degrees of freedom and adjusts for sample size (Steiger, 1990). Because the RMSEA thus estimates the "badness of fit," lower RMSEA values are better and a common cut-off is 0.08 (Browne & Cudeck, 1993; Hu & Bentler, 1999; Steiger, 1989), but the cut-off is less stringent when either the number of degrees of freedom is low ( $<20$ ) or the sample size is small ( $<100$ ; Kenny, Kaniskan, & McCoach, 2015). The comparative fit index (CFI) is the ratio of improvement obtained when a model generated from the data is compared to a null model that assumes no shared variance among measures; a CFI greater than 0.95 is generally taken to indicate a good fit (Hu & Bentler, 1999; Raykov & Marcoulides, 2006). Finally, the standardized root mean residual (SRMR) compares an observed correlation matrix to a model-implied correlation matrix and estimates the difference by averaging

the absolute values of the correlation residuals. As with the RMSEA, lower SRMR values indicate better fit and a value of 0.08 or less is generally considered acceptable (Kline, 2005).

## Results

### Experiment 1

The four stimuli featured in this experiment are shown schematically along the sides of Figure 2. Counting from the start of each dominance period to the start of the next dominance period for the opposite percept, the mean percept duration, averaged across all included observers, ranged from 2.7 s for the large grating stimulus to 3.2 s for the small dot stimulus, with intermediate values for the remaining stimuli. Our main measure of interest is a corrected version (see Methods) of the logarithm of each individual's mean dominance duration for each condition. Figure 2 shows a correlation matrix to quantify the relation between this variable as measured during each of the four binocular rivalry conditions tested. On the main diagonal is the reliability of this variable within each condition. This reliability is high for all conditions (in the 0.8–0.9 range—"good" to "excellent" by conventional standards).

The figure also shows substantial correlations across distinct binocular rivalry conditions (all  $r$ s are highly significant; two-tailed  $p < 0.00001$ ). This finding is consistent with existing work that examines correlations between different binocular rivalry variants (Law, Miller, & Ngo, 2017; Cao et al., 2018). More surprisingly, visual inspection of the correlation matrix suggests that substantially higher correlations are obtained when comparing between stimuli that only differ in retinal location (i.e., between the small and large grating stimulus or between the small and large dot stimulus), than when comparing between stimuli that differ in feature content. This impression is confirmed when comparing sets of correlations using Steiger's test for the equality of two dependent correlations (Steiger, 1980). For instance, taking the small grating stimulus as the reference point, the correlation with the stimulus that differs only in location ( $r = 0.86$ ) is significantly larger than the correlation with the stimulus that differs only in features ( $r = 0.62$ ;  $z = 4.4$ ; two-tailed  $p = 0.00001$ ). Similarly, taking the large dot stimulus as the reference point, the correlation with the stimulus that differs only in location ( $r = 0.83$ ) is significantly larger than the correlation with the stimulus that differs only in features ( $r = 0.61$ ;  $z = 3.7$ ; two-tailed  $p = 0.0002$ ). Evidently, part of the between-observer variability in

rivalry percept durations reflects a factor that is relatively sensitive to stimulus features, but not so sensitive to retinal location.

To examine whether changing retinal location impacts individual differences in binocular rivalry percept duration at all, we divided the data for the small grating condition into two halves (by separating each observer's odd and even trials) and then used Steiger's test to evaluate whether the correlation between these two halves of the small grating data ( $r = 0.68$ ) was any different from the correlation between the first half of these data and all of the data from the large grating condition ( $r = 0.73$ ). This difference was not significant ( $z = -0.27$ ; two-tailed  $p = 0.79$ ), thus showing no impact of changing retinal location for the grating stimulus. Similarly, for the dot stimulus conditions, the analogous analysis showed no significant difference when comparing the correlation between two halves of the data from the small dot condition ( $r = 0.85$ ) to the correlation between one of those halves and all of the data from the large dot condition ( $r = 0.83$ ;  $z = 0.03$ ; two-tailed  $p = 0.98$ ).

This lack of evidence for any impact of changes in retinal location suggests that the only reason that the large and small grating conditions show a correlation less than 1 may be measurement error, and the same for the large and small dot conditions. To examine this idea we used Spearman's disattenuation formula to correct these correlation coefficients upward based on the reliabilities of the individual measures (which provide an estimate of the degree of measurement error). The disattenuated correlation coefficients obtained in this fashion are quite close to 1: 0.96 for the comparison between the large and small grating stimulus conditions, and 0.93 for the comparison between the large and small dot stimulus conditions. To put these numbers into context: The disattenuated correlation coefficient for the comparison between the large dot stimulus and the large grating stimulus is 0.67, and for the comparison between the two small stimuli, it is 0.71. Considered together, these various analyses suggest that changes in retinal location impact individual differences in binocular rivalry percept duration only very slightly, if at all, whereas changes in feature content have a much larger impact.

These results suggest that, for any given binocular rivalry stimulus, one factor underlying individual differences in percept duration is highly specific, in the sense that it is not even shared with other variants of binocular rivalry that differ in stimulus features. At the same time, however, correlations remain substantial even when stimulus features do differ, implying the existence of a general factor as well. This would imply that, for an observer viewing a specific rivalry stimulus, dominance durations are explained by a combination of at least two factors: a general factor and a feature-

specific factor. For our data set in its entirety this would amount to a total of three factors: a general factor as well as two that are specifically associated, respectively, with the grating conditions and with the dot conditions.

To further examine this possibility we first employed exploratory factor analysis, but the results were difficult to interpret. For completeness, we will nevertheless document these results here, before moving on to a more interpretable confirmatory factor analysis. An initial exploratory factor analysis indicated only a single factor underlying the data but provided a very poor fit ( $\chi^2[2] = 20.9$  and  $p < 0.0001$ ; data not shown), precluding any strong conclusions. We then performed a second, more guided, exploratory factor analysis in which we imposed a total number of factors of three (motivated by the idea, outlined above, of one general factor and two specific factors underlying our data set). To allow enough degrees of freedom to perform such an analysis, data from each condition (six trials total) were split into three odd trials and three even trials for each observer, thus increasing the total number of measurements available for constraining the model from four to eight (symbolized by the eight icons along the left side of Figure 4A). The results of this analysis, illustrated in Figure 4A, were suggestive but, again, not conclusive. In particular, the model fit was fair ( $\chi^2[7] = 11.1$  and  $p = 0.14$ ) and the loadings for Factor 1 and Factor 3 provided some indication of a separation between a feature-specific "gratings" factor and a feature-specific "dots" factor. In Figure 4A this is highlighted by the gray boxes: the loadings within these boxes tend to be high, whereas the remaining loadings for these two factors tend to be low. At the same time, evidence for a general factor was mixed in this analysis: The loadings for Factor 2 were hard to interpret and not consistent with it corresponding to such a general factor, yet we did find that Factor 1 and Factor 3 were highly correlated with each other ( $r = 0.70$ ), which supports the idea of shared variance across all eight measurements, consistent with a general factor.

