Binocular rivalry and multi-stable perception: Independence and monocular channels

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When discrepant images are shown to the two eyes, each can intermittently disappear. This is known as binocular rivalry (BR). The causes of BR are debated. One view is that BR is driven by a low-level visual process, characterized by competition between monocular channels. Another is that BR is driven by higher level processes involved in interpreting ambiguous input. This would link BR to other phenomena, wherein perception changes without input changes. We reasoned that if this were true, the timing of BR changes might be related to the timing of changes in other multi-stable stimuli. We tested this using combinations of simple (orthogonal gratings) and complex (pictures of houses and faces) stimuli. We also presented simple stimuli in conjunction with a stimulus that induced an ambiguous direction of rotation. We found that the timing of simple BR changes was unrelated to the timing of either complex BR changes or to direction changes within an ambiguous rotation. However, the timings of changes within proximate BR stimuli, both simple and complex, were related, but only when similar images were encoded in the same monocular channels. These observations emphasize the importance of monocular channel interactions in determining the timing of binocular rivalry changes.

Keywords: binocular rivalry, multi-stable perception, perceptual awareness

Introduction

Debate concerning binocular rivalry (BR) has focused on two related issues: the causal neural substrate/s and the possible functional significance. Something of a contemporary consensus has emerged concerning the neural substrate, with most researchers suggesting BR is shaped by activity in multiple structures located at different levels of the human visual hierarchy (Blake & Logothetis, 2002; Haynes, Deichmann, & Rees, 2005; Lee & Blake, 1999; Tong & Engel, 2001; Watson, Pearson, & Clifford, 2004; Wunderlich, Schneider, & Kastner, 2005). However, the functional significance of BR is possibly more contentious.

Some researchers have suggested that intermittent disappearances during BR are driven by a functional process that strives to suppress conflicting defocused images from awareness (Arnold, Grove, & Wallis, 2007; Fahle, 1982). This account links BR to the inter-ocular suppression experienced by strabismics, which can ensure that strabismics *see* information encoded by their better focused eye (Schor, Landsman, & Erickson, 1987; Shors, Wright, & Greene, 1992). It would also link binocular rivalry to the inter-ocular suppression experienced in daily life, when an object selectively obstructs just one eye (Arnold et al., 2007; Arnold, Law, & Wallis, 2008; Changizi & Shimojo, 2008).

A *selective* obstruction of one eye can occur when looking at a distant object at an acute angle, past the nose, or when peeking around a corner. These scenarios are similar to BR, in that unmatched monocular images are encountered. However, unlike BR, perception tends to be persistently dominated by the distant fixated object. Perception of the nose, or of the surface that the person is peeking around, tends to be suppressed. Crucially, in these scenarios the eyes will accommodate on the distant fixated object, rendering images of the nose, or of the proximate obstructing surface, relatively blurred.

Blur is central to one of the most fundamental concepts in BR research: *signal strength* (Levelt, 1968). This refers to a collection of features known to modulate the probability of perceptual dominance during BR. Many signal strength features vary with distance in depth from fixation, including blur (Fahle, 1982; Levelt, 1968), spatial frequency content (Baker & Graf, 2009; Fahle, 1982), and chromatic (Pearson & Clifford, 2004) and luminance (Mueller & Blake, 1989) contrasts. Accordingly, it has been suggested that BR is driven by a functional process that enhances the visibility of fixated objects when conflicting monocular images are encountered, by suppressing the instantaneously weaker signal (Arnold et al., 2007).

According to another view, BR is driven by analyses that strive to interpret often ambiguous sensory input (Andrews & Purves, 1997; Leopold & Logothetis, 1999;

Logothetis, Leopold, & Sheinberg, 1996). According to this perspective, BR is related to other multi-stable phenomena (Andrews & Purves, 1997; Bonneh, Cooperman, & Sagi, 2001; Necker, 1832; Wallach & O'Connell, 1953), wherein perception alternates in the absence of sensory input changes. Evidence for linking diverse multi-stable phenomena is derived from a consideration of the durations for which intermittent perceptual states persist. These typically conform to a gamma distribution (Andrews & Purves, 1997; Carter & Pettigrew, 2003; Miller et al., 2000). Moreover, individuals who report relatively persistent percepts in one form of multi-stable perception tend to report persistent percepts in other forms of multi-stable perception (Carter & Pettigrew, 2003).

