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BRIEF REPORT

Individual differences in the temporal dynamics of binocular rivalry and stimulus rivalry

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Abstract Binocular rivalry and stimulus rivalry are two forms of perceptual instability that arise when the visual system is confronted with conflicting stimulus information. In the case of binocular rivalry, dissimilar monocular stimuli are presented to the two eyes for an extended period of time, whereas for stimulus rivalry the dissimilar monocular stimuli are exchanged rapidly and repetitively between the eyes during extended viewing. With both forms of rivalry, one experiences extended durations of exclusive perceptual dominance that fluctuate between the two stimuli. Whether these two forms of rivalry arise within different stages of visual processing has remained debatable. Using an individual-differences approach, we found that both stimulus rivalry and binocular rivalry exhibited same-shaped distributions of dominance durations among a sample of 30 observers and, moreover, that the dominance durations measured during binocular and stimulus rivalry were significantly correlated among our sample of observers. Furthermore, we found a significant, positive correlation between alternation rate in binocular rivalry and the incidence of stimulus rivalry. These results suggest that the two forms of rivalry may be tapping common neural mechanisms, or at least different mechanisms with comparable time constants. It remains to be learned just why the incidences of binocular rivalry and stimulus rivalry vary so greatly among people.

Keywords Perceptual organization · Visual perception · Visual awareness · Cognitive neuroscience

When the two eyes view dissimilar monocular images (i.e., dichoptic stimulation), those images compete for perceptual awareness. With extended viewing, one image may achieve exclusive dominance for seconds at a time, effectively suppressing the other from awareness. Sooner or later, however, the two stimuli exchange roles, with the previously suppressed image now claiming exclusive dominance. This phenomenon, referred to as *binocular rivalry*, has a long and fascinating history (Wade, 2005), and in recent years scientists and philosophers have become infatuated with rivalry as a possible tool for examining the neural correlates of consciousness (Crick & Koch, 1998; Maier, Panagiotaropoulos, Tsuchiya, & Keliris, 2012; but see Blake, Brascamp, & Heeger, 2014).

For years, a prominent view of binocular rivalry posited that alternations in perception resulted from inhibitory interactions between pools of monocular neurons separately innervated by the two eyes (e.g., Blake, 1989; Levelt, 1968; Verhoeff, 1935). These so-called *eye-based* accounts of rivalry have been opposed, however, by accounts positing that rivalry is a high-level phenomenon transpiring beyond the level of monocular processing (e.g., Walker, 1978). Probably the most impactful challenge to the notion of eye-based rivalry has been provided by Logothetis, Leopold, and Sheinberg (1996). They discovered that rivalry between two dichoptic stimuli could

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be experienced even when those competing stimuli were rapidly and repetitively swapped back and forth between the two eyes. The persistence of stimulus dominance over multiple eye swaps represented a formidable challenge to the view that rivalry is exclusively eye-based. For purposes of exposition, we shall hereafter refer to rivalry triggered by rival stimulation without eye swapping as “conventional binocular rivalry” (CBR), and rivalry triggered by rapid swapping of stimuli between the eyes as “flicker/swap rivalry” (FSR), with the term “flicker” denoting that the incidence of this form of rivalry is maximized when the stimuli being swapped are themselves also flickered very rapidly on and off (Lee & Blake, 1999; Logothetis et al., 1996).