Summarizing the above paragraphs, analysis of the correlation matrix of Figure 2 suggests the presence of both a set of feature-specific factors that can differ between stimuli and a more general factor that is shared across stimuli, yet the results of our exploratory factor analyses did not clearly support or contradict this idea. We therefore turned to confirmatory factor analysis to evaluate the specific model suggested by the correlation matrix in a more direct manner. This bifactor model, illustrated in Figure 4B, assumes three latent variables or factors: one that explains variance across all conditions of Experiment 1, and two specific ones that are associated exclusively with, respectively, either the two grating conditions or the two dot conditions, while not explaining any variance for the

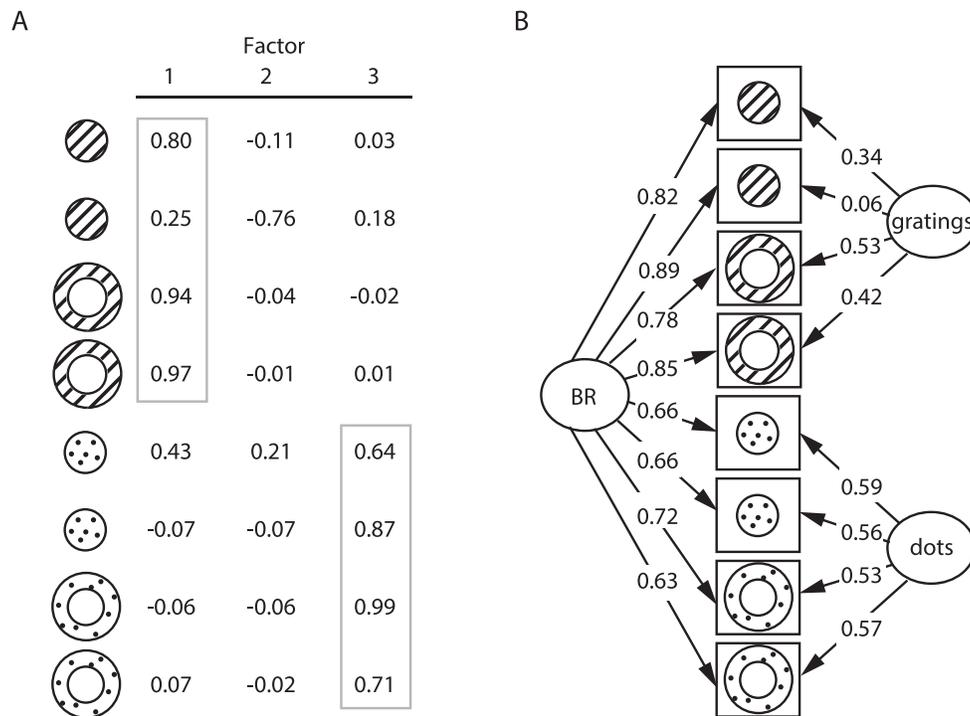


Figure 4. Exploratory and confirmatory factor analysis for Experiment 1. (A) Pattern matrix for an exploratory factor analysis where the number of factors was imposed to be three. With one data point per observer for each of our four conditions there are not enough degrees of freedom to perform this analysis, so we split each observer's data for a given condition in two (odd versus even trials); hence the increase to eight measured variables in this figure. (B) Results of a confirmatory factor analysis on a model in which the measured variables are explained by three latent variables: one that is common across all conditions, one that is shared by the conditions that involve a grating stimulus, and one that is shared by the conditions that involve a dot stimulus. To allow sufficient degrees of freedom the data for each condition were again split into odd and even trials.

other conditions. We again split data from each condition into odd and even trials for each observer to allow enough degrees of freedom to evaluate the model; hence the total number of eight, rather than four, measured variables indicated in the figure. Various indices (see Methods section for their respective interpretations and limitations) show the model fit to be good ( $\chi^2[16] = 25.05$  and  $p = 0.069$ ; RMSEA = 0.085; CFI = 0.99; SRMR = 0.028), and the appropriateness of the model is further indicated by the fact that all factor loadings are positive, and all but one are statistically significant (two tailed,  $\alpha = 0.05$ ; the exception being the loading of the second half of the data from the small grating condition on the grating factor).

We also compared this bifactor model to two nested models to verify the necessity of the bifactor structure (i.e., a structure that includes a general factor as well as a set of mutually independent specific factors). The bifactor model fit the data significantly better, both than a model that has only the general binocular rivalry factor (model comparison:  $\chi^2[8] = 197.69$ ,  $p < 0.00001$ ), and a model that has only the two feature-specific factors (model comparison:  $\chi^2[8] = 47.85$ ,  $p < 0.00001$ ). Consistent with this, the model with only the general

binocular rivalry factor provided a poor fit to the data ( $\chi^2[24] = 222.74$  and  $p < 0.00001$ ; RMSEA = 0.326; CFI = 0.85; SRMR = 0.12), and so did the model with only the two feature-specific factors ( $\chi^2[24] = 72.90$  and  $p < 0.00001$ ; RMSEA = 0.162; CFI = 0.93; SRMR = 0.37). In other words, the results of this confirmatory factor analysis corroborate the idea of a general factor as well as a set of feature-specific factors.