While the similar dynamics of diverse multi-stable phenomena might suggest a link (Andrews & Purves, 1997; Carter & Pettigrew, 2003; Miller et al., 2000; Van Ee, 2005), there are also important differences. For instance, BR is less susceptible to control via selective attention than are other multi-stable phenomena (Meng & Tong, 2004; van Ee, van Dam, & Brouer, 2005).

Given the conflicting evidence concerning a link between diverse multi-stable phenomena, we felt it might be beneficial to contrast multi-stable stimuli in a more direct fashion than previously attempted. We envisage three plausible relationships. If diverse multi-stable phenomena are driven by a common process, perceptual alternations in different multi-stable stimuli might synchronize. Alternatively, they might be negatively correlated, as the single mechanism that drives perceptual alternations can only induce one change at a time. A third possibility is that the timing of alternations in different multi-stable stimuli will be unrelated, because diverse multi-stable phenomena are not in fact driven by a common process.

Experiment 1

Observers

Participants included the first author, in addition to six observers who were naive as to the purpose of the experiment. All observers had normal, or corrected-to-normal, visual acuity and stereo vision.

Stimuli

Stimuli were generated using Matlab software in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and displayed on a 19-inch Sony Trinitron G420 monitor (1024 × 768 resolution; 75-Hz refresh rate). All stimuli were viewed from a distance of ~50cm, through an individually adjusted mirror stereoscope, with the participants' head restrained by a chin rest. Stimuli were shown against a black background.

There were three experimental conditions. In all, one of two multi-stable stimuli consisted of pairs of orthogonally oriented Gabor patches. These subtended ~2.3° of visual angle (dva) at the retina, a spatial envelope with a standard deviation subtending ~0.38 dva, a spatial frequency of 2 cycles/dva, a Michelson luminance contrast of 100%, and were centered ~1.25 dva from fixation. We refer to these as the Standard pair. These were positioned either above or below green fixation points (which subtended ~0.6 dva), determined at random on a trial-by-trial basis. Comparison multi-stable stimuli were shown on the opposite sides of the fixation points.

In the Simple BR condition, comparison stimuli were identical to the standard (see Figure 1). In the Complex BR condition, comparison stimuli consisted of pairs of grayscale images, of a house and human face (see Figure 2). The mean luminance of these images was 25 cd/m^2, and they were matched in size to the standard images.
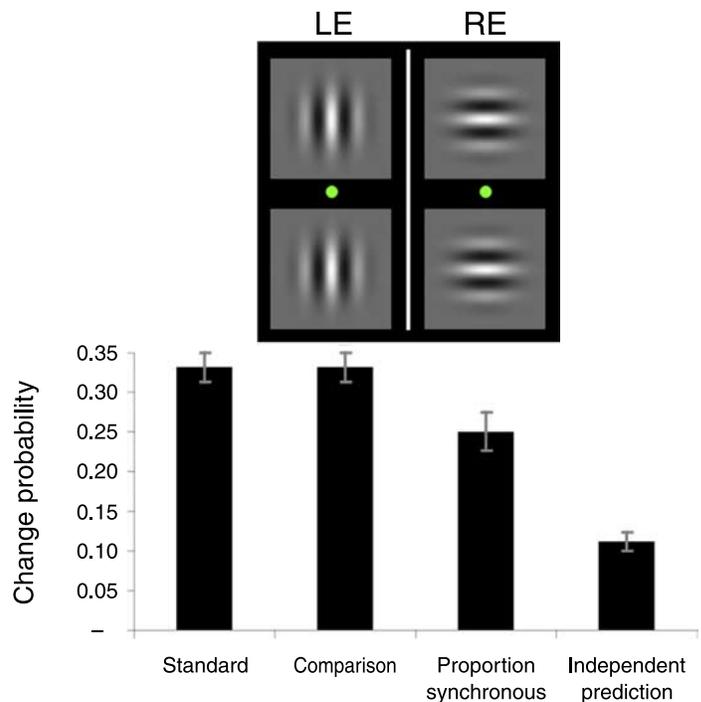