This method described by Logothetis and colleagues for producing slow alternations with dichoptic rival stimulation, together with other intriguing findings implicating interocular grouping during CBR (e.g., Kovács, Papathomas, Yang, & Feher, 1996), has forced a reconsideration of the neural mechanisms of rivalry. To accommodate evidence favoring eye-based rivalry and evidence favoring stimulus-based rivalry, the notion has emerged that CBR and FSR arise from competitive interactions between conflicting neural interpretations emerging at multiple sites within the visual hierarchy (Bhardwaj, O’Shea, Alais, & Parker, 2008; Blake & Logothetis, 2002; Denison & Silver, 2012; Nguyen, Freeman, & Alais, 2003; Tong, Meng, & Blake, 2006; Wilson, 2003). This hybrid view has promoted a satisfying reconciliation of two seemingly incompatible notions of rivalry. At the same time, however, this compromise left many questions unanswered, one of which motivated the experiment reported in this article: Namely, are the dynamics of rivalry produced by the eye-swapping procedure (FSR) comparable to the dynamics of rivalry produced without eye swaps (CBR)? The question is a simple one, but the answer could provide important clues about the nature of the processes involved in these seemingly distinct forms of rivalry. To be sure, we know that dominance fluctuates unpredictably over time with both CBR and FSR (Logothetis et al., 1996). What we did not know before now, however, was whether the temporal patterns of rivalry alternations for a given individual were comparable for the two forms of rivalry. By “temporal patterns,” we mean the rate at which perceptual dominance alternates over time. It is well established that alternation rates vary significantly among individuals when one views a CBR display (Carter & Pettigrew, 2003; Hancock, Gareze, Findlay, & Andrews, 2012). In the present study, we asked whether this is also true for the alternations associated with FSR and, moreover, whether the fluctuations in rate for the two forms of rivalry are correlated among individuals. The results reported here provide affirmative answers to both questions.

Method

Participants

Thirty adult volunteers (21 female, nine male) participated in this experiment, and all but three were naive as to the purpose of the study (the nonnaive participants were the authors). Each participant was screened for good acuity and stereoscopic depth perception. All aspects of the study were preapproved by the Vanderbilt University Institutional Review Board.

Equipment and stimuli

All aspects of the experiment were controlled by a Macintosh computer running MATLAB and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Rival stimuli were presented in the two halves of a gamma-corrected video monitor (21-in. Sony MultiScan; refresh rate: 100 Hz). Sitting in a darkened room, the observer viewed those stimuli through a stereoscope with his or her head position stabilized by a chin and forehead rest situated so that the viewing distance was 96 cm.

For both CBR and FSR, the dichoptically viewed rival stimuli (shown schematically in Fig. 1) were orthogonally oriented, circular sinusoidal grating patterns (diameter = 2.4°, spatial frequency = 3 c/deg, contrast = 30 %, mean background luminance = 32 cd m^{-2}). The contours of one of the gratings were oriented 45 deg clockwise (CW) from vertical, and the contours of the other were oriented 45 deg counterclockwise (CCW) from vertical. One pattern was tinted green and the other was tinted red, and the gratings flickered on/off at 18 Hz. A 3.0° square surrounded each rival stimulus.

For the CBR trials, the assignment of the two dichoptic gratings to the two eyes remained unchanged throughout an entire 1-min trial. For the FSR trials, the dichoptic gratings were exchanged between the eyes rapidly and repetitively (every 333 ms) during the 1-min trial. Extensive pilot work guided by previous studies (Bonneh, Sagi, & Karni, 2001; Denison & Silver, 2012; Lee & Blake, 1999; Logothetis et al., 1996) was carried out prior to the main experiment to identify stimulus conditions that promote robust, unambiguous rivalry for both CBR and FSR.

For the CBR trials, the color and orientations of the rival gratings were counterbalanced between the eyes across trials. For the FSR trials, orientation and color were counterbalanced across trials (meaning on some trials the CW grating was red and on other trials it was green, and vice versa for the CCW grating). The entire experiment consisted of 24 trials, with 12 trials apiece devoted to CBR and to FSR.

