MECHANISMS UNDERLYING BINOCULAR RIVALRY

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ABSTRACT

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When observers view a perceptually bistable stimulus, their perception changes stochastically. Various studies have shown across-observer correlations in the percept durations for different bistable stimuli including Necker cube, binocular rivalry (BR) and bistable moving plaids (MP), which suggests a shared mechanism underlying perception in these paradigms. In this project we explore such shared mechanisms by examining what determines whether a given set of bistable perception paradigms will exhibit correlations in percept durations, and also by examining correlations with other perceptual phenomena that do not directly involve bistability. In our first experiment, we hypothesize that the presence or absence of a certain type of motion can influence whether different bistable paradigms will exhibit correlated percept durations. We found that the correlations between some bistable stimuli are strong, but others are fragile and inconsistent, which prevents us from drawing direct conclusions. In the second experiment, we examine whether between-observer variability in cortical inhibition underlies correlated percept durations between binocular rivalry and bistable moving plaid perception. As a behavioral measure of cortical inhibition, we used center-surround suppression of perceived contrast. While we were able to successfully replicate the correlations between bistable paradigms, there was no correlation between center-surround suppression strength and percept durations for any bistable paradigm. Moreover, the results from a mediation analysis indicate that center-surround suppression is not the mediating factor in the correlation between BR and MP, suggesting that cortical inhibition cannot explain the correlation between various bistable paradigms.

This thesis is dedicated to the Jagtaps and Deshmukhs and everyone else with a red line under their names in Microsoft Word.

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Introduction

Ambiguous figures are images that support more than one interpretation such that each interpretation gives rise to one percept and usually one interpretation is seen at a given moment in time. Therefore, depending on the total number of stable interpretations, the image can be either bistable (with two compatible percepts) or multistable (more than two compatible percepts). Binocular rivalry is one example of a multistable stimulus in which stochastic fluctuation of perception occurs when interocularly conflicting visual information is presented to the two eyes (Blake & Logothetis, 2002). An observer can perceive a total of three percepts- two exclusive percepts, each associated with the image presented to one eye, and a third percept which is a mixture of the images presented to both eyes. This phenomenon has been widely studied, which has provided some insight into its mechanisms. For instance, some studies have indicated that the rate of percept switching is dependent on local features of the stimulus such as spatial frequency (Adelson & Movshon, 1982) etc., and other studies point to a role of higher-level factors like attention (Girgus, Rock & Egatz, 1977), expectation, intention, prior exposure, and learning (Hochberg & Peterson, 1987). Still, understanding of the mechanisms underlying the perceptual fluctuations in binocular rivalry remains incomplete (Kang & Blake, 2010; Logothetis & Leopold, 1996). Previous studies about perceptual switches have shown that there is a large extent of inter-individual variability in the number of switches per minute, as a result, some participants may be categorized as “slow switchers” while the others as “fast switchers” (Washburn, Mallay & Naylor, 1931). Investigating which other visual or cognitive phenomena are correlated with the perceptual time course of binocular rivalry can increase scientific understanding of binocular rivalry as well as the other phenomena, by identifying common factors that drive both. The present study consists of two separate experiments that both take this approach. The first experiment examines how the perceptual time course during binocular rivalry is correlated with the perceptual time course observed for other bistable perception paradigms. The second experiment examines how the perceptual time course during binocular rivalry is correlated with the strength of center-surround suppression in contrast perception, which is thought to form an index of cortical inhibition strength.