Figure 1. Graphical depiction of, and data from, the Simple BR condition of Experiment 1. The bar plot depicts probabilities of perceptual changes being reported within each 1-s epoch of a stimulus presentation. Observed data are reported for standard and comparison stimuli (see main text). Proportion synchronous refers to the proportion of epochs in which both standard and comparison stimulus changes were reported. The independent prediction refers to the proportion of trials in which this should have been reported if these changes were unrelated. Error bars depict ±1 SEM.
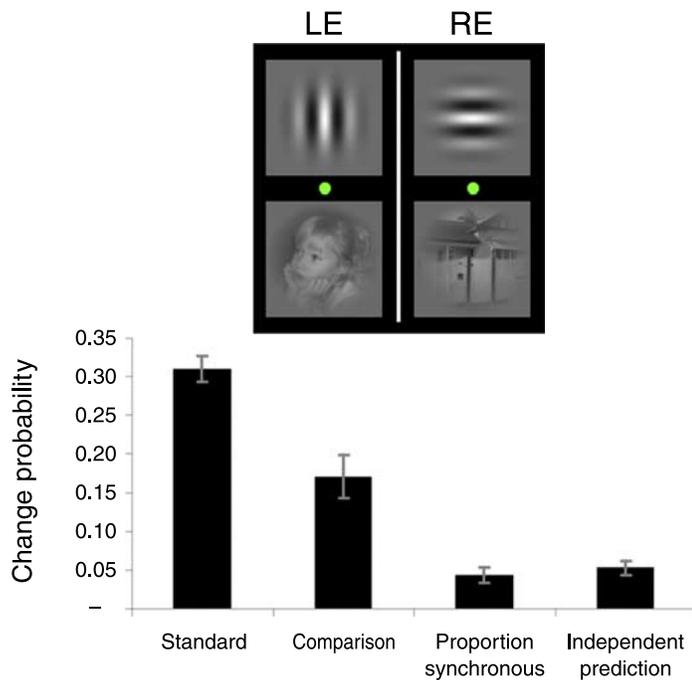
Figure 2. Graphical depiction of, and data from, the Complex BR condition of Experiment 1. Further details as for Figure 1.

Figure 3. Graphical depiction, and data from, Ambiguous Rotation condition of Experiment 1. Further details as for Figure 1.

In the Ambiguous Rotation condition, comparison stimuli consisted of two identical fields, one shown to each eye, of 20 red dots (each subtending ∼0.6 dva), which translated back and forth in a sinusoidal fashion (frequency of 0.75 Hz). Dot starting positions, in terms of the sinusoidal movement cycle, were randomized. Viewing these stimuli created an impression of a rotating cylinder that subtended ∼2.3 dva in width and height (see Figure 3). Crucially, although this stimulus seems to rotate about a vertical axis, the direction of rotation (clockwise or counterclockwise) is ambiguous and seems to intermittently reverse (Miles, 1931).

Procedure

In all conditions, participants simultaneously tracked the perceptual state of each multi-stable stimulus, by pressing one of four keyboard buttons to indicate that a particular perceptual state was dominant. Participants were instructed not to respond if the perceptual state was either mixed or ambiguous. Each stimulus presentation persisted for 2 min. During a run of trials each of the three conditions was presented twice in a random order. Each participant completed three runs of trials.

Results

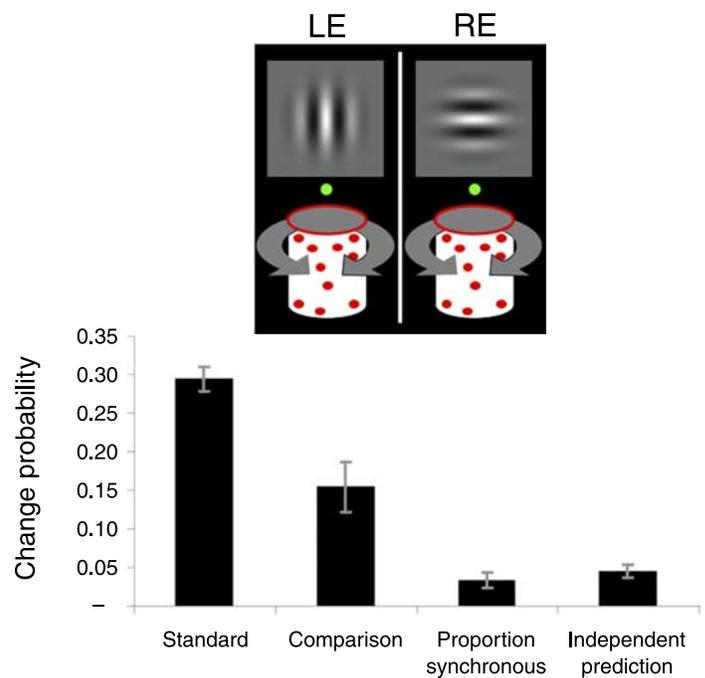We recorded dominance onset times for each perceptual state in each of the three experimental conditions. From these, we calculated individual probabilities for dominance changes being reported in each 1-s epoch during a stimulus presentation. The probability of dominance changes being reported for standard stimuli was 0.33 (±0.02), 0.31 (±0.02), and 0.29 (±0.02) in the Simple BR (see Figure 1), Complex BR (Figure 2), and Ambiguous Rotation (Figure 3) conditions, respectively. The corresponding comparison dominance change probabilities were 0.33 (±0.02), 0.17 (±0.03) , and 0.15 (±0.03).