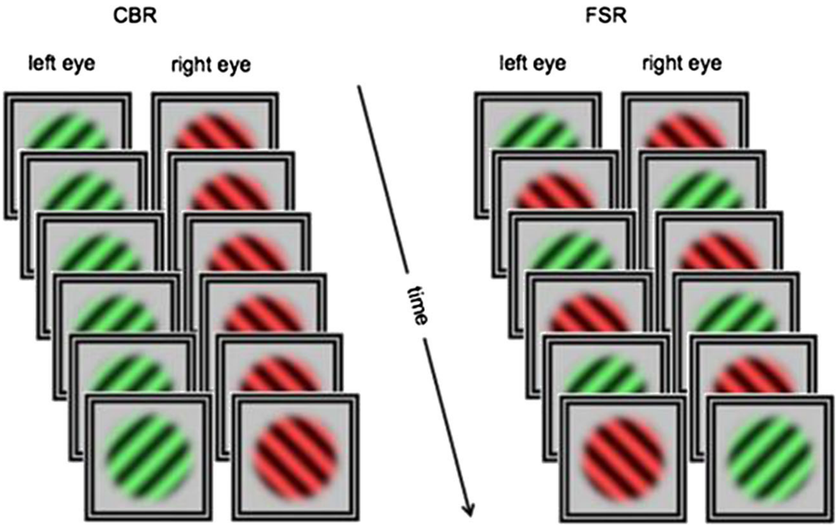

Fig. 1 Schematic of the dichoptic stimuli used in the conventional binocular rivalry condition (CBR) and in the flicker-and-swap rivalry condition (FSR). Red/black and green/black orthogonally oriented gratings (–45° and +45° from vertical) were presented to participants dichoptically. For both the CBR and FSR trials, both gratings flickered on and off at 18 Hz, and during FSR the two gratings were repetitively interchanged between the eyes three times per second

Procedure

At the beginning of the test session, the observer carefully adjusted the mirrors of the stereoscope to achieve accurate binocular alignment of the two dichoptic stimuli, as indicated by constant, unvarying perception of the visual direction of the stimuli when the two eyes' views were alternately covered and uncovered in a reciprocal, repeated fashion. The observer was instructed to report at any time during the test session if binocular alignment was compromised (as indicated by diplopia); this very rarely happened, and when it did the alignment procedure was repeated before testing resumed. After the initial adjustment of the mirrors, the observer next performed a color nulling task in which the relative intensities of the red and green guns of the video monitor were adjusted to achieve an appearance of neutral yellow when the two colors were rapidly interchanged at 15 Hz (heterochromatic flicker photometry). The results from this nulling technique were used to set the intensities of the red and green gratings for that observer.[1] This was then followed by two successive 1-min practice trials in which the observer was introduced to CBR and to FSR. After practice, the two blocks of trials (CBR and FSR) for the main experiment were administered, with the order of blocks being determined for each observer by a coin flip. We blocked these trials, rather than randomly intermixing them, because the tracking instructions were different for FSR and CBR, as we will describe in the next paragraph.

For the CBR block of trials, observers pressed one of two computer keys to track fluctuations in dominance between the red grating (the "1" key) and the green grating (the "3" key). Observers were urged to establish and maintain a fixed criterion for the "dominance" of a colored grating. The relatively small size of the rival targets minimized mixture states, making this instruction easy to understand and follow. For the FSR block of trials, observers used those same two keys to track the dominance of the red and green gratings. In addition, they were instructed to press "2" when they experienced rapid flicker between the red and green gratings (a perceptual state unique to FSR but never experienced with CBR). Fast alternations were carefully explained and illustrated before formal data collection.

For both CBR and FSR trials, a tracking period lasted at least 60 s, with the trial ending once the observer released a key after 60 s had expired (ensuring that the last state duration was not truncated by ending the trial). The CBR and FSR blocks of trials each consisted of 12 60-s tracking periods separated by short rest periods when needed. Within a block of trials, color and orientation were counterbalanced, as was eye for the CBR condition.

