Revisiting individual differences in the time course of binocular rivalry

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Simultaneously showing an observer two incompatible displays, one to each eye, causes binocular rivalry, during which the observer regularly switches between perceiving one eye's display and perceiving the other. Observers differ in the rate of this perceptual cycle, and these individual differences have been reported to correlate with differences in the perceptual switch rate for other bistable perception phenomena. Identifying which psychological or neural factors explain this variability can help clarify the mechanisms underlying binocular rivalry and of bistable perception generally. Motivated by the prominent theory that perceptual switches during binocular rivalry are brought about by neural adaptation, we investigated whether perceptual switch rates are correlated with the strength of neural adaptation, indexed by visual aftereffects. We found no compelling evidence for such correlations. Moreover, we did not corroborate previous findings that switch rates are correlated between binocular rivalry and other forms of bistable perception. This latter nonreplication prompted us to perform a meta-analysis of existing research into correlations among forms of bistable perception, which revealed that evidence for such correlations is much weaker than is generally believed. By showing no common factor linking individual differences in binocular rivalry and in our other paradigms, these results fit well with other work that has shown such common factors to be rare among visual phenomena generally.

Introduction

Binocular rivalry is a perceptual phenomenon that arises when providing incompatible inputs to the two eyes (Blake & Logothetis, 2002). This configuration causes the observer to experience an ongoing cycle, during which perception is alternately dominated by the left eye's input, the right eye's input, or—less frequently—a mixture of both. Interestingly, the rate of this perceptual cycle varies widely across individuals with differences as large as a factor of five being routinely observed (Carter & Pettigrew, 2003; Gallagher & Arnold, 2014), yet it is relatively stable within individuals (although systematic changes over time do happen; Ukai, Ando, & Kuze, 2003; van Ee, 2005; Suzuki & Grabowecky, 2007). Investigating what makes one person a "fast switcher" and another a "slow switcher" can increase scientific understanding of binocular rivalry by identifying factors that drive its perceptual cycle. With this in mind, we set out to use individual differences in binocular rivalry switch rate as a tool to examine the role of neural adaptation in binocular rivalry.

Our starting point was a long-standing theory that holds that binocular rivalry involves two neural populations that correspond to the two predominant percepts and that engage in an interaction governed by mutual inhibition and adaptation (Lehky, 1988; Noest, van Ee, Nijs, & van Wezel, 2007; Wilson, 2007; Seely & Chow, 2011). In particular, the theory states that observers generally perceive only one of the monocular displays at a time because its representation exerts inhibition on the representation that corresponds to the other display. It also states that perception switches after a gradual accumulation of neural adaptation weakens the currently dominant representation to a point at which the alternative representation can overcome the now reduced inhibition. Of note, several studies that focus on individual differences in switch rate have provided support for the inhibition aspect of this theory. In particular, perceptual switch rate has

been reported to correlate with the strength of dichoptic masking, another psychophysical phenomenon thought to be tied to inhibition (Baker & Graf, 2009), and also with the concentration of the inhibitory neurotransmitter GABA in the visual cortex (van Loon et al., 2013; although see Sandberg et al., 2016; Sy, Tomarken, Patel, & Blake, 2016). Although the idea of adaptation as the second key factor is supported by a diverse set of findings (summarized in our Discussion section), existing research has not tested the implication that interindividual differences in binocular rivalry rate may, in part, reflect differences in the dynamics of neural adaptation. Examining this implication was our first objective, so in addition to binocular rivalry, we tested observers on a battery of tasks that included visual aftereffect paradigms that we used as a proxy for indexing the strength of adaptation.

Our second objective was related to the fact that an observer's perceptual switch rate for binocular rivalry has been reported to be predicted by his or her switch rate for other "bistable perception" phenomena (Carter & Pettigrew, 2003; Sheppard & Pettigrew, 2006; Shannon, Patrick, Jiang, Bernat, & He, 2011; Baker, Karapanagiotidis, & Coggan, 2015; Patel, Stuit, & Blake, 2014; but see Gallagher & Arnold, 2014). Like binocular rivalry, these other phenomena, for example, motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001) or Necker cube perception (Boring, 1942), involve a perceptual cycle, during which the observer alternately experiences one or the other interpretation. We reasoned that the reported correlation in switch rates across binocular rivalry and other kinds of bistable perception might reflect a common reliance on mechanisms that center on inhibition and, more importantly in our present context, adaptation. Accordingly, we included two other bistable perception paradigms in our battery with the goal of evaluating correlations among these three forms of bistable perception as well as the ability of our indices of adaptation to explain these correlations.

Finally, in designing our project, we heeded recent evidence that interindividual differences in the reported binocular rivalry cycle are partly explained by interindividual differences in key-press behavior rather than by actual differences in perception (Gallagher & Arnold, 2014). This raises the possibility that any correlations we might find between reported binocular rivalry dynamics and other measures would partly reflect nonperceptual factors that are not our present interest. With that evidence in mind, our battery also included a type of "replay" paradigm (Blake & Fox, 1974). The latter paradigm allowed us to estimate across-observers differences in key-press behavior in the same fashion as Gallagher and Arnold (2014). The paradigm required observers to report perception of an on-screen movie that was meant to mimic the binocular

rivalry experience but that involved no actual conflict or ambiguity, thus providing a ground truth to which to compare reported perception. In other words, we included this replay paradigm to hone in more effectively on individual differences in the actual perception of binocular rivalry, relatively free from any differences in the way different observers report what they see.

Methods

General approach

To examine the questions laid out in the Introduction section, we performed two separate experiments.

In Experiment 1, observers completed a battery of tasks that included, along with a binocular rivalry task and a rivalry replay task, two additional bistable perception tasks and three visual adaptation tasks. (The battery also included further tasks not relevant in the present context.) The bistable perception paradigms were motion-induced blindness (Bonneh et al., 2001) and ambiguous structure from motion (Wallach & O'Connell, 1953). In the former paradigm, a stationary peripheral target is surrounded by a moving "mask" pattern, resulting in alternate perceptual disappearance and reappearance of the target. In the latter paradigm, observers view a two-dimensional sequence of moving elements that is equally consistent with two distinct three-dimensional interpretations, and perception alternates between those interpretations. To assess visual adaptation, we measured the strength of negative afterimages, of a tilt aftereffect, and of a motion aftereffect. These three phenomena are all thought to reflect adaptation in the visual system but in different parts of the visual system. Negative afterimages—the illusory "photo negatives" that can be perceived following exposure to a stationary visual pattern—are thought to reflect adaptation of visual processing channels that encode local luminance (Brindley, 1962; Virsu & Laurinen, 1977). The tilt aftereffect occurs following exposure to an oriented pattern (e.g., clockwise-tilted lines) and is characterized by a shift in perceived orientation away from the orientation of that pattern (e.g., vertical lines are now perceived as tilted counterclockwise; Gibson & Radner, 1937; Clifford, Wenderoth, & Spehar, 2000). The phenomenon is thought to reflect adaptation in orientation-sensitive visual neurons. The motion aftereffect, in turn, follows exposure to an initial moving pattern (e.g., downward motion) and is characterized by a change in the perceived motion direction of a subsequent pattern away from the direction of the adapting pattern (e.g., a stationary image is now perceived as moving upward;

Barlow & Hill, 1963; Anstis, Verstraten, & Mather, 1998). Analogous to the tilt aftereffect, the motion aftereffect is thought to reflect adaptation in motion-sensitive visual neurons.

Observers in Experiment 2 completed a reduced battery that included only the binocular rivalry task, the rivalry replay task, the motion-induced blindness task, the tilt aftereffect task, and the negative afterimage task.

Observers

For Experiment 1, we recruited 131 healthy participants (100 females) from the psychology subject pool at Michigan State University. Average age was 20.2 years (standard deviation 2.9 years, range 18–36 years). For Experiment 2, we recruited 118 healthy participants (98 females) in the same way. The average age in that experiment was 19.6 years (standard deviation 1.6 years, range 18–29 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 tasks were preceded by an informal practice period during which observers performed a shorter version of the task to familiarize themselves with it.