The analyses reported so far converge on the notion that individual differences in the perception of a given binocular rivalry stimulus reflect a specific factor that is different depending on stimulus features, but also a general factor that influences binocular rivalry broadly. Existing work has shown that binocular rivalry percept durations correlate with percept durations for some other paradigms of perceptual bistability (but not all; see Brascamp et al., 2018 for an overview, and see Fesi & Mendola, 2014; Cao et al., 2018; and Chen et al., 2018 for relevant papers not included in that overview). This raises the following question: Is the more general factor identified here also responsible for those across-paradigm correlations? Or, alternatively, should we consider three different factors from specific to general: one specific to particular binocular rivalry variants, one that is shared across all forms of binocular rivalry, and

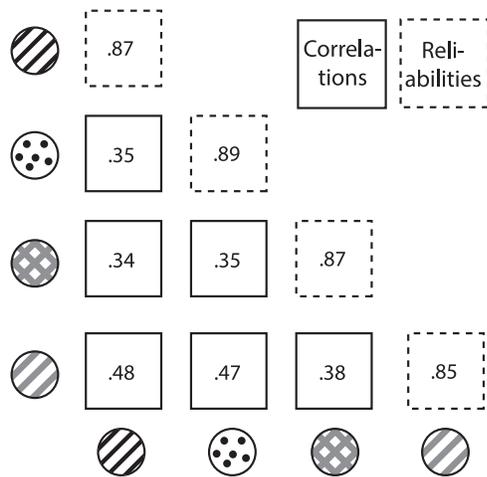


Figure 5. Correlation matrix of average percept durations for the four stimuli of Experiment 2, indicated schematically along the sides of the matrix (the binocular rivalry icon that looks most like the moving plaid icon corresponds to the newly added binocular rivalry stimulus that shares the plaid stimulus' features). Cells on the diagonal show reliabilities; off-diagonal cells show Pearson correlation coefficients.

an even more general one that is shared across different paradigms of perceptual bistability including binocular rivalry? Experiment 2 was designed to answer this question.

## Experiment 2

One perceptual bistability paradigm for which perceptual dominance durations are plausibly correlated with those for binocular rivalry, is moving plaid rivalry (Figure 1B; Cao et al., 2018; Sheppard & Pettigrew, 2006). Thus, in Experiment 2 we included a plaid rivalry condition, while also retaining the binocular rivalry conditions with the small grating stimulus and with the small dot stimulus. In addition, motivated by the relevance of stimulus features that was apparent in Experiment 1, we included a third binocular rivalry condition that used gratings that were identical in every respect to the gratings that made up the bistable moving plaid, except for being presented dichoptically (one grating to each eye) to elicit binocular rivalry.

Figure 5 shows the correlation matrix for these four conditions. As in Experiment 1, reliabilities, shown on the main diagonal, are high, and all between-condition correlations are positive and significant (all two-tailed  $p < 0.004$ ). Although significant, correlations are substantially lower than in Experiment 1 even though two of the conditions involved are the same—a point to which we will return in the Discussion section. The significance of all correlations, including the ones

involving the moving plaid condition, is consistent with the previous finding (Sheppard & Pettigrew, 2006; Cao et al., 2018) that perceptual dominance durations are correlated between binocular rivalry and moving plaid rivalry.

Experiment 1 provided evidence that individual differences in binocular rivalry percept durations reflect, at least, both a specific factor that is sensitive to stimulus features and a second, more general, factor that is common across binocular rivalry variants irrespective of feature content. The data of Experiment 2 now allow us to extend on this finding by arbitrating between two possibilities. The first possibility is that there exist three factors: one factor that is specific to particular binocular rivalry variants, a second one that is general across all binocular rivalry variants but not other forms of bistability, and a third one that generalizes across several kinds of bistability. This third factor would be responsible for the correlations between binocular rivalry and moving plaid rivalry that are evident from Experiment 2. An alternative possibility is that only the first and third of these factors exist, and that there is no general binocular rivalry factor that, in terms of generality, lies between the feature-specific factor and the general bistability factor. In the correlations of Experiment 2 the three-factor scenario would be evidenced by relatively lower correlations for comparisons that include the moving plaid condition (which would be driven only by the general bistability factor but not by either of the binocular rivalry factors) than for comparisons that include only binocular rivalry variants (which would be driven by both the general bistability factor and the general binocular rivalry factor). Under the two-factor scenario, on the other hand, one would expect correlations between different binocular rivalry variants (that have different features, thereby eliminating the feature-specific factor) to be comparable to correlations between a binocular rivalry condition and the plaid rivalry condition. Visual inspection of the figure shows some indication that correlations involving the moving plaid condition are relatively low, but not overwhelmingly so. We took two separate approaches to examining this issue more formally.

First we again used Steiger's test for pairwise comparisons between dependent correlations, asking whether a given binocular rivalry variant is more strongly correlated with a second binocular rivalry variant than it is with the moving plaid condition. Because Experiment 2 included three different binocular rivalry variants and a single moving plaid variant, one can ask this question for six different pairs of correlations. None of these six pairs shows a significant difference when tested in this way (all  $z \leq 1.19$ ; two-tailed  $p > 0.23$ ; the closest to significance comes the comparison involving the correlation between the two

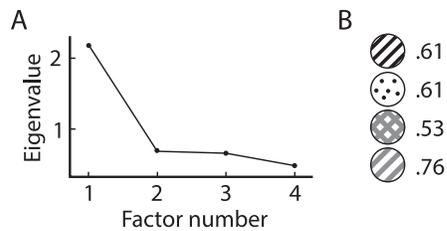


Figure 6. Exploratory factor analysis on the data of Experiment 2. (A) The eigenvalues of the first four factors suggest that only the first factor is important. (B) Factor loadings for the four conditions for the one-factor model.

binocular rivalry grating conditions on the one hand, and the correlation between the original small grating condition and the plaid condition on the other). In other words, this first analysis provides no evidence that correlations between binocular rivalry variants are larger than those involving both a binocular rivalry variant and the moving plaid condition. This finding does not support the idea of a factor that underlies dominance durations for all binocular rivalry variants yet not for the plaid condition.

To examine the same question from a different perspective, and mirroring our approach to the analysis of Experiment 1, we performed an exploratory factor analyses to determine what factor model best explains the data summarized in Figure 5. Based on the pairwise comparisons described above, one might expect this to be a model consisting of a single factor, with comparable factor loadings for all four conditions. Alternatively, the model might also include an additional factor with high loadings for the binocular rivalry conditions but not the moving plaid condition: a general binocular rivalry factor. Figure 6 shows the results of this analysis. Panel A shows the eigenvalues of the first four factors (i.e., a measure of the fraction of the total variance explained by each of the four factors). Two rules of thumb for distinguishing between important and nonimportant factors on the basis of such a plot are to either look for the inflection point in the curve, or to identify which eigenvalues lie above 1. Both rules of thumb would suggest only a single important factor in this case. Figure 6B shows the loadings for this one factor: Data from all four conditions are substantially and positively correlated with it. Finally, the fit between this model and the data is good ( $\chi^2[2] = 0.376$ ;  $p = 0.83$ ), again indicating that a single factor is adequate to explain these data. A confirmatory factor analysis further corroborates this idea by showing that a model with a single, general factor fits the data very well ( $\chi^2[2] = 0.38$  and  $p = 0.83$ ; RMSEA  $< 0.001$ ; CFI = 1.00; SRMR = 0.014). In sum, these results are not consistent with a multiple-factor model, and instead support the idea of only a single factor, shared across all four paradigms examined.