Results

We began by examining the distributions of dominance durations associated with CBR and FSR, to compare how our results stacked up against previous results showing that those durations are reasonably well approximated by a gamma distribution (Logothetis et al., 1996; but see Brascamp, van Ee, Pestman, & van den Berg, 2005, for alternative candidate distribution models for rivalry). To generate those histograms, the dominance durations for each observer were normalized by dividing each individual dominance duration, for both the FSR and CBR conditions, by that person's median for his or her CBR and FSR trials combined. By normalizing in this way, we were able to pool results over observers despite individual differences in the actual durations (a point that we

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[1] This procedure, which was performed for each individual in order to match the two colors in effective strength, means that a given observer's two eyes did not necessarily view equal-luminance gratings, nor did all observers view the same luminance values for red and for green.

return to in a moment), while preserving any relative differences between the CBR and FSR durations. As can be seen in Fig. 2, the durations obtained with CBR and with FSR both conform to the typical distribution found for bistable perceptual phenomena (Brascamp et al., 2005). It is worth noting that these distributions also closely resemble the FSR distributions previously reported in the literature (Kang & Blake, 2008; Logothetis et al., 1996), confirming that our displays and tracking instructions are suitable for the purpose of comparing CBR and FSR. In a moment we will comment on the differences in positions of the CBR and FSR distributions along the abscissa.

Our main question of interest concerned the relation between the rivalry dynamics associated with CBR and FSR, and to answer that question we performed a series of different analyses. To start, we computed the Pearson correlation coefficient between the median dominance durations for CBR and FSR across our sample of 30 observers. Note that this correlation was based on the actual median dominance durations, not the normalized values. In calculating median dominance durations, any duration less than a third of a second was excluded, since that would signify a duration faster than the actual swapping time in the FSR condition. The resulting correlation (see Fig. 3) was positive and statistically significant (*r* = .74, *p* < .0001). A similar, strong correlation was found between the FSR and CBR durations across observers when computing correlations on the basis of mean (not median) dominance durations (*r* = .73, *p* < .0001). Moreover, removal of the notable outlier in the data set had virtually no effect on the strength of the relation between the two (*r* = .67, *p* < .0001). To learn whether biases for eye, color, or orientation might be contributing to this highly significant correlation, we computed a bias index for each observer that expresses the extent to which that individual's CBR dominance durations favored one color over the other, favored one eye over the other, or favored one orientation over the other. This index was defined for each of the three stimulus conditions (color, orientation, and eye) as the absolute difference between the median dominance duration for one stimulus value (e.g., the right eye) and the median dominance duration for the other stimulus value (e.g., the left eye); by taking the absolute difference, we were ensuring that the bias index across observers was independent of the direction of that bias for a given observer. We then computed correlations between those bias indices and the incidence of FSR. For none of the three measures of bias was the correlation between FSR incidence and the bias in dominance durations significantly different from zero (color, *r* = –.28, *p* = .14; orientation, *r* = .04, *p* = .83; eye dominance, *r* = –.20, *p* = .29). We concluded that the strong relation evidenced in Fig. 3 was not attributable to systematic, interobserver differences in bias during CBR.