Experiment 1a

The perceptual time course associated with various bistable stimuli

This experiment was inspired by a recent study by Cao et al. (2018). Cao et al. (2018) investigated switch rates associated with many different bistable stimuli and found that some stimuli were correlated with each other in terms of switch rate while others were not, hence forming two separate groups of stimuli with strong correlation within the group. One group of mutually correlated stimuli consisted of the Spinning dancer illusion (Ward & Scholl, 2015), a Lissajous figure (Weilnhammer et al., 2013) and a structure-from-motion cylinder variant, and the other group comprised of a Necker cube, binocular rivalry, Rubin's vase-face illusion and a moving plaid stimulus. Part of the motivation for the present study is an observation about the nature of the stimuli in these two groups. The homogeneity of the stimuli in the former group (all of them involve ambiguous three-dimensional motion as a factor that leads to a bistable percept) provides a ready explanation for the presence of a correlation between the switch rates for those stimuli. For the latter group, however, such a clear explanation does not present itself when casually comparing the stimuli involved (Necker cube, binocular rivalry, Rubin's vase-face illusion and a moving plaid). Indeed, it would appear that the processes that give rise to their multistability are quite different for this group, henceforth referred to as the 'cluster of interest': interocular contour conflict leads to fluctuating perception in case of binocular rivalry; alternating border ownership assignment, and an associated change in the figure/ground status of parts of the stimulus, give rise to bistability for Rubin's vase-face illusion; the lack of unambiguous depth cues in the presence of contours that suggest a 3D structure leads to bistability for the Necker cube; and finally the moving plaids involve an ambiguity in terms of the direction of motion as well as the depth ordering. This heterogeneity renders the 'cluster of interest' worthy of further study: what is the shared mechanism that brings about the observed correlation among a group of such diverse stimuli, and why does that mechanism not apply to other stimuli, which fall outside of the cluster? Our present approach to examining that question was inspired by a second finding in the study by Cao et al.: the finding that the perceptual switch rates for a structure-from-motion stimulus are correlated with those for the Necker cube, but not with those for any of the other stimuli in the cluster of interest. There are clear similarities between the structure-from-motion stimulus and the Necker cube in terms of the nature of ambiguity: in both cases there is a two-dimensional stimulus which gives rise to the perception of a three-dimensional object but with ambiguity about the layout of that object. In fact, in a sense both stimuli lie on a sort of continuum: from a moving object without bounding contours on one end (the structure-from-motion stimulus) to a static object with bounding contours on the other end (the Necker cube). In our experiment we exploit this fact: we re-examine the (lack of) correlation in percept dynamics among the 'cluster of interest', a structure-from-motion stimulus, as well as a new stimulus that interpolates along the continuum between the structure-from-motion stimulus and the Necker cube. This new stimulus is simply a Necker cube that is animated so that the cube is seen to rotate (in a direction that is ambiguous). Our question, then, is: how does this rotating Necker cube fit into the pattern of correlations? A presence or absence of correlation with the 'cluster of interest' can help us distinguish between two possible explanations as to why the structure-from-motion falls outside of the 'cluster of interest' while the Necker cube does not: a) three-dimensional motion renders the structure-from-motion stimulus (cylinder) to be different from the other stimuli and therefore the structure-from-motion stimulus (cylinder) draws on a completely different neural substrate; b) the contours in the Necker cube might act as anchor points for surface based processing which the structure-from-motion stimulus (cylinder) lacks. By discriminating between those possibilities, we also aim to gain insight into the question of what makes the stimuli in the 'cluster of interest' correlate to begin with.

Cortical inhibition and bistable perception

The second experiment in this project also capitalizes on inter-observer differences in the temporal dynamics of bistable perception, and how such across-observer variance correlates with variance in other measures. This experiment uses this approach to address a specific hypothesis about the neural substrate of bistable perception and, in particular, of binocular rivalry. This hypothesis holds that inhibition among cortical neurons is a central component in shaping the perception during binocular rivalry. More specifically, theories about binocular rivalry posit that neural inhibition at multiple levels in the visual hierarchy could be responsible for suppressing the representation of one of the eyes' images during binocular rivalry, thus playing an important role in the perceptual cycle (Tong et al., 2006; van Loon et al., 2013). Indeed, a change in the excitatory-inhibitory balance in the cortical areas (especially visual cortex) has been suggested to influence the perceptual fluctuations of binocular rivalry. Consistent with this idea, evidence from previous studies (McKendrick et al., 2019; van Loon et al., 2013, although see Sandberg et al. 2016) indicates that as the concentration of GABA (the brain's main inhibitory neurotransmitter) in the visual cortex increases, there is a decrease in perceptual switch rate during binocular rivalry. Furthermore, a study on older adults (Pitchaimuthu et al., 2017) reported that the concentration of GABA is significantly greater in older adults as compared to younger adults and that older adults report fewer perceptual switches as compared to younger adults. Additionally, disorders like schizophrenia and autism spectrum disorder (ASD) are linked to a disturbance in the excitatory-inhibitory balance (Spiegel et al., 2019; Yoon et al., 2010), and also with altered binocular rivalry dynamics. At least two studies have found that patients suffering from schizophrenia had lower switch rates for binocular rivalry as compared to their healthy counterparts (Xiao et al., 2018; Ye et al., 2019). Similarly, a study of binocular rivalry in ASD observed that there is a significant reduction in the alternation rates in this population (Spiegel et al., 2019). Yet another study found similar results and reported that an inverse relationship between the concentration of cortical GABA and the proportion of perceptual suppression during rivalry, which is observed in healthy controls, is absent in ASD patients, thus suggesting that the disturbance in excitatory-inhibitory balance in the autistic brains leads to a reduced effect of GABA on perceptual suppression (Robertson et al., 2016).