Based on standard and comparison change probabilities, we were able to *predict* probabilities of synchronous standard and comparison changes being reported (within the same 1-s epoch) assuming independence (standard probability * comparison probability). These were 0.11 (±0.01), 0.05 (±0.01), and 0.04 (±0.01) for the Simple BR (see Figure 1), Complex BR (Figure 2), and Ambiguous Rotation (Figure 3) conditions, respectively. We contrasted these predictions with the proportions of synchronous changes actually reported, being the proportion of epochs in which both standard and comparison changes were reported. These were 0.25 (±0.02), 0.04 (±0.01), and 0.03 (±0.01) for the corresponding conditions. We then calculated individual difference scores and conducted single sample *t*-tests against a value of 0.

The mean difference score for the Simple BR condition (0.14 ± 0.02) was significantly greater than 0 ($t_6 = 6.64$, $p < 0.001$), indicating that synchronous Simple BR changes were reported in spatially offset stimuli more frequently than predicted by the chance co-occurrence of independent events.

Bin size (s)	Proportion synchronous	Independent prediction	Probability
0.75	0.099	0.044	0.011
1.00	0.251	0.112	0.001
3.00	0.664	0.577	0.007

Table 1. Different bin size analyses for Simple BR condition. Data show the proportion of synchronous changes observed, and the proportion predicted, averaged across observers. Probability values relate to the results of one-sample *t*-tests. See main text for further description.

Bin size (s)	Proportion synchronous	Independent prediction	Probability
0.75	0.010	0.013	0.522
1.00	0.043	0.053	0.111
3.00	0.343	0.331	0.442

Table 2. Different bin size analyses for Complex BR condition. Details are as for Table 1. See main text for further description.

Bin size (s)	Proportion synchronous	Independent prediction	Probability
0.75	0.006	0.010	0.172
1.00	0.033	0.045	0.139
3.00	0.257	0.253	0.407

Table 3. Different bin size analyses for Ambiguous Rotation condition. Details are as for Table 1. See main text for further description.

Difference scores in the Complex BR (-0.01 ± 0.01) and Ambiguous Rotation (-0.01 ± 0.01) conditions were *not* significantly different to 0 (Complex BR $t_6 = 1.87$, $p = 0.111$; Ambiguous Rotation $t_6 = 1.70$, $p = 0.139$), indicating that the probability of these changes being reported in the same epoch was consistent with independent events co-occurring at chance.

To demonstrate the generality of our findings, we also conducted analyses wherein we examined the probabilities of both Standard and Comparison changes being reported during 0.75- and 3.0-s epochs. The results of these analyses are depicted in Tables 1–3 for the Simple BR, Complex BR, and Ambiguous Rotation conditions, respectively. As can be seen, the patterns of results for these analyses were qualitatively similar to that obtained in our initial 1.0-s epoch analysis.

Discussion

The results of Experiment 1 suggest that the probability of synchronous perceptual changes, in proximate multi-stable stimuli, was at chance for different forms of multi-stable perception but highly related for identical stimuli.

This last observation is potentially important. In its absence, one might assume that perceptual changes in diverse multi-stable stimuli are governed by common, but spatially localized, processes. Thus, the apparent independence of distinct forms of multi-stable perception, in terms of change timing, would be related to spatial separation, and not to their being governed by distinct processes.

In part, we can counter this criticism by pointing to the diminutive size, and spatial separation, of our stimuli. However, there is also a dissociation, between the independence of change timings in diverse multi-stable stimuli (see Figures 2 and 3) and the high correlation of change timings in identical spatially offset stimuli (see Figure 1). This provides strong evidence for change timings in different forms of multi-stable perception being governed by distinct processes.