Considered together, the results of Experiment 2 suggest the existence of a mechanism that is shared across distinct binocular rivalry variants as well as plaid motion rivalry, regardless of feature content. They do not provide substantial evidence for any mechanism that would be shared across all binocular rivalry variants yet that is not involved in plaid motion rivalry.

Another issue that Experiment 2 allows us to address is that of feature selectivity. It is conceivable that a mechanism that affects percept durations for both binocular rivalry and moving plaid rivalry is tuned to stimulus features, just like the feature-tuned mechanism underlying binocular rivalry percept durations identified in Experiment 1. If this were the case, then we might expect a relatively high correlation between moving plaid rivalry and the new binocular rivalry stimulus that is made up of the exact same gratings as the moving plaid. But our data provide no evidence for this. Steiger's test showed no significant difference when comparing this correlation to the correlation between the plaid rivalry condition and the original small grating rivalry condition ( $z = 0.35$ ; two-tailed  $p = 0.72$ ), nor when comparing this correlation to the correlation between the plaid rivalry condition and the original small dot rivalry condition ( $z = 0.26$ ; two-tailed  $p = 0.79$ ). Incidentally, the results of the factor analyses reported above, which provided no evidence for a second factor of any kind underlying the data of Experiment 2, also argue against the idea of a feature-specific factor at work in this experiment.

## Discussion

Consistent with existing work (Law, Miller, & Ngo, 2017; Cao et al., 2018), our Experiment 1 shows that individual differences in binocular rivalry percept durations are correlated across different variants of the paradigm. Beyond existing work, the experiment shows these correlations to be substantially reduced when comparing across variants that differ in feature content, but not to be detectably reduced when comparing across variants that differ in retinal location. Our Experiment 2, again consistent with existing work (Sheppard & Pettigrew, 2006; Cao et al., 2018), shows significant correlations between percept durations for binocular rivalry and for a bistable moving plaid paradigm. Again going beyond existing work, this second experiment provides no compelling evidence that such across-paradigm correlations are any smaller than correlations among binocular rivalry variants that differ in stimulus features. The experiment also provides no evidence that the across-paradigm correlations are sensitive to featural overlap between

the binocular rivalry stimulus and moving plaid stimulus used. Taken together, the two experiments invite the view that binocular rivalry is driven by two separable mechanisms: a feature-tuned mechanism that is specific to binocular rivalry and not moving plaid rivalry, and a more general mechanism that is common across both binocular rivalry and moving plaid rivalry and that is insensitive to stimulus features.

The recent Cao et al. (2018) study included a control experiment that is relevant to the present conclusions. Like our study the control experiment involved binocular rivalry variants that could differ in retinal location and/or feature content, and also involved moving plaid rivalry. Apparently at odds with our present findings, the results of that control experiment showed no evidence that differences in stimulus features impact correlations in percept duration any more than changes in retinal location do: Correlations among all binocular rivalry variants were numerically similar to each other and also numerically larger than those between variants of binocular rivalry and of moving plaid rivalry (their figure 9). The best explanation we have for this apparent discrepancy is the relatively low statistical power of that control experiment (the experiment included only 13 participants—considerably fewer than that study’s main experiment and also than our own experiments). Nevertheless, the issue warrants further examination.

Regarding the finding that retinal location plays little to no role in the correlations we observe, it should be remarked that this may change if one considers larger retinal separations than we did. In our Experiment 1 the outer edge of the small stimuli and the inner edge of the large stimuli were nearly abutting, meaning that a subset of retinally tuned neurons would be expected to respond to stimuli of either size. This plausibly reduces the impact of retinal location on our measures. On the other hand, there are certainly also substantial populations of retinally tuned neurons that respond to only the small stimuli or only the large stimuli we used (especially in early visual cortex), yet we observed the impact of retinal location not to be merely small, but to be virtually absent. This would suggest that even larger retinal separations might have little effect. Tentative evidence for this comes from the control experiment by Cao et al. (2018) that was mentioned in the previous paragraph: that experiment yielded little evidence for a role of retinal location even though the separations used were larger than the ones used here.

Another point of discussion is the fact that correlations between binocular rivalry variants were considerably smaller in our Experiment 2 than in our Experiment 1, even when considering the same pair of variants (i.e., the small dot stimulus condition and the small grating stimulus condition). While we are surprised by the size of this difference, there may be a

methodological explanation. In Experiment 1, where all conditions involved two percepts that differed in color, we could give observers general instructions (“report which color you see”) once at the beginning of the experiment and then randomly interleave trials of all conditions, with each condition occurring multiple times across short and randomly placed trials. In Experiment 2 we instead opted to present trials for a given condition in a block-wise fashion, motivated by the fact that instructions necessarily differed between conditions (some percepts were distinguished by motion direction, others by orientation, others by color). Previous research has indicated that an observer’s percept durations can gradually change over the course of an experiment (Mamassian & Goucher, 2005; Van Ee, 2005; Suzuki & Grabowecki, 2007), and this suggests a way in which this difference in design might have caused the observed differences in correlation strengths. In particular, a gradual drift in average percept duration over the course of an experiment session would affect all conditions similarly in the quasi-random design of Experiment 1, but it would differentially impact different conditions in the blocked design of Experiment 2, potentially explaining why between-condition correlations were lower in the latter case. To test the viability of such an explanation, we examined correlations in percept duration between pairs of trials that both used the same stimulus. In both of our experiments each stimulus was presented in six individual trials, and for this analysis we rank-ordered these trials chronologically from one to six for each combination of experiment, observer and stimulus. This allowed us to quantify the across-observer correlation in average percept duration between the two members of a pair of trials that used the same stimulus, and to examine whether this correlation was impacted by how far apart in time the two trials occurred during an experiment session. If gradual changes do cause reduced correlations when comparing data collected farther apart in time, then we expect correlations to be higher for pairs of trials that followed each other more closely in the chronological sequence. The analysis confirmed this expectation: For each of the eight stimuli used across the two experiments, between-trial correlations became smaller as the difference in rank number between the two trials being compared went up. Specifically, the sign of this relationship was numerically negative in all cases ( $-0.59 < r < -0.15$ ), and significantly so in two cases ( $p < 0.05$ , for Experiment 1’s large dot stimulus and Experiment 1’s small grating stimulus). One might, furthermore, suspect this negative dependence to be stronger for Experiment 1, where a given difference in rank number corresponds to a relatively larger separation in time (because trials that used a different stimulus could intervene). Further analyses provide