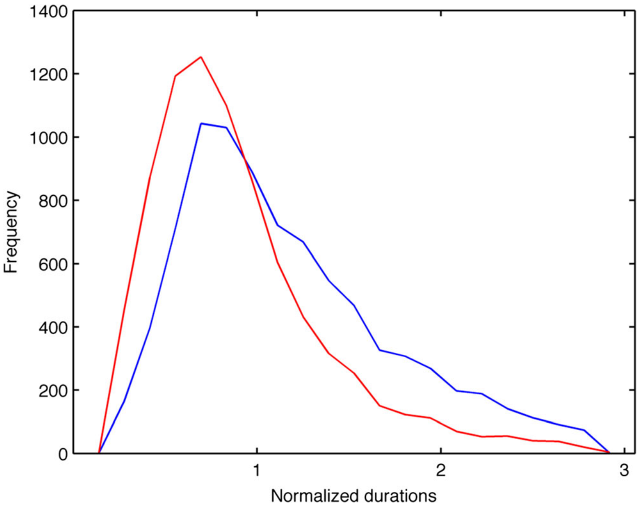

Fig. 2 Normalized frequency histograms of dominance durations measured for CBR (cooler curve) and for FSR (warmer curve). The actual duration values varied substantially among observers (see Fig. 3), so to pool the data over all 30 observers, each observer's individual durations were normalized by dividing each value by that observer's overall median for all of his or her dominance durations for both CBR and FSR. Frequencies were computed over normalized durations, within equally spaced, 0.25-s bins. The rightward displacement of the CBR relative to the FSR curve denotes the overall longer dominance durations obtained with CBR (see Fig. 3)

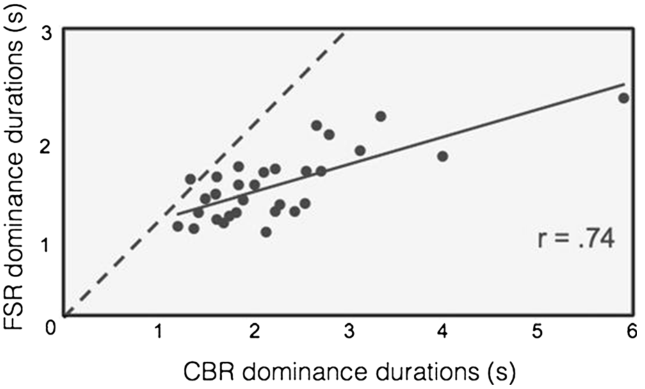

Fig. 3 Scatterplot of median dominance durations for each observer for the CBR condition (abscissa) and the FSR condition (ordinate). The solid line denotes the best-fit linear regression to those data points, the dashed unity line is presented for comparison, and the Pearson correlation value is given in the inset (*r* = .74, *p* < .0001)

From the scatterplot in Fig. 3, it is obvious that the slope of the best-fit regression line falls below the unity line (i.e., the solid line is shallower than the dashed line), implying that the durations of dominance during CBR were longer on average than the durations of dominance during FSR. This difference in average durations was also observed in an earlier study from our lab (Brascamp, Sohn, Lee, & Blake, 2013). In the present data set, the dominance durations measured for CBR were longer, on average, than those for FSR in 29 out of the 30 observers; a *t* test performed on those two arrays of averages returned a highly significant *p* value (*p* < .001).

Next we approached the relation between CBR and FSR from a different angle, hoping to solve a mystery that has puzzled our laboratory for years. In previous work, we have consistently found that some observers have great trouble experiencing stimulus rivalry under seemingly optimal conditions—they primarily perceive very rapid perceptual switches between the two rival targets, as if they are seeing one eye's display or the other's (Brascamp et al., 2013; Kang & Blake, 2008; Lee & Blake, 1999). Why do some people readily experience stimulus rivalry when viewing FSR, whereas others have difficulty seeing anything other than rapid switches? Seeking clues to this puzzle, we used the results from the present study to learn whether there are potentially revealing relations between the incidence of FSR and the rivalry dynamics measured during CBR.

We started by considering the possible perceptual outcomes that one may experience when viewing FSR. One can perceive stimulus rivalry—that is, periods of exclusive visibility of one stimulus or the other, indicating stimulus dominance that transcends multiple swaps of the stimulus between the eyes. Those durations of stimulus dominance, however, are punctuated by periods of time during which one perceives rapid, repetitive interchange between the two rival targets, a perceptual experience that no doubt signifies the dominance of a given eye for a period of time. So, what can we say about those two alternative perceptual experiences and why they differ in incidence among observers?