One reason why change timings in spatially offset Simple BR stimuli might have been correlated relates to facilitation along collinear image contours (Alais & Blake, 1999; Alais, Lorenceau, Arrighi, & Cass, 2006; Das & Gilbert, 1995; Field, Hayes, & Hess, 1993). To assess whether this was the only factor contributing to synchronized perceptual changes in spatially offset BR stimuli, we conducted a second experiment wherein the orientations of spatially offset Gabors were not collinear (see Figure 4). In addition, we included conditions wherein identical Complex BR stimuli were presented (see Figure 5) and we manipulated whether identical images were shown to the same or different eyes.

Experiment 2

Methods

Methods for Experiment 2 were similar to those for Experiment 1, with the following exceptions.

There were four experimental conditions, Matched Simple BR (see Figure 4a), Mixed Simple BR (see Figure 4c), Matched Complex BR (see Figure 5a), and Mixed Complex BR (see Figure 5c). In the Matched conditions, identical images were presented above and below fixation points viewed by the same eye. Thus, in these conditions, identical images were encoded within the same monocular channels. In Mixed conditions, dissimilar images were presented to the same eyes, resulting in dissimilar images being encoded within monocular channels.

Reporting criteria were simplified, with observers required to press a button when the appearance of a BR stimulus changed, rather than persistently tracking the perceptual status of both stimuli.

During a run of trials, each of the four conditions was presented once, in random order. Each participant
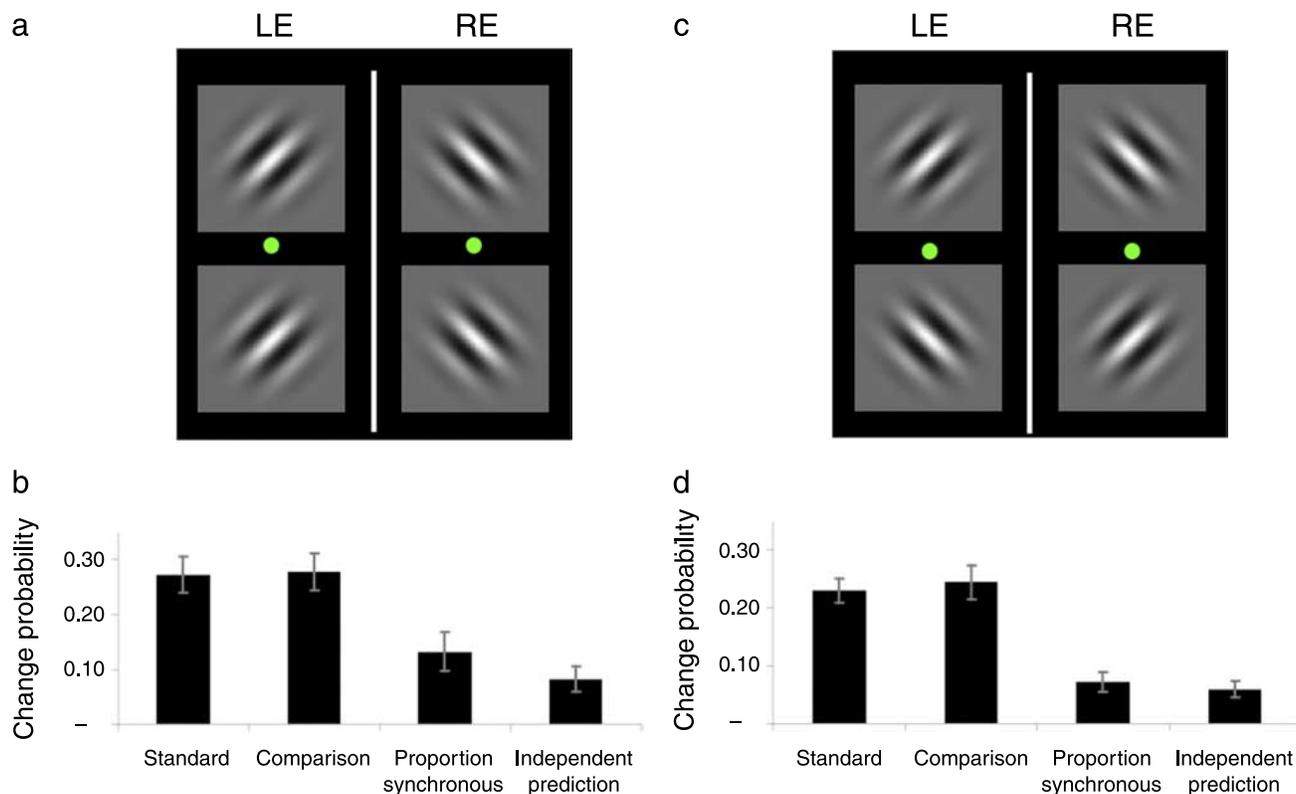
Figure 4. (a) Graphical depiction of the Matched Simple BR condition of Experiment 2. (b) Data from the Matched Simple BR condition of Experiment 2. (c) Graphical depiction of the Mixed Simple BR condition of Experiment 2. (d) Data from the Mixed Simple BR condition of Experiment 2. Further details are as for Figure 1.