Binocular rivalry

Observers in our binocular rivalry experiment were seated in front of a mirror setup (Brascamp & Naber, 2017) that allowed each eye to view a separate computer monitor. Each monitor displayed a sinusoidal grating (1.2 cycles/degrees of visual angle [c/dva], Michelson contrast 0.5, mean luminance same as background luminance) presented within an annular aperture (inner radius 0.5 dva, outer radius of 1.25 dva). Grating orientation (−45° and 45° 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 to achieve a diagonally upward or downward translation, orthogonal in the two eyes (1.1 dva/s, direction alternated between trials). Background luminance was 31.8 cd/m^2 formed by blending equal luminances from the red and green channels, resulting in a brownish shade. Both gratings were presented within the same set of three nested square frames to facilitate alignment of the eyes. The

three frames had inner and outer diameters, respectively, of 3.8 and 5.8 dva, of 6.8 and 8.5 dva, and of 9 and 12 dva. Each frame was filled with a black and white pattern (one Michelson contrast): a coarse square wave grating for the outermost frame (0.12 cycles/dva), a finer square wave grating for the middle frame (0.8 cycles/dva), and random pixel noise for the innermost frame. Finally, observers were instructed to fixate their gaze on a round fixation mark (radius 0.2 dva) shown in the center of both screens' displays.

During Experiment 1, the stimuli were presented for a total of 12 trials of 45 s each, divided into two sessions. During Experiment 2, trial duration was increased to 50 s, and everything else remained the same. During each trial, observers used three keyboard keys to report their first perception at the start of the trial as well as all perceptual changes. The keys indicated the start of all-red percepts, the start of all-green percepts, and the start of periods during which a mix of both colors was seen.

Binocular rivalry replay

During the replay condition, observers viewed an animation that alternated between the two gratings that were presented dichoptically during binocular rivalry and were now presented binocularly. The animation also included periods during which a mixture of both gratings was shown. In both Experiments 1 and 2, the replay condition was administered as the first and last trial of each binocular rivalry block (so four trials total, 45 s each), and observers were not informed that it was different from the binocular rivalry condition. Animations were constructed by alternating periods of exclusive visibility of either grating (of random duration, uniform distribution between 1 and 4 s) with periods of mixed perception. In an attempt to mimic the spatiotemporal nature of such mixture periods during binocular rivalry (Wilson, Blake, & Lee, 2001), these latter periods started with a segment of the currently nonvisible grating appearing as a straight wave front at the edge of the currently visible grating and moving inward in one of the four cardinal directions (i.e., moving inward from the top, bottom, left, or right edge, randomly chosen). In a further attempt to mimic the unpredictable nature of periods of mixed perception during binocular rivalry (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006), these mixture periods were built up of three consecutive phases, each with random properties. During each phase, the wave front moved at a speed that was randomly chosen (uniform distribution between 0.5°/s and 2.2°/s) except that, in half of the cases, it stood still during the second phase. In another half of those cases, the wave direction reversed for the third phase, thus resulting in a period of mixed visibility inserted between

two periods during which the same grating was seen exclusively (Mueller & Blake, 1989). The duration of the first two phases was randomly selected (uniform distributions between 0.75 and 1.25 s and between 0.5 and 1.75 s, respectively); the third phase lasted however long it took for the wave front to engulf the stimulus entirely.

Motion-induced blindness

Our motion-induced blindness display consisted of a mask and a single target. The mask was a grid of 11 × 11 gray plus signs (6 cd/m^2, diameter 1.1 dva) presented on a lighter gray background (20 cd/m^2), spaced evenly to form a square grid (diameter 12 dva) centered on a round fixation mark (radius 0.4 dva), on which observers were instructed to fix their gaze. The grid revolved around its center at a rate of 0.4 revolutions per second. The target was a Gaussian blob (peak luminance 45 cd/m^2, standard deviation 0.2 dva) presented at 3.5 dva eccentricity. During Experiment 1, observers completed 10 trials of 60 s each, distributed across two sessions. For Experiment 2, the number of trials was increased to 12, and everything else remained the same. Observers were instructed to, during each trial, press and hold down a designated keyboard key whenever they did not perceive the target. Target location alternated between top right (45° from straight above fixation) and top left (−45°) across trials, and the grid's rotation direction alternated between clockwise and counterclockwise every two trials.

Ambiguous structure from motion

Observers viewed a motion sequence that corresponds to an orthographic projection of a transparent sphere (radius 2 dva) with dots randomly speckled on its surface and revolving around its vertical central axis (0.25 revolutions per second). This sequence consisted of 100 white disks (60 cd/m^2, radius 0.05 dva) moving horizontally with a sinusoidal speed profile on a gray background (20 cd/m^2). Observers perceived this display as a three-dimensional sphere that alternated in rotation direction. Observers were instructed to fixate their gaze on a round black fixation mark at the center of this display (1 cd/m^2, radius 0.05 dva) and indicate each trial's initial perceived rotation direction as well as any subsequent perceived reversals using two keyboard keys. During Experiment 1, observers completed a total of 10 trials of 60 s each across two sessions; the condition was not included in Experiment 2.

Negative afterimages

On each trial, observers viewed a Gabor patch for 1.5 s, created by presenting a sine wave grating (Michelson contrast one, mean luminance same as background luminance) within a Gaussian envelope upon a gray background (35 cd/m^2). The relation between the grating's spatial frequency (0.25 c/dva) and the Gaussian's standard deviation (1 dva) was such that less than one grating cycle was visible, resulting in the half dark, half light appearance. The afterimage of such an adapter also looks like a Gabor patch but one that is bright where the adapter was dark and vice versa. We assessed the strength of the afterimage on each trial with a nulling method, in which the display after adaptation immediately changes into a pattern that is a photo negative of the afterimage or, in other words, a low-contrast version of the original adapting pattern itself. By varying the contrast of such a more null pattern across trials and asking observers which side of the display appears lighter, one obtains an index of afterimage strength in terms of the more null contrast required to cancel it out (Leguire & Blake, 1982; Georgeson & Turner, 1985; Kelly & Martinez-Uriegas, 1993). Our nulling procedure had one twist relative to this conventional procedure, motivated by the fact that some observers during pilot work had trouble focusing on the relatively weak and fleeting perceptual impression during the more null period and, instead, reported the appearance of the adapting image itself. To avoid this confusion, we modified the stimulus used during the nulling period. The purpose was to achieve a percept during nulling that could not be confused with the adapting Gabor patch, thus making it easier to instruct observers as to which time period to respond. Our stimulus during the nulling period consisted of a superimposed combination of a Gabor patch that would conventionally be used to null our observers' afterimages and a second Gabor patch that was similar but orthogonal to the more null. This second Gabor patch played no role in canceling the afterimage, and its Michelson contrast was fixed at 0.3. Importantly, however, the inclusion of this second component resulted in a percept, during nulling, of a type of dipole that could not be confused for the adapter stimulus. This dipole was characterized by a dark corner and a bright corner, and the perceived location of the bright corner (or, equivalently, of the dark corner) on a given trial was now diagnostic of whether the more null overpowered the afterimage or not. Accordingly, observers were asked to report on each trial which of four corners (top left, top right, bottom left, or bottom right) appeared brightest. Note that, on any given trial, only two out of these four options could possibly be correct because the orthogonal stimulus unambiguously ruled out the other two. Across consecutive trials, the adapting stimulus was alternately oriented vertically or horizontally (because of our particular more null method, this did not impact the observer's task), and more null contrast was chosen quasi-randomly

from a preset range of values. During Experiment 1, these were 0, 0.12, 0.24, 0.36, 0.48, and 0.60; during Experiment 2, they were 0, 0.10, 0.20, 0.30, 0.40, 0.50, and 0.60. The contrast polarities of the adapter as well as of the orthogonal component during nulling were independently randomized across trials. In both experiments, each more null contrast was presented 12 times. The more null display lasted 0.5 s, immediately followed by a checker pattern aimed at masking any remaining afterimage. The intertrial interval was 3 s, and observers were given a self-timed break after every sequence of 20 trials. Trials were distributed equally across three sessions. Observers were instructed to fixate their gaze at the center of the display throughout each trial, and this was facilitated by a circle (radius 2.2 dva) that framed the stimulus area and a circular fixation mark at its center (radius 0.15 dva).