tentative support for this suspicion: When combining data from all four stimuli used in Experiment 1 the slope of the relationship between correlation coefficient and rank number difference was  $-0.028$ , and this correlation was highly significant ( $p = 0.006$ ). When combining across the four stimuli in Experiment 2 in the same fashion, the slope was numerically less negative ( $-0.020$ ) and the statistical significance of the correlation was marginal ( $p = 0.06$ ). A formal comparison between the two experiments was not possible, however, because of the different stimuli used in the two experiments. In sum, these analyses confirm that the time interval that separates two periods in which percept durations are measured during an experiment session impacts the degree of correlation between the two periods' data, supporting the idea that the comparatively modest between-condition correlations observed in Experiment 2 may be explained by that experiment's use of a blocked design. Aside from supporting this explanation, this analysis provides a qualification to the general understanding (Pettigrew & Miller, 1998; Shannon, Patrick, Jiang, Bernat, & He, 2011; Katyal, He, He, & Engel, 2019), that test–retest reliability of bistable perception dominance durations is high. The test–retest reliabilities are, apparently, affected by the separation in time (within an experiment session) between test and retest.

So, how should the present findings be interpreted in terms of the neural mechanisms responsible for binocular rivalry and those responsible for moving plaid rivalry? There is substantial evidence that binocular rivalry relies in part on events that transpire early in the visual processing hierarchy, with a plausible involvement of inhibition between monocular neurons such as found in primary visual cortex (Blake, 1989; Polonsky, Blake, Braun, & Heeger, 2000; Sengpiel, Bonhoeffer, Freeman, & Blakemore, 2001; Tong & Engel, 2001; Baker & Graf, 2009; Klink, Brascamp, Blake, & van Wezel, 2010). We tentatively identify the specific factor implicated in Experiment 1, which is not shared between binocular rivalry versions that differ in feature content, let alone between binocular rivalry and moving plaid rivalry, with such an early neural mechanism. The idea that a factor associated with early visual processing could be feature-specific, is consistent with existing work on individual differences in basic visual functions. For instance, individual differences in grating detection thresholds at various spatial frequencies are best explained by a model with a number of distinct factors, each associated with a different spatial frequency range (Sekuler, Wilson, & Owsley, 1984; Peterzell & Teller, 1996). Similarly, Cappe, Clarke, Mohr, and Herzog (2014) found correlations to be small or absent among a set of tests of visual performance that used different visual stimuli, even though several of the tests would seem to draw on

visual acuity. In other words, early vision seems to be governed by many, highly specific factors, and this might extend to the feature-specific factor we identified for binocular rivalry. When considered from this perspective, our observation that differences in retinal location do *not* affect correlations in binocular rivalry percept durations, might be more surprising than the observation that differences in feature content do. Rather than interpreting this as evidence that neurons without retinotopic tuning are involved, we speculate that between-observer variance is shared across neurons tuned to various retinal locations. That is, we posit that an individual's neurons that respond to grating stimuli (with a given spatial frequency, etc.) behave somewhat similarly across the retina, but may behave differently than the individual's neurons that respond to moving dot fields.

This leaves the second, more general factor implicated by our work: a factor that lacks feature specificity and that is shared across binocular rivalry and moving plaid rivalry. We propose that this factor maps onto a neural mechanism involved in the representation of surfaces at a binocular level. (We do not suspect even more central variables such as those related to motor behavior, both because we controlled for differences in motor behavior [see Methods] and because we have previously shown a lack of correlation when comparing a very similar binocular rivalry paradigm to yet other forms of perceptual bistability; Brascamp et al., 2018). Several authors have emphasized that binocular rivalry's characteristics do not point exclusively to spatially local mechanisms such as inhibition between monocular neurons that respond to an image's local features. Instead, these characteristics also implicate mechanisms that are responsible for filling in across space the representation of the image surface (Ooi & He, 2005, 2006) or, according to a somewhat different view, for integrating across space the boundaries that delineate the surface (Grossberg, Yazdanbakhsh, Cao, & Swaminathan, 2008). Such mechanisms are not unique to binocular rivalry but rather are plausibly involved generally in segmenting input into surfaces while dealing with occlusions and transparencies (Nakayama, Shimojo, & Silverman, 1989; Shimojo & Nakayama, 1990; Grossberg, Mingolla, & Viswanathan, 2001; Graf & Adams, 2008). The mechanisms have been proposed to operate at a binocular rather than monocular level, perhaps in cortical area V2 (Grossberg, 1987; Van Bogaert, Ooi, & He, 2008; Grossberg et al., 2008). A role of this type of mechanism, not only in binocular rivalry, but also in moving plaid rivalry is plausible given that moving plaid rivalry, while unrelated to interocular conflict, depends on the segregation of surfaces in the face of potential transparencies and occlusions.

Other indirect evidence is also consistent with the idea that our second factor corresponds to some process of achieving or maintaining coherence across space. In binocular rivalry one can sometimes see the currently suppressed visual pattern break into dominance in a local image region and then gradually engulf the entire image as its dominance spreads across space (Wilson, Blake, & Lee, 2001). The speed of this spread turns out to vary between individuals and, indeed, to be strongly predictive of individual variation in average dominance duration (Kang, Heeger, & Blake, 2009). This supports the idea that part of the variation we are measuring in our binocular rivalry conditions is explained by a process of spatial integration, rather than by spatially local mechanisms. Also consistent with this idea is the fact that rivalry dominance depends considerably on the degree of continuity (in terms of, for example, contour orientation or surface curvature) between nearby stimulus regions, rather than on local image features alone (Alais & Blake, 1999; Bonneh, Sagi, & Karni, 2001; Graf & Adams, 2008). With regard to the idea that a putative spatial integration process involved in binocular rivalry would also affect moving plaid rivalry: This idea fits well with evidence that during binocular rivalry such a process seems to operate at a binocular, rather than monocular, level. In particular, when creating a binocular rivalry stimulus in which the component parts of a coherent surface are distributed between the two eyes' images, so that each monocular image includes a complementary set of surface fragments, observers do tend to perceive this coherent surface, indicating that their visual systems can group corresponding image segments regardless of eye of origin (Kovács, Papathomas, Yang, & Fehér, 1996; Alais, O'Shea, Mesana-Alais, & Wilson, 2000; S.-H. Lee & Blake, 2004). In fact, such a tendency toward coherent surface perception is even observed when complementary fragments of a coherent surface are engaged in different forms of bistability (binocular rivalry, monocular rivalry, and “stimulus rivalry”; Pearson & Clifford, 2005), consistent with the view that distinct forms of bistability may draw on a common process of surface integration across space.