completed three runs of trials. The second author participated in this experiment, in addition to the observers who had participated in Experiment 1.

Results

Details concerning data analyses were similar to those described for the Simple BR condition of Experiment 1.

The probability of perceptual changes being reported for standard stimuli was 0.27 (±0.03), 0.23 (±0.02), 0.19 (±0.03), and 0.16 (±0.02) in the Matched Simple BR (see Figure 4b), Mixed Simple BR (see Figure 4d), Matched Complex BR (Figure 5b), and Mixed Complex BR (Figure 5d) conditions, respectively. The corresponding comparison change probabilities were 0.28 (±0.03), 0.24 (±0.03), 0.20 (±0.03), and 0.16 (±0.02).

Probabilities for reporting synchronous standard and comparison changes, assuming independence, were 0.08 (±0.02), 0.06 (±0.01), 0.04 (±0.01), and 0.03 (±0.01) for Matched Simple BR (see Figure 4b), Mixed Simple BR (see Figure 4d), Matched Complex BR (Figure 5b), and Mixed Complex BR (Figure 5d) conditions, respectively. We contrasted these predictions with the proportion of epochs in which synchronous standard and comparison changes were reported. These were 0.13 (±0.04), 0.07 (±0.02), 0.08 (±0.02), and 0.03 (±0.01) for the

corresponding conditions. We then calculated individual difference scores and conducted single sample t-tests against a value of 0.

The mean difference scores for the Matched Simple BR (0.05 ± 0.02) condition was significantly greater than 0 ($t_7 = 2.79$, $p = 0.027$). So too was the mean difference score for the Matched Complex BR (0.03 ± 0.01) condition ($t_7 = 2.63$, $p = 0.034$). These data show that synchronous changes were reported in spatially offset stimuli more frequently than predicted by chance when identical spatially offset images were shown to the same eyes and therefore encoded in the same monocular channels. However, difference scores in the Mixed Simple BR (0.01 ± 0.01) and Mixed Complex BR (0.002 ± 0.005) conditions were not significantly different to 0 (Mixed Simple BR $t_7 = 1.19$, $p = 0.27$; Mixed Complex BR $t_7 = 0.44$, $p = 0.68$), indicating that the probability of synchronous changes being reported in these conditions was at chance.