Tilt aftereffect

On each trial, observers viewed an adapting stimulus composed of a sine wave grating (1.6 c/dva, radius 5 dva, Michelson contrast of one, mean luminance same as background luminance), oriented at 20° (in either direction away from vertical, randomly selected each trial) and presented on a gray background (35 cd/m^2) for 4 s. The adapting grating's phase jumped randomly between eight evenly spaced values every 0.02 s in an effort to provide as strong an adapting stimulus as possible and thereby maximize adaptation. After a blank screen of 0.3 s, the adapter stimulus was followed by a nulling stimulus that lasted 0.2 s with orientations that varied randomly from trial to trial (between −1°, 0°, 1°, 2°, 3°, and 4°, counterbalanced between trials— here 0° means physically vertical, and positive numbers indicate tilts in the direction of the adapting grating). Observers were asked to report the tilt (clockwise or counterclockwise from vertical) during each nulling period. Observers were again instructed to fixate their gaze at the center of the display throughout each trial, and stimuli were again presented within a circle (radius 5 dva) and with a circular fixation mark shown at the center of the display (radius 0.15 dva). In order to discourage observers from reporting the appearance of the adapting stimulus itself, we again took measures aimed at clearly distinguishing the adapting pattern and the nulling pattern. For this reason, the nulling pattern was a type of annulus, formed by presenting a grating pattern (of the same spatial frequency as the adapter, 0.2 Michelson contrast, mean luminance same as background luminance) within a radial Gaussian envelope (envelope centered on a ring with radius 3.1 dva with a standard deviation of 0.73 dva in the radial direction). In addition, the ring surrounding the stimulus area turned from white to green at the moment the more null stimulus appeared. After the

observer responded, the next adapter stimulus appeared 4 s later. Finally, because we initially had the intention to also assess the potential influence of cognitive response biases associated with having seen a tilted adapting stimulus, the trials described above were interleaved with a type of baseline trial. These trials were essentially the same as normal trials, but the adapter stimulus was tilted at a much steeper angle (65° from vertical). Adaptation at such a steep angle typically has little influence on the perception of near-vertical orientations (e.g., Clifford, 2002; O. Schwartz, Hsu, & Dayan, 2007), so any systematic tendency to report vertical, more null stimuli as tilted during these baseline trials could suggest a cognitive response bias. However, no analysis of responses on these baseline trials is included in the present report. Both normal trials and baseline trials were presented nine times per more null orientation during Experiment 1 and 12 times per more null orientation during Experiment 2. In both cases, trials were distributed evenly across three separate sessions and included a self-paced break every nine trials.

Motion aftereffect

Here, the adapting stimulus was a Gabor patch oriented either horizontally or vertically (sinewave grating: 1 c/dva, contrast one Michelson, standard deviation of Gaussian envelope 1.5 dva) with its phase shifting by a quarter period every 0.05 s, corresponding to a 5 dva/s translating motion along a cardinal axis. The stimulus was viewed for 1.5 s, followed after 0.1 s by a more null stimulus. In some experiments that null a motion aftereffect, the more null stimulus moves in the same direction as the adapting stimulus and is aimed at canceling out the illusory motion of the aftereffect (Hiris & Blake, 1992; Lankheet & Verstraten, 1995), analogous to our approach to negative afterimages and the tilt aftereffect. Pilot experiments suggested, however, that motion aftereffects measured in this fashion require adaptation times that were prohibitively long for our project. For this reason, we measured what has been called the "rapid motion aftereffect," which is quantified using a test stimulus of which the perceived direction of motion is bistable, allowing perception to be pushed toward one interpretation or the other depending on the system's adaptation state (von Grunau, 1986; Culham, Verstraten, Ashida, & Cavanagh, 2000; Kanai & Verstraten, 2005). Our test stimulus had the same spatial layout and orientation as the adapter (but lower contrast: 0.5 Michelson), but its phase shifted by steps that were close to half a period (180°) and that occurred every 0.1 s. Because a phase step of 180° is identical regardless of its direction, the motion direction of this type of test stimulus is ambiguous. For phase steps

close to 180°, the visual system tends toward motion perception in the direction corresponding to the shorter phase steps (say, 175° in one direction instead of 185° in the other). Accordingly, we quantified the effect of adaptation by varying the phase step size of the test stimulus across trials (Castet, Keeble, & Verstraten, 2002) to find the point at which both motion directions were perceived equally often (between 47.25°, 33.75°, 22.5°, 13.5°, 2.25°, and −11.25° when expressed in terms of the deviation from 180° and with positive numbers indicating deviations that counteract the effect of adaptation). Analogous to the method described in the section about negative afterimages and for the same reason as given there, in actuality our display during the test period consisted of a superimposition of the test stimulus described above and an orthogonal grating that moved unambiguously (with quarter-period phase steps). The overall appearance was, thus, of a kind of checkerboard with checks that moved diagonally (the combination of unambiguous motion along one cardinal axis and ambiguous motion along the other). Observers indicated, on each trial, which of four possible directions they perceived (top right, bottom right, bottom left, or top left). Note that, analogous to the situation for negative afterimages, only two out of these four options could reasonably be correct on any given trial because the unambiguous orthogonal motion ruled out the other two. The test display was presented for a total of six phase shifts of the ambiguously moving grating. After the observer responded, the next adapter appeared 3 s later, and observers were allowed a self-paced break every six trials. Observers completed a total of 12 trials per test phase step size across three different blocks. The orientation of the adapter alternated across trials between horizontal and vertical, and the directions of the adapter and the orthogonal grating were varied randomly and independently between trials. None of these variables influenced the nature of the observer's task: to report the diagonal motion direction of the checkerboard seen during the test period.

Data analysis

For binocular rivalry and motion-induced blindness, the time course was divided into periods of exclusive and mixed perception on the basis of the key-press records (after reducing sequences of consecutive presses of the same key to only the first key press). As our main measure, we calculated each observer's average percept duration by averaging each interval duration, separating the start of an exclusive percept and the start of the next other exclusive percept (see section "The rivalry replay condition" for an alternative approach). Because the across-observers distribution of resulting average

durations was right-skewed, we took the logarithm before performing further analyses. As our main measure for motion-induced blindness, for each observer we calculated the average duration between each moment of reported disappearance and the subsequent moment of reappearance. We again took the logarithm before further analyses.

For each of the paradigms measuring visual adaptation, we constructed a psychometric curve for each participant. The *y*-axis variable was the proportion of trials on which reported perception of the more null display matched the physical characteristics of the preceding adapting stimulus (i.e., matching either in contrast polarity, orientation, or motion direction, depending on the paradigm), and the *x*-axis variable was the value of the parameter that was varied to cancel out the effect of adaptation (i.e., more null contrast, orientation, or motion step size, depending on the paradigm). Note that, for the negative afterimage paradigm and the motion aftereffect paradigm, with which two out of four response options were objectively incorrect on any given trial (see above), these incorrect responses were not included in this analysis. We fitted a cumulative Gaussian function to the data with an additional free parameter to scale the range of the function to accommodate the fact that the curve may not span the full zero to one range if an observer makes key-press errors no matter how clear the percept is. Aftereffect strength was quantified as the fitted mean parameter, which corresponds to a *y*-axis value of 0.5 or, in other words, to a more null strength that balances out the aftereffect.