If correlations in average percept duration between distinct forms of bistability are, indeed, explained by a relatively universal mechanism involved in representing surfaces, then it becomes interesting that some forms of visual bistability do *not* share this correlation. Although correlations in percept durations have been reported among a variety of perceptually bistable phenomena (e.g., Carter & Pettigrew, 2003; Shannon et al., 2011; Kondo et al., 2012; Fesi & Mendola, 2014; Patel, Stuit, & Blake, 2014), there is now fairly strong evidence that binocular rivalry shows no, or a very small, correlation in percept durations with at least two other bistable phenomena, notably those known as

motion-induced blindness and structure-from-motion rivalry (Gallagher & Arnold, 2016; Brascamp et al., 2018; Cao et al., 2018). It seems reasonable to expect processes involved in the integration and representation of surfaces to also play a role in those phenomena (Graf, Adams, & Lages, 2002; Hsu, Yeh, & Kramer, 2004; Brouwer & van Ee, 2006; Klink, Noest, Holten, Van Den Berg, & Van Wezel, 2009; Devyatko, Appelbaum, & Mitroff, 2016), so our present proposal does not explain this evident lack of correlation. Clearly, further research is needed to more fully understand the specific processes responsible for the observed correlations and why these processes apply to some forms of bistability but not others.

In sum, our results show that at least two factors explain individual differences in binocular rivalry percept durations. One factor is specific to binocular rivalry and, in fact, does not even generalize across binocular rivalry versions that differ in image features; the second is shared between binocular rivalry and moving plaid rivalry and is independent of image features. These results are consistent with the general idea (Blake & Logothetis, 2002; Tong et al., 2006) that binocular rivalry relies both on early mechanisms at monocular processing levels and on later mechanisms that are independent of eye of origin. We specifically propose that these later mechanisms are related to the spatially coherent representation of surfaces.

*Keywords:* binocular rivalry, bistable perception, individual differences, moving plaid rivalry

## Acknowledgments

The authors would like to thank Michael Wertheimer, Julia Evanski, David Clancy, Michelle Rozwadowski, and Nabil Hamati for their role in collecting data for this study.

Commercial relationships: none.

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## References

- Alais, D., & Blake, R. (1999). Grouping visual features during binocular rivalry. *Vision Research*, *39*(26), 4341–4353.
- Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared

- stimulus complexity. *Vision Research*, 47(2), 269–279, <http://doi.org/10.1016/j.visres.2006.09.003>.
- Alais, D., O’Shea, R. P., Mesana-Alais, C., & Wilson, I. G. (2000). On binocular alternation. *Perception*, 29(12), 1437–1445, <http://doi.org/10.1068/p3017>.
- Andrews, T. J., & Purves, D. (1997). Similarities in normal and binocularly rivalrous viewing. *Proceedings of the National Academy of Sciences, USA*, 94(18), 9905–9908.
- Baker, D. H., & Graf, E. W. (2009). On the relation between dichoptic masking and binocular rivalry. *Vision Research*, 49(4), 451–459, <http://doi.org/10.1016/j.visres.2008.12.002>.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145–167.
- Blake, R., & Fox, R. (1974, May 31). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature*, 249(5456), 488–490, <http://doi.org/10.1038/249488a0>.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3(1), 13–21, <http://doi.org/10.1038/nrn701>.
- Bonneh, Y., Sagi, D., & Karni, A. (2001). A transition between eye and object rivalry determined by stimulus coherence. *Vision Research*, 41(8), 981–989.
- Bonneh, Y. S., Donner, T. H., Cooperman, A., Heeger, D. J., & Sagi, D. (2014). Motion-induced blindness and troxler fading: Common and different mechanisms. *PLoS One*, 9(3):e92894, <http://doi.org/10.1371/journal.pone.0092894>.
- Brascamp, J., Sohn, H., Lee, S.-H., & Blake, R. (2013). A monocular contribution to stimulus rivalry. *Proceedings of the National Academy of Sciences, USA*, 110(21), 8337–8344, <http://doi.org/10.2307/42656724>.
- Brascamp, J. W., Becker, M. W., & Hambrick, D. Z. (2018). Revisiting individual differences in the time course of binocular rivalry. *Journal of Vision*, 18(7): 3, 1–20, <https://doi.org/10.1167/18.7.3>. [PubMed] [Article]
- Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The “laws” of binocular rivalry: 50 years of Levelt’s propositions. *Vision Research*, 109, 20–37, <http://doi.org/10.1016/j.visres.2015.02.019>.
- Brascamp, J. W., Van Ee, R., Noest, A. J., Jacobs, R. H., & van den Berg, A. V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. *Journal of Vision*, 6(11):8, 1244–1256, <https://doi.org/10.1167/6.11.8>. [PubMed] [Article]
- Brouwer, G. J., & Van Ee, R. (2006). Endogenous influences on perceptual bistability depend on exogenous stimulus characteristics. *Vision Research*, 46(20), 3393–3402, <http://doi.org/10.1016/j.visres.2006.03.016>.
- Browne, M. W., & Cudeck, R. (1993). Alternative ways of assessing model fit. In K. A. Bollen & J. S. Long (Eds.), *Testing structural equation models* (pp. 136–139). Newbury Park, CA: Sage.
- Cao, T., Wang, L., Sun, Z., Engel, S. A., & He, S. (2018). The independent and shared mechanisms of intrinsic brain dynamics: Insights from bistable perception. *Frontiers in Psychology*, 9, 32–11, <http://doi.org/10.3389/fpsyg.2018.00589>.
- Cappe, C., Clarke, A., Mohr, C., & Herzog, M. H. (2014). Is there a common factor for vision? *Journal of Vision*, 14(8):4, 1–11, <https://doi.org/10.1167/14.8.4>. [PubMed] [Article]
- Carter, O. L., & Pettigrew, J. D. (2003). A common oscillator for perceptual rivalries? *Perception*, 32(3), 295–305.
- Chen, B., Zhu, Z., Na, R., Fang, W., Zhang, W., Zhou, Q., . . . Rao, Y. (2018). Genomic analyses of visual cognition: Perceptual rivalry and top-down control. *The Journal of Neuroscience*, 38(45), 9668–9678, <http://doi.org/10.1523/JNEUROSCI.1970-17.2018>.
- Devyatko, D., Appelbaum, L. G., & Mitroff, S. R. (2016). A common mechanism for perceptual reversals in motion-induced blindness, the Troxler effect, and perceptual filling-in. *Perception*, 46(1), 50–77, <http://doi.org/10.1177/0301006616672577>.
- Fesi, J. D., & Mendola, J. D. (2014). Individual peak gamma frequency predicts switch rate in perceptual rivalry. *Human Brain Mapping*, 36(2), 566–576, <http://doi.org/10.1002/hbm.22647>.
- Gallagher, R. M., & Arnold, D. H. (2014). Interpreting the temporal dynamics of perceptual rivalries. *Perception*, 43(11), 1239–1248, <http://doi.org/10.1068/p7648>.
- Graf, E. W., & Adams, W. J. (2008). Surface organization influences bistable vision. *Journal of Experimental Psychology: Human Perception and Performance*, 34(2), 502–508, <http://doi.org/10.1037/0096-1523.34.2.502>.
- Graf, E. W., Adams, W. J., & Lages, M. (2002). Modulating motion-induced blindness with depth ordering and surface completion. *Vision Research*, 42(25), 2731–2735.
- Grossberg, S. (1987). Cortical dynamics of three-dimensional form, color, and brightness perception: II. Binocular theory. *Perception & Psychophysics*, 41(2), 117–158, <http://doi.org/10.3758/bf03204875>.
- Grossberg, S., Mingolla, E., & Viswanathan, L. (2001). Neural dynamics of motion integration and seg-