To pursue an answer to that question, we started by deriving an index of the likelihood of experiencing stimulus rivalry during FSR. That index was defined as the ratio of the sum of the durations of exclusive dominance during an FSR trial to the total duration of that trial; the closer this index came to unity, the greater would be the incidence of stimulus rivalry. Consistent with earlier findings in our laboratory, the incidence of stimulus rivalry varied greatly within our sample of observers, ranging from 94 % down to 31 %. Now, it stands to reason that the incidence of stimulus rivalry during FSR should be inversely related to the average duration of periods during which one experiences rapid alternations, for those durations of rapid alternations contribute to the denominator but not to the numerator of the incidence index. As a sanity check, we computed that correlation among observers, and it was indeed negative and highly significant ($r = -.69$, $p < .00003$).

Next, we asked whether the durations of dominance during FSR were related to the durations of rapid alternations between the two rival targets during FSR. Looking at just the average duration values, periods of rapid alternation were 45 % longer, on average, than were the durations of exclusive dominance during FSR (2.49 vs. 1.72 s, respectively—a difference that is significantly different at the .0003 level, based on a two-tailed t test). Nonetheless, the correlation between those two duration measures revealed that they were positively related ($r = .68$, $p < .0001$). Putting this finding together with the negative correlation between incidence of FSR and the duration of rapid alternation, we arrived at this conclusion: People who more readily experience rivalry when viewing FSR tend to have brief individual periods of exclusive dominance, interspersed with somewhat longer but still relatively brief periods of rapid alternations, whereas people who have trouble experiencing rivalry during FSR (meaning that they predominantly see rapid alternation) have relatively long but infrequent periods of stimulus dominance and long periods of rapid alternations.

Finally, we asked how these individual differences in the incidence of stimulus rivalry when viewing FSR related to individual differences in the rivalry dynamics measured during CBR. For this purpose, we derived an index of the alternation rate obtained with CBR for each observer by dividing the number of state changes per tracking period by the duration of that tracking period; larger values of this index denoted faster alternation rates. The index expressing the likelihood of experiencing stimulus rivalry during FSR was described in an earlier paragraph. The correlation calculated between these two indices revealed that the alternation rate during CBR was positively related to the incidence of stimulus rivalry during FSR ($r = .48$, $p < .0075$). In other words, people who experience faster alternations during CBR tend to be those who are likely to experience stimulus rivalry more often during FSR. In the Discussion section, we consider how these findings can be tied together within a common theoretical framework.

Discussion

Our new finding is the robust correlation among observers in their rivalry dynamics measured with CBR and with FSR. In one respect, this result is not surprising, for it is known that (a) the statistical properties of perceptual state durations are quite similar for a variety of different multistable visual phenomena (Brascamp et al., 2005; Logothetis, 1998), and (b) that individual differences in the dynamics of perceptual alternations are correlated in other tasks involving bistable perception (e.g., Carter & Pettigrew, 2003). Nonetheless, the present findings are important because they clarify what has been a debatable issue ever since Logothetis and colleagues (1996) reported FSR: We now have strong statistical evidence for the existence of a link between CBR and FSR. What can be said about that link? To address that question, we start with an overview of current thinking about the neural bases of rivalry.

One view of rivalry treats CBR and FSR as different manifestations of a common, underlying neural architecture whose function is to derive perceptual interpretations of sensory information (Dayan, 1998; Hohwy, Roepstorff, & Friston, 2008; Leopold & Logothetis, 1999; Sterzer, Kleinschmidt, & Rees, 2009). According to this notion, competition between perceptual interpretations arises when the brain is confronted with conflicting and/or ambiguous sensory signals about what in the world is giving rise to those sensory signals, with the manifestation of this competition being fluctuations in perception over time. CBR and FSR provide two related ways to provoke that competition—related in the sense that both exploit dichoptic stimulation to introduce conflict. The most parsimonious account of CBR and FSR would be to ascribe both forms of rivalry to the same neural mechanisms. Indeed, that was the interpretation initially drawn by Logothetis et al. (1996), and it is also the interpretation recently voiced by Brascamp et al. (2013), albeit with a different narrative twist. For the last decade or so, however, parsimony has taken a back seat for some theorists, the dominant idea being that rivalry associated with dissimilar monocular stimulation results from cooperative/competitive interactions within a distributed network comprising feedforward and feedback connections, with CBR and FSR being mediated by different neural populations within this network (Blake & Logothetis, 2002; Denison & Silver, 2012; Tong et al., 2006; Wilson, 2003). Our results do not settle the question of whether CBR and FSR arise from a single mechanism or from a cascade of distributed mechanisms, but our results do suggest how both forms of rivalry may be interrelated.