General discussion

Our first experiment suggested that the timings of perceptual changes in distinct multi-stable stimuli were
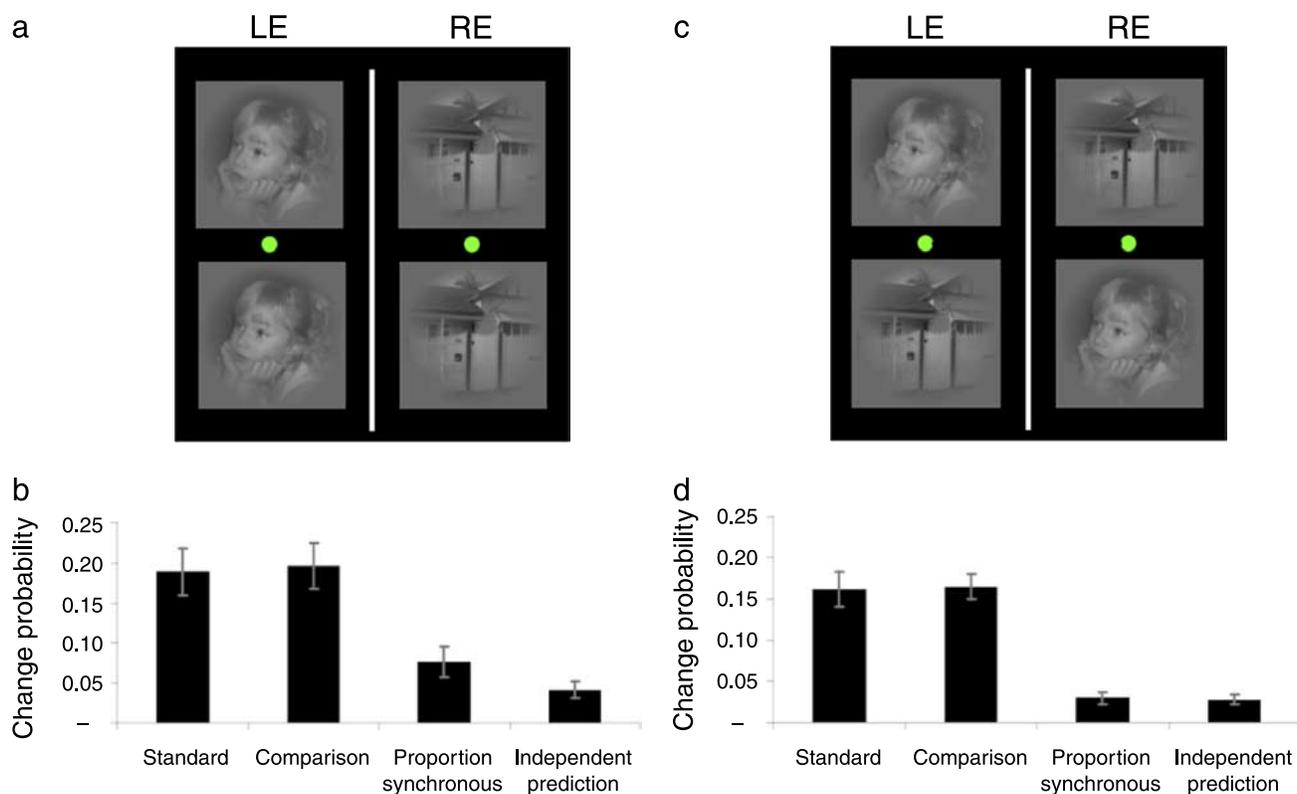
Figure 5. (a) Graphical depiction of the Matched Complex BR condition of Experiment 2. (b) Data from the Matched Complex BR condition of Experiment 2. (c) Graphical depiction of the Mixed Complex BR condition of Experiment 2. (d) Data from the Mixed Complex BR condition of Experiment 2. Further details are as for Figure 1.

independent of one another (see Figures 2 and 3). However, they also suggested that the timings of changes in identical, but spatially offset, multi-stable stimuli were related (see Figure 1).

In our second experiment, we explored this last observation in greater detail. We showed that synchronized changes in identical, but spatially offset, multi-stable stimuli could not be solely attributed to the effects of facilitation along collinear contours (see Figures 4a–4b and 5a–5b). Moreover, we found that a critical factor, leading to synchronized perceptual changes, was that identical images be encoded within the same monocular channels (see Figures 4 and 5).

In general, our data are not consistent with the timing of perceptual changes in different multi-stable stimuli being determined by a common high-level process. Moreover, they add to the body of evidence concerning the importance of monocular channel interactions for BR (Arnold, James, & Roseboom, 2009; Kang, Heeger, & Blake, 2009; van Boxtel, Alais, & van Ee, 2008; van Boxtel, Knapen, Erkelens, & van Ee, 2008; Watson et al., 2004).

The fact that perceptual switches, between face and house dominance, only tended to synchronize when identical images were encoded in the same monocular channels (see Figure 5) is particularly striking. These data suggest that the dominance of even complex images,

known to induce activity in higher levels of the human visual system (Kanwisher, McDermott, & Chun, 1997), involves monocular channel specific interactions. These data are reminiscent of results obtained using biological motion stimuli (Watson et al., 2004). In that context, it was found that motion grouping could induce sets of different colored dots to rival, but this only happened when the sets of dots that defined the biological movement were encoded in the same monocular channels (Watson et al., 2004).

We found no evidence for synchronized perceptual changes when similar images (faces, houses, or simple oriented images) were encoded by different monocular channels. This does not preclude the possibility of such an effect being observed. However, our data suggest that the encoding of similar inputs within common monocular channels must be a stronger determinant of synchronized perceptual changes than is similar appearance per se.