For all bistable perception paradigms, an observer's data were discarded if he or she reported fewer than two perceptual dominance periods in total. Also, for binocular rivalry and ambiguous structure from motion, data were excluded if an observer had an overly asymmetrical alternation cycle (more extreme than 3:1 overall predominance ratio for the two percepts). For motion-induced blindness, data were excluded if an observer reported subjective invisibility less than 5% of the time, indicating no robust motion-induced blindness. For each visual adaptation paradigm, data were excluded if the estimated aftereffect strength lay far outside the range of more null strengths actually measured (negative afterimages: Michelson contrast smaller than −0.1 or larger than 0.7, tilt aftereffect: angle smaller than −2.5° or larger than 5°, motion aftereffect: step size smaller than −11° or larger than 48°—negative values here mean in the direction that actually augments the aftereffect rather than counteracting it). For these paradigms, data were also excluded if the psychometric function fitted poorly (sum of squared errors larger than 0.2) or if it was very shallow (standard deviation larger than 0.35, than 3.5°, or than 23° for the three paradigms in order). Finally,

Legend cell: n, r_s, p | n, $\rho^*_{xx'}$

	BR	MIB	SFM	NAI	TAE	MAE
BR	*115* / *.93*					
MIB	102 / .20 / .05	*112* / *.95*				
SFM	108 / .17 / .08	102 / .00 / 1.0	*120* / *.92*			
NAI	102 / -.17 / .09	106 / -.09 / .36	103 / -.12 / .23	*113* / *.86*		
TAE	92 / -.10 / .34	88 / -.24 / .02	100 / .04 / .69	88 / .21 / .05	*103* / *.83*	
MAE	79 / -.02 / .86	74 / .03 / .80	78 / .20 / .08	75 / -.01 / .93	70 / .11 / .36	*82* / *.38*

Bistable perception: BR, MIB, SFM — Adaptation: NAI, TAE, MAE

Table 1. Correlations among bistable perception paradigms and visual adaptation paradigms in Experiment 1. *Notes*: We quantified observers in the former paradigms by the logarithm of their percept duration and in the latter paradigms by the strength of visual aftereffects as measured using a nulling procedure. Cells with solid borders show numbers of observers (top left), Pearson correlation coefficients (r_s; center) and *p* values (bottom right), uncorrected for multiple comparisons. Cells with a *p* value below 0.05 are shown in gray. Cells with dashed borders show numbers of observers (top left) as well as statistical reliability (bottom right) based on split-half correlations corrected using the Spearman–Brown prediction formula ($\rho^*_{xx'}$). BR = binocular rivalry; MIB = motion-induced blindness; SFM = structure from motion; NAI = negative afterimages; TAE = tilt aftereffect; MAE = motion aftereffect.

for the negative afterimage and motion aftereffect paradigms, with which two out of four response options on any given trial were objectively incorrect (see above), data were discarded from observers who gave erroneous responses on more than 33% of the trials. We also repeated our analyses without discarding any data, and this did not change our overall pattern of results.

To calculate statistical reliability for Tables 1 and 2, we separated the data for each condition and observer into two nonoverlapping halves (balancing more null strength values between the two halves when appropriate) and calculated the Pearson correlation coefficient between the two resulting data sets. These correlation coefficients were then converted to reliability values using the Spearman–Brown prediction formula. For the meta-analysis referred to in Figure 2, we calculated *z*-transformed correlation coefficients by applying Fisher's *r*-to-*z* transformation (Field, 2001) to the original studies' *r* values and calculated 95% confidence intervals as described in the same paper. We evaluated whether the data of Figure 2C were homogeneous by calculating Cochran's *Q* statistic (Cochran, 1954) and tested its significance by comparison to a chi-square distribution, in both cases

following descriptions by Field (2001) and Huedo-Medina, Sánchez-Meca, Marín-Martínez, and Botella (2006). Because the hypothesis of homogeneity was rejected, we used Hedges and Olkin's (1985) random-

Legend cell: n, r_s, p | n, $\rho^*_{xx'}$

	BR	MIB	NAI	TAE
BR	*103* / *.96*			
MIB	93 / -.05 / .63	*108* / *.95*		
NAI	85 / -.16 / .14	94 / -.17 / .10	*99* / *.88*	
TAE	87 / .04 / .71	87 / -.08 / .46	78 / -.02 / .86	*95* / *.80*

Bistable perception: BR, MIB — Adaptation: NAI, TAE

Table 2. Correlations among bistable perception paradigms and visual adaptation paradigms in Experiment 2. *Notes*: All methods were the same as for Experiment 1, but Experiment 2 involved different participants and fewer tasks.

effects approach to calculate the across-study effect size and its confidence interval, following the description provided by Field (2001).

Results

Correlations among binocular rivalry, other forms of bistable perception, and visual adaptation

As detailed in the Methods section, the task battery of Experiment 1 included binocular rivalry, two other forms of bistable perception (motion-induced blindness and ambiguous structure from motion), and three tasks aimed at gauging visual adaptation (a negative afterimage task, a tilt aftereffect task, and a motion aftereffect task). This set of tasks allowed us to investigate our two main questions: whether the extent to which an individual exhibits visual adaptation predicts his or her binocular rivalry switch rate and whether such an adaptation factor might explain correlations in switch rate across distinct forms of bistable perception. The task battery of Experiment 1 also included a rivalry replay condition, the results of which are discussed in the following section.

For each bistable perception paradigm, our main measure was the logarithm of each observer's average interval duration between the start of a given percept and the start of the subsequent alternative percept. We took the logarithm because these average durations have a non-normal, right-skewed distribution. Note that we only considered the start times of exclusive (i.e., nonmixture) percepts in this measure so that any time periods during which the observer reported perceiving a mixture percept were simply included in the duration of the preceding exclusive percept. This choice did not importantly affect our results, but for an in-depth discussion on the treatment of mixture percepts, see the following section. For each visual adaptation paradigm, our main measure was the strength of the nulling stimulus needed to cancel out the aftereffect (see Methods).

Table 1 shows the result of Experiment 1. Each cell with a solid border shows the correlation coefficient between two measures at its center, as well as the number of included observers (top left) and the associated *p* value, uncorrected for multiple comparisons (bottom right). For cells on the main diagonal, the bottom right shows a measure's statistical reliability: the correlation coefficient between two data sets formed by taking nonoverlapping halves of each observer's data for a given measure corrected upward for the fact that the correlations of interest are based on all (not

half) of the data. The top left of those cells shows how many observers produced usable data for that measure.

A first conclusion from this table is that all measures have acceptably high reliability, with $\rho_{xx'}^*$ values of 0.83 and higher except motion aftereffect strength ($\rho_{xx'}^* = 0.38$). Given that these reliability values provide a type of upper limit on the correlation coefficient that can be obtained in comparisons involving a given measure, this means that comparisons involving our motion aftereffect strength measure in Table 1 are not very informative. In other words, because of low reliability, this measure cannot correlate very highly with any other measure.

The table also shows that correlations between all pairs of measures from Experiment 1 are near zero to medium in magnitude with absolute correlation coefficients ranging from 0.00 to 0.24. As a result, only three correlations reach a significance level of $p < 0.05$ without correction for multiple comparisons. These are a positive correlation between log percept duration for binocular rivalry and for motion-induced blindness ($r = 0.20, p = 0.04$), a positive correlation between tilt aftereffect strength and negative afterimage strength ($r = 0.21, p = 0.05$), and a negative correlation between tilt aftereffect strength and log percept duration for motion-induced blindness ($r = -0.25, p = 0.02$). None of the correlations is significant after correcting for multiple comparisons.

Thus, the results of Experiment 1 do not provide support for our hypothesis that an individual's binocular rivalry switch rate would be predicted by his or her strength of visual adaptation as indexed by our three aftereffect tasks. In addition, although we had expected to replicate the prior finding that switch rates are robustly correlated between binocular rivalry and other forms of bistable perception, evidence for such correlations is limited in these data with a modest and only marginally significant correlation between binocular rivalry and motion-induced blindness and a slightly weaker and nonsignificant correlation between binocular rivalry and ambiguous structure from motion.

On the other hand, reflecting on these results, we noticed that the three correlations that, although of modest strength, do reach statistical significance in these data (without correction for multiple comparisons) are all consistent with reasonable prior expectations. In particular, the correlation between binocular rivalry rate and motion-induced blindness rate is consistent with the prior report that percept durations may be correlated across distinct bistable perception paradigms, the correlation between tilt aftereffect strength and negative afterimage strength is consistent with the idea that visual adaptation strengths may be correlated across distinct aftereffect paradigms, and the correlation between tilt aftereffect strength and motion-

induced blindness rate is consistent with the idea that observers with stronger adaptation might experience more frequent perceptual switches during bistable perception.

Because we were uncertain about the interpretation of the results of Experiment 1, we performed a second experiment with new participants. We present the results of this experiment here to the extent that they help resolve this uncertainty regarding potential correlations between our tasks and only then move on to presenting findings regarding the rivalry replay condition (which was part of both Experiments 1 and 2).