Putting these pieces of evidence together, in this second experiment we aim to investigate whether inter-observer differences in the temporal dynamics of binocular rivalry perception might partly reflect inter-observer differences in cortical inhibition strength.

Perceptual time course associated with various bistable stimuli

As indicated earlier, various studies have found a positive correlation between the percept durations of Necker cube and structure-from-motion paradigms, as well as among the Necker cube, binocular rivalry and bistable moving plaids, yet a lack of correlation of structure-from-motion with either binocular rivalry or bistable moving plaids (Brascamp et al., 2018, 2019; Cao et al., 2018; Gallagher & Arnold, 2014; Kang & Blake, 2010; Sheppard & Pettigrew, 2006). This experiment aims to understand the stimulus properties that could have led to this pattern of results. In particular, the aspect of the data that we are interested in is that binocular rivalry and moving plaids are correlated, in terms of percept durations, with the Necker cube but not with structure-from-motion paradigms, which involve stimuli that are quite similar to the Necker cube. One hypothesis is that rotation in depth is the property that makes the structure-from-motion stimulus stand apart, leading to the lack of correlation between percept durations for the structure-from-motion stimulus and those observed during binocular rivalry and bistable moving plaid perception (i.e. two paradigms in the 'cluster of interest'). As briefly explained above, we tested this idea by designing a new stimulus, a rotating Necker cube, that has properties that are intermediate between those of a Necker cube and those of structure-from-motion stimuli. If it is, indeed, the presence of rotation in depth that makes structure-from-motion stimuli draw on such distinct neural processes that no perceptual correlation with some other stimuli remains, then no correlation should be observed for the rotating Necker cube either. If, on the other hand, other factors are critical, for instance the fact that the structure-from-motion stimulus has no contour lines, then the predicted outcome is different.

Methods

Participants

We recruited 113 participants, aged between 18 and 25, from the psychology subject pool of Michigan State University. Of these 113 participants, 79 were females and all the participants had normal or corrected-to-normal vision. This experiment was conducted over 2 sessions and the task order within each session was fixed but the order of sessions was counterbalanced across participants. The sessions also included other experiments that were unrelated to the present study. One of the sessions comprised binocular rivalry and bistable moving plaids paradigm whereas the other session included structure-form-motion, Necker cube and rotating Necker cube paradigm. Not all the recruited participants showed up to (all of) the testing sessions and hence data was collected from 103 participants for binocular rivalry, Necker cube and rotating Necker cube paradigm and 102 participants for bistable moving plaids and structure-from-motion stimulus. Some participants were further dropped after the preliminary analysis of the data (see below for the exclusion criteria) and the final sample included 88 participants for binocular rivalry, 93 participants for bistable moving plaids, 96 participants for structure-from-motion, 92 participants for Necker cube and 81 participants for rotating Necker cube.

All the experiments in this study were approved by the Michigan State University institutional review board. Written informed consent was obtained from all the participants prior to testing. Participants fulfilled course requirements through their participation.

Stimuli and Task

Binocular rivalry

The specifications of this stimulus were identical to those of one of the stimuli ("small grating stimulus") used in a previous study (Brascamp et al., 2019). Sinusoidal gratings (spatial frequency of 2.0 c/dva, Michelson contrast 0.5, mean luminance same as background luminance) were presented within an annular aperture (inner radius 0.37 dva, outer radius of 0.85 dva) on two separate monitors viewed through a mirror stereoscope. Interocular conflict was created by presenting different grating orientations (-45 and +45 degrees from vertical) and grating colors (using either only the monitor's red channel or only the monitor's green channel) to each eye. Both eyes were presented with a grating that drifted diagonally upward or downward, at 0.24 dva/s to minimize the formation of negative afterimages. The vertical direction of this movement was always the same in both eyes and was varied from trial to trial.