To understand the strong relation between periods of exclusive dominance with CBR and with FSR, it is useful to consider what conventional models of CBR have to say about the neural events governing dominance durations during rivalry. In those models, dominance durations are governed by two neural processes, adaptation and inhibition. We consider each of these within the context of our findings, starting with adaptation.

A number of models of rivalry assume that the neural representation of the currently dominant stimulus undergoes self-adaptation, with transitions in rivalry states occurring when the neural activity associated with the dominant stimulus decreases to a point at which the balance of activity is tipped in favor of the previously suppressed stimulus (Alais, Cass, O'Shea, & Blake, 2010; van Ee, 2011); in some models, that tipping point is abetted by intrinsic variability of activity (i.e., noise) within those neural responses (Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009; van Ee, 2009). One influential rivalry model posits that self-adaptation is mediated by slow after-hyperpolarizing potential currents with time constants around 1 s (Wilson, 2003). This form of self-adaptation is plausibly attributable to endogenous, calcium-mediated potassium channels (Liu & Wang, 2001). In the context of CBR and FSR, those endogenous adaptation mechanisms, to the extent that they are under general genetic control throughout the brain, should yield related dominance durations within a given individual. At the same time, the CBR dominance durations for a given individual are reliably longer than the durations for FSR, implying that those adaptation mechanisms are being driven to different degrees dependent on the nature of the stimulus regime provoking rivalry—that is, continuous exposure of a given stimulus to a given eye versus rapid swapping of those stimuli between the eyes.

The second neural ingredient that putatively influences rivalry dynamics is the strength of inhibition exerted by one population of neurons (those activated by the currently dominant stimulus) on another population of neurons (those activated by the currently suppressed stimulus). Specifically, the stronger the inhibition exerted by the dominant stimulus on the suppressed one, the longer on average it will take that suppressed stimulus to overcome the inhibition; this relation between stimulus inhibition and duration is a natural outcome in reciprocal inhibition models of rivalry (e.g., Stollenwerk & Bode, 2003). Perhaps, then, shorter durations of suppression of a given stimulus, which would produce faster alternation rates in CBR, are symptomatic of weaker inhibition that also favors dominance with the FSR regime. This speculation is entirely consistent with the modeling work of Wilson (2003), in which FSR blunts the generation of strong inhibition, and with the psychophysical results of Klink, Brascamp, Blake, and van Wezel (2010) implicating weaker suppression with increased mixture states in CBR. Moreover, this speculation squares with previous findings concerning the depths of suppression (and, by inference, the strengths of inhibition) measured during CBR and during FSR using test-probe techniques. Specifically, suppression depth, as indexed by impairments in probe detection during suppression relative to dominance, is weaker for FSR than for CBR (Bhardwaj et al., 2008; Stuit, Cass, Paffen, & Alais, 2009), implying that inhibition is more potent during CBR than during FSR.

In conclusion, we can now know that CBR and FSR are closely related processes within individuals. What remains to be learned is why the incidence of rivalry alternations, both CBR and FSR, varies so widely among people. A recent study by van Loon et al. (2013) showed a tantalizing correlation between levels of gamma-amino-butyric acid (GABA) concentrations in visual cortex and rates of alternations during bistable perception, including binocular rivalry. So a good place to start the pursuit of individual differences in binocular rivalry would likely be an examination of individual differences in GABA, the main inhibitory neurotransmitter in the brain. We and several other laboratories are currently pursuing this line of investigation.

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