Experiment 2 involved a reduced battery of only the four tasks that were highlighted as potentially associated by the results of Experiment 1, namely those involving binocular rivalry, motion-induced blindness, negative afterimages, and tilt aftereffects. The results of Experiment 2 are shown in Table 2, following the same format as Table 1. Consistent with Experiment 1, the reliabilities of these measures are acceptably high, and correlations among them are small-to-medium in magnitude. Critically, however, none of the correlations reaches a significance level of $p < 0.05$, including those correlations that did reach significance (uncorrected for multiple comparisons) in Experiment 1. In fact, out of those three correlations, the only one that even has the same sign in both experiments is the one between motion-induced blindness rate and tilt aftereffect strength; the other two do not have the same sign in Table 2 as they did in Table 1.

Considering the data across Experiments 1 and 2 together, there is little evidence that binocular rivalry switch rate is predicted by visual adaptation strength as indexed by our tasks. In addition, there is little evidence that switch rates are correlated between binocular rivalry and other forms of bistable perception or, for that matter, between motion-induced blindness and ambiguous structure from motion. This failure to compellingly corroborate prior reports of correlations between distinct bistable perception paradigms is surprising in light of the good statistical reliability of our measures and also in light of the fact that the data sets of Experiments 1 and 2 are both among the largest used for assessing such correlations in the literature, in terms of both the number of observers and the measurement time per observer (to our knowledge, the only studies with similar observer numbers are those by Shannon et al., 2011, and by Kondo, Kitagawa, Kitamura, Koizumi, Nomura, & Kashino, 2012; the former having a considerably shorter measurement time per observer). The present lack of compelling correlations between bistable perception paradigms is consistent, however, with a previously reported nonreplication (Gallagher & Arnold, 2014). We examine this comparison with existing literature more closely in a later section.
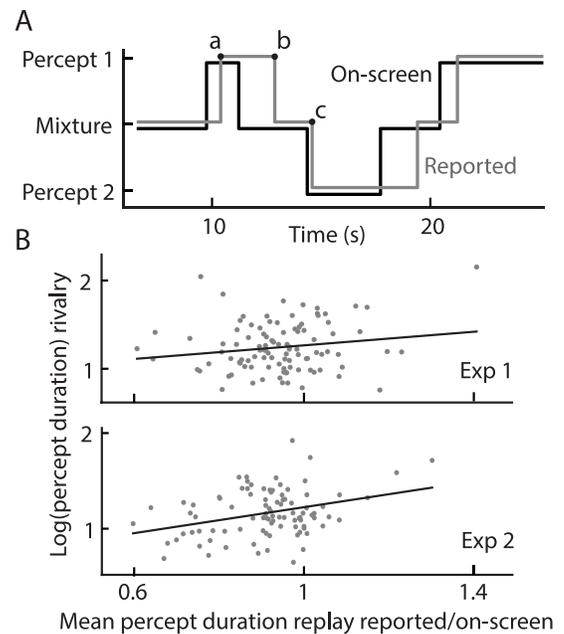

Figure 1. The binocular rivalry replay condition. (A) Example segment of the time course shown in an on-screen animation during the replay condition (black line) and the time course that would be inferred from the observer's key responses to that animation (gray line). See text for the relevance of the letters "a," "b," and "c" along the time course. (B) The *x*-axes of these plots show, for each individual observer, the ratio between the mean percept duration that would be inferred when relying on his or her key presses during the replay condition and the actual mean percept duration of the animation shown on the screen. Individual differences in this value indicate differences in key-press behavior, not perception. The *y*-axes of these plots show the logarithm of individual observers' mean percept durations during actual binocular rivalry as inferred from key presses. The slight positive correlations indicate that variance in key-press behavior explains some proportion of what would otherwise be considered variance in binocular rivalry percept durations. In the main text, we discuss the fact that this proportion is much larger when quantifying percept durations in a different way than we did.

The rivalry replay condition

Both Experiments 1 and 2 included a rivalry replay condition. During this condition, observers binocularly viewed a video in which a stimulus unpredictably alternated between the same two displays that, during the binocular rivalry task, were shown dichoptically (see the section on binocular rivalry replay for details). Observers reported perception in the same way as during the binocular rivalry task: by indicating the onsets of either exclusive percept as well as the onsets of any mixture periods (see Figure 1A for an example). Whereas, during actual binocular rivalry, such key-

press reports would typically be the only index of an observer's perceptual sequence, the video provides a ground truth as to the perceptual sequence during replay. A comparison between this actual sequence and an observer's key presses, therefore, can provide information about that observer's ability to accurately report binocular rivalry–like sequences.

As briefly mentioned in the Introduction section, our battery included a replay condition because Gallagher and Arnold (2014) reported that observers systematically differ in the accuracy with which their key presses represent the actual switch rate shown in a video and, importantly, that this interindividual variance in key-press behavior explains a substantial amount of the interindividual variance in measured perceptual switch rate during actual binocular rivalry. This latter variable is, by necessity, also derived from key-press reports, raising the possibility that any correlation between measured binocular rivalry switch rate and a second variable is, in part, due to nonperceptual factors. Our original intention, therefore, was for the replay condition to allow us to control for nonperceptual contributions to any correlations that we would find involving binocular rivalry (i.e., the replay condition was meant as a safeguard against false positives). In light of the fact that our data do not compellingly show such correlations (Tables 1 and 2) the relevant question becomes whether any such correlations appear after correcting for nonperceptual factors (i.e., the replay condition can act as a safeguard against false negatives).

Figure 1B shows each observer's measured binocular rivalry percept duration as a function of the degree to which that observer's key presses during replay misrepresent the actual duration of on-screen animated percepts (x values smaller than one mean the key presses lead to an underestimation; x values larger than one mean an overestimation). In both Experiments 1 and in 2 (top and bottom panels, respectively), the correlation is positive (Experiment 1: $r = 0.16$, $p = 0.11$; Experiment 2: $r = 0.33$, $p = 0.001$). In other words, observers who reported an average perceptual duration that was longer (or shorter) than the veridical on-screen duration tended to be the same observers who were classified as having longer (or shorter) percept durations in the binocular rivalry task. This result corroborates the conclusion of Gallagher and Arnold (2014) that differences in key-press behavior can contribute to differences in measured binocular rivalry percept duration (which is necessarily inferred from key presses in almost all studies).

We then repeated the analyses underlying Tables 1 and 2 by replacing our original measure of binocular rivalry percept duration with the y-axis residuals of the correlations shown in Figure 1B in an attempt to factor out any contamination of our binocular rivalry data by

variance in key-press behavior. However, this did not importantly impact the results reported in Tables 1 and 2, thus providing no evidence that our lack of observed correlations involving binocular rivalry has to do with individual differences in perception being washed out by individual differences in key-press behavior (data not shown).

At this point it is worth recalling a methodological detail: In the analyses underlying all results shown so far (Table 1, Table 2, and Figure 1B), we have quantified a percept duration as the time interval between the onset of an exclusive percept (e.g., point *a* in Figure 1A) and the onset of the following alternative exclusive percept (e.g., point *c* in Figure 1A). In other words, our definition of a perceptual dominance period, which we call a start-to-start definition, did not treat periods of mixed perception as distinct, instead counting them as part of the preceding exclusive percept. An alternative approach is to quantify a percept duration as the time interval between the onset of an exclusive percept (e.g., point *a* in Figure 1A) and the end of that exclusive percept (e.g., point *b* in Figure 1A): a start-to-finish definition. We mention this distinction because the analysis of Figure 1B turns out more extreme when using this start-to-finish definition, with correlation coefficients of $r = 0.27$ ($p = 0.007$) and $r = 0.53$ ($p < 0.00001$) for the two experiments, respectively. In other words, when using a start-to-finish definition of binocular rivalry percept duration, nonperceptual factors form a larger contribution than they do when using a start-to-start definition. Of note, none of the results of Tables 1 and 2 changes much (data not shown) when using the start-to-finish definition of percept duration regardless of whether we factor out the contribution of key-press behavior, thereby again providing no evidence that our lack of observed correlations involving binocular rivalry has to do with contamination of our data by nonperceptual factors. Nevertheless, this result is important because it warrants further caution regarding the interpretation of existing and future reports of correlations involving individual differences in the time course of binocular rivalry. In particular, the results show that the contribution of nonperceptual factors to those differences can be quite large and depends on the exact way of quantifying this time course. In the Discussion section, we address in more detail the implications of these results beyond the present study.