A mimic condition was also included in which a single stimulus was shown binocularly, as opposed to two gratings being shown dichoptically at the same time. This stimulus could, at different times, consist of either of the grating patterns or a patchwork of both. The latter mimicked a mixture percept of the binocular rivalry stimulus. We mention this mimic condition here because it was part of the same experiment blocks as the binocular rivalry condition, but the data from the mimic condition were not analyzed in the context of this study.

During either condition, observers had to indicate the onset of the red pattern, the onset of the green pattern and also the onset of mixture percepts where both of the patterns were partly visible, using three separate keys on the keyboard. Each block started with a 20 second practice trial with the rivalry stimulus, and the data for this practice trial were not analyzed. Each subsequent trial lasted for 45 seconds, followed by a forced break of 10 seconds (longer if the observer wanted). There were 6 trials of the binocular rivalry condition and 4 trials of the mimic condition that were randomly interleaved within the experimental block. Each participant ran a single experiment block.

Bistable moving plaids

The stimulus specifications for the bistable moving plaids were identical to those used in a previous study (Brascamp et al., 2019). The stimulus consisted of two overlapping square wave gratings oriented at ±26.6 degrees relative to vertical (spatial frequency: 2.0 c/dva; 0.5 Michelson contrast). They were made in grayscale and had a uniform gray background of 35.2 cd/m^2 (same as the average grating luminance). The gratings shifted diagonally upward at 0.48 dva/s. The luminance of the locations where the two gratings overlapped was adjusted to promote perception of transparency (see below for possible percepts). This was done by first calculating the difference in log space between the luminance of the dark stripes and that of the light stripes of the gratings. The luminance of the intersection area between two bright stripes was then set such that, again in log space, the difference between the intersection luminance and the luminance of the bright stripes was the same. This stimulus gave rise to periods when observers perceived a coherent, solid, diamond pattern moving straight upward, as well as periods when they perceived two transparently superimposed gratings moving in two different directions. A schematic of this stimulus and percepts is presented in figure 1. The task of the participant was to indicate the onset of either of the aforementioned percepts, as well as the onset of mixture percepts, using three separate keys on the keyboard (the only difference between this task and the one in the 2019 study was this ability to report mixed percepts.). Each trial was 60 seconds long, followed by a 10 second forced break (longer, if the observer wanted). Each observer completed a practice trial followed by a single block with six trials.