Perhaps the most surprising aspect of our data is that it suggests the existence of processes that enhance the probability of seeing similar images, be they faces or oriented input, when these images are encoded within a common monocular channel. Pattern-based interactions at this level of processing could enhance visibility in cluttered settings, making it easier to detect a continuation of a pattern behind monocular occlusions (Arnold et al., 2007, 2008; Changizi & Shimojo, 2008). Given the

efficacy of facial images in this context, it is tempting to conclude that these pattern-based monocular interactions involve feedback, from binocular face coding mechanisms to monocular V1 channels. However, we cannot exclude an alternate possibility that these interactions occur within the monocular layers of V1, based on matched orientations and frequency spectra.

Our data are less consistent with the results of another study that looked at the grouping of similar percepts across distinct multi-stable stimuli (Pearson & Clifford, 2005). In that study, perceptual rivalry between pairs of orthogonal gratings was induced via three distinct presentation protocols, resulting in what are commonly referred to as monocular (Mackey, 1960), binocular (Helmholtz, 1962), and stimulus (Logothetis et al., 1996) rivalries. Despite distinct presentation protocols in different stimulus regions, similarly oriented and colored gratings tended to dominate across the entire display (Pearson & Clifford, 2005).

There are at least two important differences between our study and the former study that suggested perceptual grouping across different forms of perceptual rivalry (Pearson & Clifford, 2005). First, we have focused on the timing of perceptual changes. If the dominance of a percept in one multi-stable stimulus prompted dominance of a similar percept in another stimulus section after a variable delay, we might not have detected the relationship. Note, however, that we would have detected any tendency to report just one perceptual change per 1-s epoch. This would have resulted in a lower proportion of synchronous changes being reported than predicted by chance.

A second critical difference is that the former study only used stimuli containing collinear contours, which can lead to interactions that mutually enhance contrast detection sensitivity (Das & Gilbert, 1995; Field et al., 1993) and the probability of synchronous perceptual dominance during binocular rivalry (Alais & Blake, 1999; Alais et al., 2006). While we used stimuli containing collinear contours in the Simple BR condition of Experiment 1 (see Figure 1), we avoided doing so in the Matched Simple BR condition of Experiment 2 (see Figures 4a and 4b). The latter condition resulted in proportionally fewer reports of synchronous changes in spatially offset stimuli (0.13 ± 0.04 as opposed to 0.25 ± 0.02), suggesting that collinear contour interactions *do* encourage synchronized perceptual changes (see also Alais et al., 2006). It is possible that such interactions were primarily responsible for driving grouping across different multi-stable stimuli in the former study (Pearson & Clifford, 2005).

According to this last suggestion, the synchronization of perceptual changes across distinct multi-stable stimuli may reflect the degree to which interactions can induce synchronous changes in signal strength. Contrasting very similar perceptual representations, across distinct presentation protocols, might maximize the probability of this happening (Pearson & Clifford, 2005). This need not

imply that the critical modulation is driven by higher level processes. Collinear facilitation could, for instance, be driven by gain modulations of orientation-tuned V1 cells.

The contemporary consensus regarding the neural substrates of BR is that it is multi-faceted, with changes driven by activity in multiple structures located at different levels of the visual hierarchy (Blake & Logothetis, 2002; Haynes et al., 2005; Lee & Blake, 1999; Tong & Engel, 2001; Watson et al., 2004; Wunderlich et al., 2005). While high-level grouping processes undoubtedly shape BR (Alais & Melcher, 2007; Dorrenhaus, 1975), in our view a question remains concerning whether they do so because they are directly responsible for determining perceptual dominance, or because they indirectly modulate activity at a critical low-level site via feedback. Already evidence concerning face adaptation has linked at least some of the efficacy of complex images to feedback (van Boxtel, Alais et al., 2008). More recently, members from our laboratory have shown that propagation along monocular channels is integral to the spread of triggered dominance changes through facial images (Arnold et al., 2009). These and other situations, wherein stimuli encoded by high-level processes engage in monocular channel-specific interactions (Experiment 2, see also van Boxtel, Knapen et al., 2008; Watson et al., 2004), suggest that the efficacy of high-level BR coding effects may rely on feedback to monocular levels of processing.

Conclusions

We found that the timing of simple BR changes was unrelated to the timing of either complex BR changes or to direction changes within an ambiguous rotation. This suggests that perceptual changes in diverse multi-stable stimuli are not driven by a common process. However, the timing of changes within identical BR stimuli were related, but only when similar images were encoded in the same monocular channels. These observations implicate interactions involving monocular channels as being integral to determining the timing of changes during BR.

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