Meta-analysis of correlations between distinct bistable perception paradigms

The present combination of good statistical reliability but no compelling correlations among bistable perception paradigms (Tables 1 and 2) is surprising
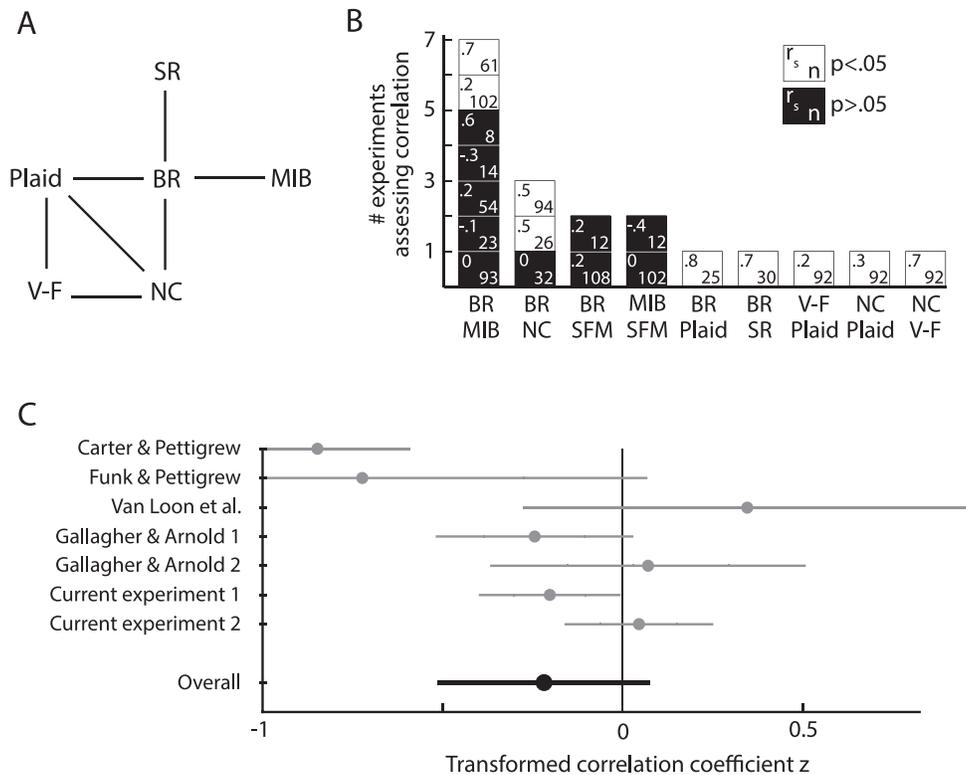
Figure 2. Meta-analysis. (A) Illustration of casual impression from the literature. Each line connects two bistable phenomena between which percept durations have been reported to be significantly correlated. (B) Tally of experiments that reported a significant (white) or a nonsignificant (black) correlation in perceptual switch rate across pairs of perceptual bistability paradigms. Each box corresponds to a single experiment, with Pearson's *r*, rounded to the nearest 10th, in the top left and the number of observers in the bottom right. (C) Meta-analysis of experiments assessing correlations between the switch rates of binocular rivalry and motion-induced blindness. The *x*-axis shows Pearson's correlation coefficients, transformed using Fisher's *r*-to-*z* transform. Error bars indicate 95% confidence intervals. Gray symbols correspond to individual experiment; the correlation estimated on the basis of all experiments together is indicated in black. Experiments included besides our current ones: Carter and Pettigrew (2003), Funk and Pettigrew (2003), Sheppard and Pettigrew (2006), Shannon et al. (2011), Kondo et al. (2012), van Loon et al. (2013), Gallagher and Arnold (2014), Baker et al. (2015), and Patel et al. (2014). Note that the correlation statistics from van Loon et al. (2013) were not reported in that paper but were communicated to us by Anouk van Loon, that the correlation from Funk and Pettigrew (2003) is included as having a *p* value of 0.10 based on the correlation strength and observer number reported in the paper even though the *p* value reported in the paper is smaller, and that for the comparisons from Kondo et al. (2012) that involve a bistable plaid we used averages across the two distinct bistable plaid tasks that were included in their battery. BR = binocular rivalry; MIB = motion-induced blindness; SFM = structure from motion; SR = stimulus rivalry (Logothetis et al., 1996); Plaid = bistable plaid (Hupé & Rubin, 2003); V-F = Rubin's vase–face illusion (Rubin, 1915); NC = Necker cube.

given the general understanding in the literature that substantial correlations exist (e.g., see review pieces by Blake & Wilson, 2011; Blake, 2014; Brascamp, Klink, & Levelt, 2015). The present nonreplication as well as the earlier nonreplication by Gallagher and Arnold (2014) motivated us to more thoroughly examine the findings that underlie this general understanding. In Figure 2A, each line connects a pair of bistable perception phenomena that have been reported to be correlated in terms of perceptual time course (BR stands for binocular rivalry; see caption for the meaning of other abbreviations). Based on a cursory look at the literature, then, the impression would arise of essentially one interconnected family of phenomena

whose time courses are all predictive of each other. Figure 2B qualifies this impression. For each pair of bistable phenomena that have been compared, this figure tallies the number of experiments that did (white) or did not (black) find a statistically significant (*p* < 0.05) correlation in perceptual switch rate or an equivalent measure (our own Experiments 1 and 2 included). Although not a formal meta-analysis, this examination suggests a different story because it shows that several pairs of phenomena have been compared only a single time and that those pairs that have been compared multiple times have all yielded an appreciable proportion of null results (the figure includes null results from Gallagher & Arnold, 2014, and the present

work as well as some that were not explicitly reported as null results in the original studies; see figure caption).

Figure 2C shows a more formal meta-analysis of the comparison between binocular rivalry and motion-induced blindness. We chose this pair because it is the only one that has been examined in a sufficient number of experiments to warrant such an analysis. Existing experiments are ordered chronologically along the *y*-axis, and the *x*-axis shows the correlation coefficient obtained in each experiment (transformed, negative numbers mean a positive correlation), including 95% confidence intervals. The figure also shows the correlation coefficient as computed across all studies (black). A first observation is that the 95% confidence interval of this across-experiment correlation coefficient includes zero, thus providing no support for the idea that the time courses of binocular rivalry and motion-induced blindness are correlated on an observer-to-observer basis. A second observation is that there are substantial differences across experiments: distinct experiments are associated with quite different correlation coefficients even in cases in which the confidence intervals are narrow. This second observation is corroborated by statistical analysis: Cochran's *Q* (Cochran, 1954) is 35.4, rejecting the hypothesis that these experiments differ only by sampling error while all estimating the same population effect size (*p* < 0.00001). We return to potential reasons for this heterogeneity in the Discussion section.

Discussion

Our experiments assessed across-observers correlations among six measures: the time courses of three different kinds of perceptual bistability and the strengths of three different kinds of visual aftereffects. Our original objectives were to evaluate (a) whether individual differences in the time course of binocular rivalry are associated with individual differences in adaptation strength as indexed by visual aftereffects and (b) whether such a contribution of adaptation could explain correlations in time course between binocular rivalry and other forms of bistable perception. Although all but one measure had good statistical reliability, the data revealed no compelling evidence for correlations among any of the measures (Tables 1 and 2). Not only did this offer no support for our hypothesis that individual differences in adaptation dynamics contribute to differences in the temporal properties of binocular rivalry, it also did not corroborate existing reports that perceptual switch rates are correlated across forms of perceptual bistability. We did, on the other hand, find support for a previous report that individual differences in measured

binocular rivalry rate, besides reflecting genuine differences in perception, in part reflect individual differences in key-press behavior. Going beyond this observation, our results showed that the extent of this nonperceptual contribution depends on the exact measure that is used to quantify the binocular rivalry time course. Motivated by our inability to find correlations in perceptual switch rate across forms of perceptual bistability, we performed a meta-analysis of existing work and found that evidence for such correlations in the literature is mixed and overall is not compelling.