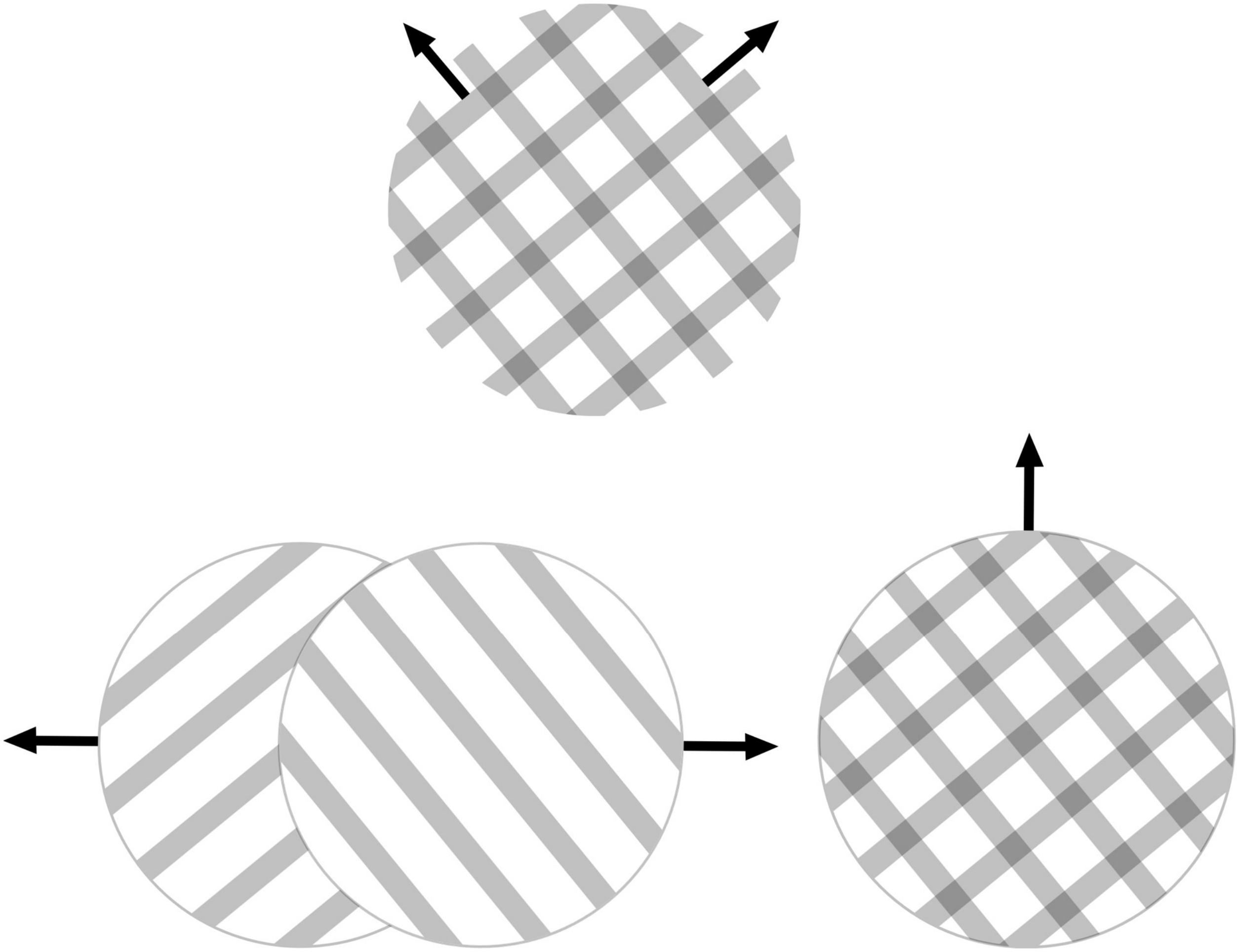


Figure 1. Bistable moving plaids.

The plaid pattern that is schematically depicted at the top was shown during the experiment. There are two compatible percepts: one where the two gratings seem to slide over each other and a second one in which the pattern seems to be moving coherently in one direction.

Structure-from-motion

This stimulus was very similar to the one used in a previous study (Brascamp et al., 2018). It consisted of horizontally moving dots (60 cd/m^2, radius 0.05 dva) with a sinusoidal speed profile across space, presented on a gray background (20 cd/m^2) (schematically represented in figure 2). The only difference between the stimulus used in this study and the one used in the previous study is that each dot had a lifetime of 2 seconds after which it was replaced by another dot at a random location. This motion sequence was perceived as an orthographic projection of a transparent, rotating, sphere with a radius of 2 dva. The observers were asked to fixate on a round fixation mark at the center of the display (1 cd/m^2; radius 0.05 dva) and to indicate the first rotation direction they perceived as well as any change in this perceived direction (clockwise, counterclockwise, or a non-exclusive mixture of these percepts) using three separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by ten 60 second trials where each pair of trials was separated by a forced break of a minimum of 10 seconds long.