- mentation within and across apertures. *Vision Research*, 41(19), 2521–2553, [http://doi.org/10.1016/s0042-6989\(01\)00131-6](http://doi.org/10.1016/s0042-6989(01)00131-6).
- Grossberg, S., Yazdanbakhsh, A., Cao, Y., & Swaminathan, G. (2008). How does binocular rivalry emerge from cortical mechanisms of 3-D vision? *Vision Research*, 48(21), 2232–2250, <http://doi.org/10.1016/j.visres.2008.06.024>.
- Hsu, L.-C., Yeh, S.-L., & Kramer, P. (2004). Linking motion-induced blindness to perceptual filling-in. *Vision Research*, 44(24), 2857–2866, <http://doi.org/10.1016/j.visres.2003.10.029>.
- Hu, L. T., & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling*, 6, 1–55, <http://dx.doi.org/10.1080/10705519909540118>.
- Hupé, J.-M., & Rubin, N. (2003). The dynamics of bistable alternation in ambiguous motion displays: A fresh look at plaids. *Vision Research*, 43(5), 531–548.
- Kang, M. S., Heeger, D., & Blake, R. (2009). Periodic perturbations producing phase-locked fluctuations in visual perception. *Journal of Vision*, 9(2):8, 1–12, <https://doi.org/10.1167/9.2.8>. [PubMed] [Article]
- Katyal, S. He, S., He, B., & Engel, S. A (2019). Frequency of alpha oscillation predicts individual differences in perceptual stability during binocular rivalry. *Human Brain Mapping*, 40(8), 2422–2433, <https://doi.org/10.1002/hbm.24533>.
- Kenny, D. A., Kaniskan, B., & McCoach, D. B. (2015). The performance of RMSEA in models with small degrees of freedom. *Sociological Methods & Research*, 44(3), 486–507.
- Keith, T. (2006). *Multiple regression and beyond*. Boston: Pearson/Allyn and Bacon.
- Kline, R. B. (2005). *Principles and practice of structural equation modeling*. New York, NY: Guilford Press.
- Klink, P. C., Brascamp, J. W., Blake, R., & van Wezel, R. J. A. (2010). Experience-driven plasticity in binocular vision. *Current Biology*, 20(16), 1464–1469, <http://doi.org/10.1016/j.cub.2010.06.057>.
- Klink, P. C., Noest, A. J., Holten, V., Van Den Berg, A. V., & Van Wezel, R. J. A. (2009). Occlusion-related lateral connections stabilize kinetic depth stimuli through perceptual coupling. *Journal of Vision*, 9(10):20, 1–20, <https://doi.org/10.1167/9.10.20>. [PubMed] [Article]
- Kondo, H. M., Kitagawa, N., Kitamura, M. S., Koizumi, A., Nomura, M., & Kashino, M. (2012). Separability and commonality of auditory and visual bistable perception. *Cerebral Cortex*, 22(8), 1915–1922, <http://doi.org/10.1093/cercor/bhr266>.
- Kovács, I., Papathomas, T. V., Yang, M., & Fehér, A. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences, USA*, 93(26), 15508–15511.
- Law, P. C. F., Miller, S. M., & Ngo, T. T. (2017). The effect of stimulus strength on binocular rivalry rate in healthy individuals: Implications for genetic, clinical and individual differences studies. *Physiology & Behavior*, 181, 127–136, <http://doi.org/10.1016/j.physbeh.2017.08.023>.
- Lee, I. A., & Preacher, K. J. (2013). Calculation for the test of the difference between two dependent correlations with one variable in common [Computer software]. Available from <http://quantpsy.org>.
- Lee, S.-H., & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research*, 44(10), 983–991. <http://doi.org/10.1016/j.visres.2003.12.007>
- Leopold, D. A., & Logothetis, N. K. (1996, February 8). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, 379(6565), 549–553, <http://doi.org/10.1038/379549a0>.
- Mamassian, P., & Goutcher, R. (2005). Temporal dynamics in bistable perception. *Journal of Vision*, 5(4):7, 7–15, <https://doi.org/10.1167/5.4.7>. [PubMed] [Article]
- Moreno-Bote, R., Shpiro, A., Rinzel, J., & Rubin, N. (2010). Alternation rate in perceptual bistability is maximal at and symmetric around equi-dominance. *Journal of Vision*, 10(11):1, 1–18, <https://doi.org/10.1167/10.11.1>. [PubMed] [Article]
- Mueller, T. J. (1990). A physiological model of binocular rivalry. *Visual Neuroscience*, 4(1), 63–73, <http://doi.org/10.1017/s0952523800002777>.
- Mueller, T. J., & Blake, R. (1989). A fresh look at the temporal dynamics of binocular rivalry. *Biological Cybernetics*, 61(3), 223–232.
- Nakayama, K., Shimojo, S., & Silverman, G. H. (1989). Stereoscopic depth: Its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception*, 18(1), 55–68, <http://doi.org/10.1068/p180055>.
- Nguyen, V. A., Freeman, A. W., & Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Research*, 43(19), 2003–2008.
- Ooi, T. L., & He, Z. J. (2005). Surface representation