We divide our discussion of these findings into methodological aspects, concerning the ways researchers investigate these topics, and conceptual aspects, concerning the implications for our understanding of binocular rivalry and other forms of perceptual bistability.

Methodological points

Replay conditions and nonperceptual factors

Our results indicate that interindividual variability in measured binocular rivalry dynamics is "contaminated" by nonperceptual factors and that the magnitude of this contamination may depend on whether one lumps periods of exclusive perceptual dominance and periods of mixed perception together (e.g., our start-to-start measure is relatively uncontaminated) or whether one keeps them separate (e.g., the start-to-finish measure is relatively contaminated). A probable reason for this is illustrated by the example time course of Figure 1A. In this example, the observer overreports the duration of exclusive percepts and underreports that of mixture percepts. Apparently, this observer employs some degree of slack in his or her criterion as to what constitutes an exclusive percept, and observers may well differ in the extent to which they do this. This provides a relatively innocuous explanation for the substantial nonperceptual contribution to measures that keep periods of mixed perception and exclusive perception separate. On the other hand, a contribution of similar magnitude to measures that lump these periods together would require something more drastic: It would require observers to altogether omit entire dominance periods in their key-press reports or to spuriously insert them. It makes intuitive sense that these more drastic events are not common and, therefore, that measures that do lump together exclusive perception and mixed perception are less contaminated by nonperceptual factors. On a side note, this observation has no bearing on the question of whether periods of mixed perception should be seen as distinct or not from a functional perspective.

In light of the above considerations, we reexamined the literature that we previously reviewed for Figure 2,

now with a focus on how individual researchers treated mixed perception in their calculation of the binocular rivalry time course. There was no consistency across studies in how mixed perception was treated, nor was there an emphasis on the potential importance of this issue. For instance, observers in Shannon et al.'s (2011) study did not have the option of reporting periods of nonexclusive perception, thus leading to a measure of perceptual switch rate that is essentially the reciprocal of our start-to-start measure. Observers in Baker et al.'s (2015) study did have this option, and the authors calculated a start-to-finish measure of percept duration. Observers in the Gallagher and Arnold (2014) study, to give a final example, did have the option of reporting mixed perception, but we could not find a description of how these reports were treated in the subsequent computation of perceptual switch rate. Considering our present findings, we recommend that researchers in future work do keep track of mixed perception separately and carefully consider options for their treatment during the data-analysis stage. This recommendation should not detract from the fact, however, that binocular rivalry showed no compelling correlations with either visual aftereffects or other forms of perceptual bistability in our data regardless of how we treated periods of mixed perception.

As a final remark about mixed perception, we note that some studies specifically examine individual differences in the predominance of mixed perception during binocular rivalry rather than focusing on the durations of exclusive percepts. For instance, several studies have examined whether this predominance is altered in autism (Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013; Said, Egan, Minshew, Behrmann, & Heeger, 2013). It should be clear from the above that the exact same nonperceptual factors that affect start-to-finish measures of perceptual dominance also influence estimates of the predominance of mixed perception so that studies in this category would particularly benefit from a replay condition to explicitly measure the extent of this influence from observer to observer (note that the Robertson et al. study did include a replay condition).

Measuring motion-induced blindness

The analyses associated with Figure 2C indicate that the results from studies comparing binocular rivalry to motion-induced blindness are heterogeneous: The outcomes of those studies vary by more than would be expected if they all provided estimates of the same population effect size. In other words, those studies do not seem to have measured the same thing. We have no definitive answer as to what causes this, but we provide two observations regarding motion-induced blindness that can help guide future research.

First, although the time course of bistable perception typically describes an alternation between two perceptual states (plus potential transition periods between them), motion-induced blindness displays can include more than one peripheral target, and the subjective visibility of these targets can fluctuate with a certain degree of independence (Bonneh et al., 2001). With more than one target, therefore, there are more than two perceptual states, characterized by combinations of visibility and invisibility of the individual targets. Several of the studies reviewed in Figure 2C (Carter & Pettigrew, 2003; Funk & Pettigrew, 2003; Gallagher & Arnold, 2014) included multiple targets in their motion-induced blindness displays and then reduced the resulting number of reportable states to two by asking observers whether all targets were simultaneously visible (one reportable state) or not (the second reportable state). In such a situation, the rate of key presses can depend in a nonobvious way on the rate at which an individual target cycles in subjective visibility—a dependence that is influenced, by both the timing of this cycle for a given target and the correlation between these cycles across different targets. This complicates interpretation of data from studies that use multiple targets in combination with such a compound report instruction, and it suggests one reason why results obtained in such studies may differ from those obtained in studies in which key reports track the visibility of an individual target.

A second observation with regard to motion-induced blindness (see J.-L. Schwartz, Grimault, Hupé, Moore, & Pressnitzer, 2012, for a related discussion) is that it is asymmetric. Although there is no inherent asymmetry between, say, perceived leftward rotation and perceived rightward rotation for an ambiguous structure-from-motion display or between the left eye and the right eye during binocular rivalry, subjective visibility and subjective invisibility during motion-induced blindness are not interchangeable. Indeed, although we could afford to discard data from individuals who had an overly imbalanced perceptual cycle during binocular rivalry or ambiguous structure-from-motion perception (see earlier data analysis section), it is typical for observers of motion-induced blindness to report more visibility than invisibility (Bonneh et al., 2001; Bonneh, Donner, Cooperman, Heeger, & Sagi, 2014). As a result, although measures of perceptual switch rate in paradigms such as binocular rivalry can provide a relatively clean index of the stability of the system, the same measures in motion-induced blindness may provide a compound index of both stability and balance. In particular, within the same individual and bistable perception paradigm, the net switch rate increases when the stimulus is adjusted to produce a more balanced alternation cycle, so it is likely that individual differences in the degree of asymmetry in the

perceptual cycle during motion-induced blindness contribute to differences in switch rate (Moreno-Bote, Shpiro, Rinzel, & Rubin, 2010; Brascamp et al., 2015). In other words, the asymmetric nature of motion-induced blindness again complicates the interpretation of data from that paradigm in the present context and provides room for apparently similar studies to reach different conclusions.

Conceptual points

Some reported correlations in perceptual switch rate are probably real[1]

Although our findings clearly suggest caution regarding potential correlations between the dynamics of binocular rivalry and motion-induced blindness and also regarding the blanket conclusion that time courses are correlated across different forms of bistable perception, it is entirely possible that some of the correlations reviewed in Figure 2 are real—that is, significantly greater than zero. For instance, one study reported correlated alternation rates between binocular rivalry and stimulus rivalry (Patel et al., 2014). Stimulus rivalry is a phenomenon that involves a very similar configuration of visual input as binocular rivalry and, irrespective of correlations in alternation rate, it has been proposed that the neural substrates of both phenomena overlap (Logothetis, Leopold, & Sheinberg, 1996; van Boxtel, Knapen, Erkelens, & van Ee, 2008; although see Lee & Blake, 1999; Pearson, Tadin, & Blake, 2007). In support of this notion, there is evidence that the duration of a given perceptual dominance period in binocular rivalry can be affected by prior dominance of the corresponding percept during stimulus rivalry (Brascamp, Sohn, Lee, & Blake, 2013). In light of existing literature, then, binocular rivalry and stimulus rivalry are a likely pair of bistable perception phenomena to show a real across-observers correlation in temporal dynamics, and other pairs of bistable perception phenomena might also exhibit such correlations in spite of the cautionary note provided by our present results.

The role of adaptation in binocular rivalry

Although we found no evidence that the time course of binocular rivalry is predicted by the strength of the visual aftereffects we measured, the idea that binocular rivalry involves adaptation is supported by many other findings (but it is not undisputed; D. Leopold & Logothetis, 1999; Miller, Liu, Ngo, Hooper, & Riek, 2000; Pettigrew, 2001; Moreno-Bote, Rinzel, & Rubin, 2007). For one, computational models based on the idea capture various characteristics of binocular rivalry (Wilson, 2007; Noest et al., 2007; Seely & Chow, 2011).