- and attention modulation mechanisms in binocular rivalry. In D. Alais & R. Blake (Eds.), *Binocular rivalry*. Cambridge, MA: MIT Press.
- Ooi, T. L., & He, Z. J. (2006). Binocular rivalry and surface-boundary processing. *Perception*, *35*, 581–603, <http://doi.org/10.1068/p5489>.
- O’Shea, R. P., Parker, A., La Rooy, D., & Alais, D. (2009). Monocular rivalry exhibits three hallmarks of binocular rivalry: Evidence for common processes. *Vision Research*, *49*(7), 671–681, <http://doi.org/10.1016/j.visres.2009.01.020>.
- Patel, V., Stuit, S., & Blake, R. (2014). Individual differences in the temporal dynamics of binocular rivalry and stimulus rivalry. *Psychonomic Bulletin & Review*, *22*(2), 476–482, <http://doi.org/10.3758/s13423-014-0695-1>.
- Pearson, J., & Clifford, C. W. G. (2005). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. *Psychological Science*, *16*(7), 516–519, <http://doi.org/10.2307/40064261>.
- Peterzell, D. H., & Teller, D. Y. (1996). Individual differences in contrast sensitivity functions: The lowest spatial frequency channels. *Vision Research*, *36*(19), 3077–3085, [http://doi.org/10.1016/0042-6989\(96\)00061-2](http://doi.org/10.1016/0042-6989(96)00061-2).
- Pettigrew, J. D., & Miller, S. M. (1998). A “sticky” interhemispheric switch in bipolar disorder? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *265*(1411), 2141–2148, <http://doi.org/10.1098/rspb.1998.0551>.
- Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience*, *3*(11), 1153–1159, <http://doi.org/10.1038/80676>.
- Qian, C. S., & Brascamp, J. W. (2017). How to build a dichoptic presentation system that includes an eye tracker. *Journal of Visualized Experiments*, *127*, e56033–e56033, <https://doi.org/10.3791/56033>.
- Raykov, T., & Marcoulides, G. A. (2006). *A first course in structural equation modeling* (2nd ed.). Mahwah, NJ: Erlbaum.
- Rubin, N., & Hupé, J.-M. (2005). Dynamics of perceptual bistability: Plaids and binocular rivalry compared. In D. Alais & R. Blake (Eds.), *Binocular rivalry*. Cambridge, MA: MIT Press.
- Sekuler, R., Wilson, H. W., & Owsley, C. (1984). Structural modeling of spatial vision. *Vision Research*, *24*(7), 689–700.
- Sengpiel, F., Bonhoeffer, T., Freeman, T. C. B., & Blakemore, C. (2001). On the relationship between interocular suppression in the primary visual cortex and binocular rivalry. *Brain and Mind*, *2*(1): 39–54.
- Shannon, R. W., Patrick, C. J., Jiang, Y., Bernat, E., & He, S. (2011). Genes contribute to the switching dynamics of bistable perception. *Journal of Vision*, *11*(3):8, 1–7, <https://doi.org/10.1167/11.3.8>. [PubMed] [Article]
- Sheppard, B. M., & Pettigrew, J. D. (2006). Plaid motion rivalry: Correlates with binocular rivalry and positive mood state. *Perception*, *35*(2), 157–169.
- Shimojo, S., & Nakayama, K. (1990). Real world occlusion constraints and binocular rivalry. *Vision Research*, *30*(1), 69–80, [http://doi.org/10.1016/0042-6989\(90\)90128-8](http://doi.org/10.1016/0042-6989(90)90128-8).
- Steiger, J. H. (1980). Tests for comparing elements of a correlation matrix. *Psychological Bulletin*, *87*(2), 245–251, <http://doi.org/10.1037/0033-2909.87.2.245>.
- Steiger, J. H. (1989). *EzPATH: A supplementary module for SYSTAT and SYGRAPH*. Evanston, IL: SYSTAT.
- Steiger, J. H. (1990). Structural model evaluation and modification: An interval estimation approach. *Multivariate Behavioral Research*, *25*, 173–180, [http://dx.doi.org/10.1207/s15327906mbr2502\\_4](http://dx.doi.org/10.1207/s15327906mbr2502_4).
- Suzuki, S., & Grabowecky, M. (2007). Long-term speeding in perceptual switches mediated by attention-dependent plasticity in cortical visual processing. *Neuron*, *56*(4), 741–753, <http://doi.org/10.1016/j.neuron.2007.09.028>.
- Tong, F., & Engel, S. A. (2001, May 10). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, *411*(6834), 195–199, <http://doi.org/10.1038/35075583>.
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, *10*(11), 502–511, <http://doi.org/10.1016/j.tics.2006.09.003>.
- Wheatstone, C. (1838). Contributions of the physiology of vision. Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, *128*, 371–394.
- Van Bogaert, E. A., Ooi, T. L., & He, Z. J. (2008). The monocular-boundary-contour mechanism in binocular surface representation and suppression. *Perception*, *37*(8), 1197–1215, <http://doi.org/10.1068/p5986>.
- Van Den Berg, A. V., & Noest, A. J. (1993). Motion transparency and coherence in plaids: The role of

- end-stopped cells. *Experimental Brain Research*, 96(3), 519–533.
- Van Ee, R. (2005). Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry. *Vision Research*, 45(1), 29–40, <http://doi.org/10.1016/j.visres.2004.07.039>.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences, USA*, 100(24), 14499–14503, <http://doi.org/10.1073/pnas.2333622100>.
- Wilson, H. R. (2005). Rivalry and perceptual oscillations: A dynamical synthesis. In D. Alais & R. Blake (Eds.), *Binocular rivalry*. Cambridge, MA: MIT Press.
- Wilson, H. R., Blake, R., & Lee, S. H. (2001, August 30). Dynamics of travelling waves in visual perception. *Nature*, 412(6850), 907–910, <http://doi.org/10.1038/35091066>.