Furthermore, a role of adaptation is apparent from the binocular rivalry cycle that is observed shortly after prolonged perceptual dominance of one of the competing monocular displays during rivalry (Blake, Westendorf, & Fox, 1990; Pastukhov & Braun, 2011; De Jong, Knapen, & van Ee, 2012) or, similarly, shortly after exposure to that monocular display in isolation without the competing display present (Blake & Overton, 1979; Kang & Blake, 2010). In both cases, the binocular rivalry cycle that follows shows longer dominance durations for the alternative percept, consistent with a role of accumulated adaptation in causing switches. Along similar lines, perceptual dominance durations during rivalry can be lengthened by artificially minimizing the accumulation of feature-specific adaptation through continuous changes to the features of the conflicting monocular displays (Blake, Sobel, & Gilroy, 2003; Haynes & Rees, 2005). Finally, although detection performance is overall better for targets presented to the currently dominant eye than to the suppressed eye, it has been reported that this difference is diminished toward the end of a dominance period, again suggesting a gradual change in neural efficacy across the dominance period (Alais, Cass, O'Shea, & Blake, 2010).

Given this diverse array of findings that suggest a role of adaptation in binocular rivalry, then, why did our results show no significant correlation between rivalry switch rate and measures of visual adaptation? One possibility is that the various paradigms we employed do all draw on adaptation but in distinct neural populations and that observers do not have a general "adaptation" factor that strongly influences adaptation across the nervous system. The fact that we found no compelling evidence for correlations across distinct forms of visual aftereffects, even though these are commonly understood to each provide an index of adaptation, is consistent with this idea. A related consideration is that the term "adaptation," even within a given part of the nervous system, does not refer to a single physiological process, but to a functional outcome that can result from a range of processes (Kohn, 2007; Clifford et al., 2007). It is, therefore, possible that binocular rivalry involves adaptation in the sense of a reduction in efficacy in a part of the nervous system over time but that this is not the same kind of adaptation that is involved in visual aftereffects. In a later section, we discuss approaches to examining such possibilities.[2]

The relation between binocular rivalry and other forms of perceptual bistability

Irrespective of the role of adaptation, there is considerable evidence that binocular rivalry and other forms of perceptual bistability are related phenomena

with similar underlying mechanisms (D. Leopold & Logothetis, 1999). Some such evidence directly suggests that the same neural structures are involved in binocular rivalry and other forms of perceptual bistability, which would seem to lead to the prediction that perceptual switch rates should be correlated between paradigms (unless there is no variance in those structures across the population). For instance, it has been reported that the switch rates of both binocular rivalry and ambiguous structure from motion depend on the functional properties of the same part of the parietal cortex (Kanai, Carmel, Bahrami, & Rees, 2011) and that the switch rates of both binocular rivalry and two other forms of perceptual bistability depend on the concentration of the neurotransmitter GABA in the visual cortex (van Loon et al., 2013; although see Sandberg et al., 2016). The majority of the available evidence, however, supports the less far-reaching idea that binocular rivalry and other forms of perceptual bistability rely on analogous mechanisms but without clear implications either way regarding the degree of overlap in terms of physical implementation. Such evidence, therefore, invites much weaker predictions regarding correlations between perceptual switch rates. An example of evidence in this latter category is psychophysical evidence that distinct forms of perceptual bistability show similar dependencies on stimulus manipulations (Klink, van Ee, & van Wezel, 2008; Moreno-Bote et al., 2010; Brascamp et al., 2015) and also on trial history (D. A. Leopold, Wilke, Maier, & Logothetis, 2002; Pearson & Brascamp, 2008). Although such evidence suggests that the neural networks responsible for these various phenomena have comparable dynamics, it does not imply that the phenomena draw on one and the same network.

Common factors in vision and suggestions for future research

The above sections converge on the position that distinct bistable perception phenomena do have similar mechanisms and that these mechanisms might well include neural adaptation yet that the neural substrates underlying these phenomena may have limited anatomical overlap. The possibility that such distinct but related visual phenomena would show little across-observers correlation is consistent with existing research that has aimed to identify common factors across visual functions. This research has shown, for instance, that within the normally sighted population correlations in performance are very limited between different visual paradigms that all center on basic functions such as detection and discrimination (Cappe, Clarke, Mohr, & Herzog, 2014). Similarly, Grzeczkowski, Clarke, Francis, Mast, and Herzog (2017) observed that correlations between the magnitudes of

distinct visual illusions are generally small or absent. These latter authors do, however, point to evidence for stronger correlations when two visual functions are extremely similar to each other; for instance, correlations between the magnitudes of different versions of the same visual illusion (Coren, Girgus, Erlichman, & Hakstian, 1976) or between visual sensitivities to different gratings with sufficiently similar spatial frequencies (Peterzell & Teller, 1996). Presumably, the key is that the neural substrates engaged in such cases are overlapping across both tasks.

This perspective leads to two tentative predictions with regard to our present topic. First, observations from a binocular rivalry paradigm and from a second paradigm may become more strongly correlated when designing stimuli to be maximally alike across both paradigms, thereby increasing neural overlap. One example to support this prediction is the aforementioned study by Patel et al. (2014), who used stimuli with the exact same spatial properties to elicit both binocular rivalry and stimulus rivalry and who did report a substantial correlation. A second example is a study by Baker and Graf (2009), who found a significant correlation between percept durations in binocular rivalry and the strength of dichoptic masking, again in an experiment that used the same stimuli to elicit both. Perhaps, then, the strength of, say, an individual's tilt aftereffect after viewing a particular grating does predict that individual's temporal properties of binocular rivalry as long as the rivalry involves a very similar grating presented at different orientations to the two eyes. The second, and perhaps more surprising, tentative prediction is that, within a single bistable perception paradigm, correlations between different versions of the paradigm might scale with the similarity between the stimuli used in the two versions. For instance, a broad range of dichoptic displays can elicit binocular rivalry, and the tentative suggestion would be that an individual who is a fast switcher for a given dichoptic display can be a slow switcher for a sufficiently different dichoptic display. This suggestion is far removed from the notion that is dominant in the literature and that we subscribed to when we began this project, namely that correlations across a range of bistable perception paradigms are substantial (let alone within them), but there is some indirect support for the suggestion. Specifically, long-term experience with a binocular rivalry stimulus (during several sessions across many days) gradually makes the observer a faster switcher for that particular stimulus, but transfer of this speeding to binocular rivalry involving different stimuli is limited (Suzuki & Grabowecky, 2007). Evidently, then, there is no general rule that an observer's switch rates should remain yoked between different versions of a given perceptual bistability

paradigm. Nevertheless, across-observers correlations between different versions of the same bistable perception phenomenon have hardly been investigated (an exception is Law, Miller, & Ngo, 2017), and determining their relation to overlap in stimulus features remains a target for future research.

Keywords: binocular rivalry, bistable perception, individual differences, motion-induced blindness, adaptation

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Footnotes

[1] While our manuscript was in production, a paper was published that included comparisons among as many as eleven paradigms of bistable perception, including the three paradigms we examined here (Cao et al., 2018). The results of that paper are consistent with our findings in showing no substantial correlations among those three paradigms, but they do show substantial correlations among other bistable perception paradigms, for instance between binocular rivalry and Rubin's vase–face illusion.

[2] An earlier section emphasizes that percept durations during binocular rivalry might draw on a different kind of adaptation than indices of aftereffect strength do, potentially explaining the present lack of correlations between those measures. It is, of course, also possible that limited statistical power is responsible. In this context, it is worth noting that other factors besides adaptation likely influence binocular rivalry percept durations so that across-observers variation in binocular rivalry percept durations only, in part, reflects across-observers variation in adaptation dynamics. Besides adaptation and inhibition strength, discussed in the Introduction section, such other factors include "noise," i.e., random fluctuations in neural activity (Kim, Grabowecky, & Suzuki, 2006; Moreno-Bote et

al., 2007). One observation consistent with a substantial role of noise in binocular rivalry is that sequential correlations in binocular rivalry percept durations, although nonzero, are small (Pastukhov & Braun, 2011). Note that our overall suggestion, in a later section, that stronger correlations between bistable perception phenomena can plausibly be obtained when using more similar visual displays across paradigms, does not critically depend on whether adaptation, a different factor, or a combination of factors dictates perceptual dominance durations.

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