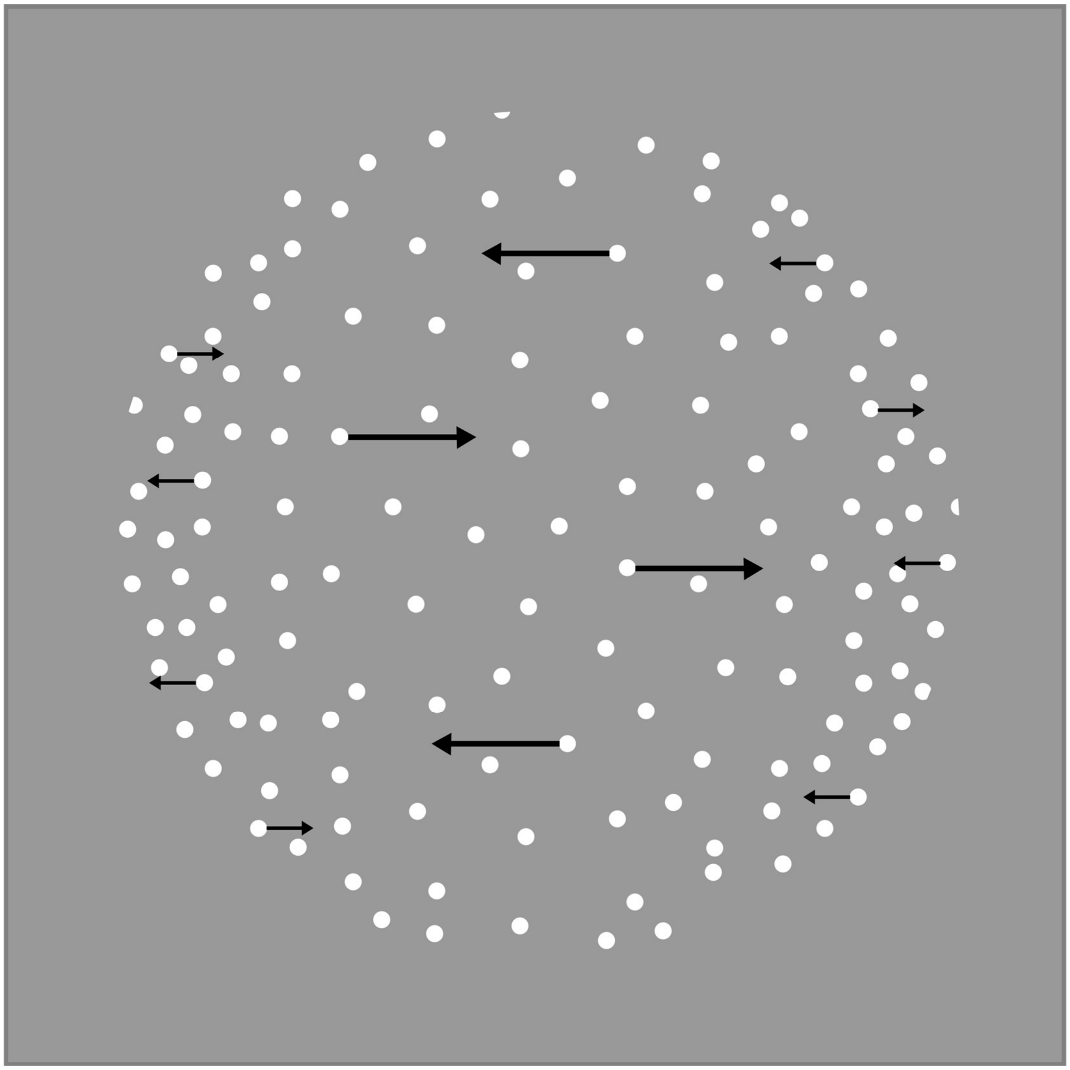


Figure 2. Structure-from-motion Stimulus.

This is a schematic of the rotating sphere stimulus, which is composed of dots moving horizontally and confined to a circular area. The speed profile of the dots, as well as dot density, was varied as a function of position within the circle, consistent with an orthographic projection of a dotted, transparent sphere. For example, dot speed was highest near the center of the circle and lowest near the outer edge of the circle. This gave rise to the perception of a rotating sphere, but the direction of rotation was ambiguous.

Necker cube

This stimulus consisted of a 2-dimensional representation of a cube. Each line that composed the cube was 0.1 dva wide and each face of the cube was 3 dva wide but the actual size of the stimulus was slightly larger than 3 dva at any moment of observation because the cube was rotated 15 degrees around the x-axis and 25 degrees on the y-axis (so that the edges do not occlude each other as they would when viewing the cube straight from the front). The observers were asked to fixate on a round fixation mark at the center of the display (1 cd/m^2; radius 0.2 dva) and to indicate the first direction in which they perceived the cube to be facing towards as well as any change in this perceived direction (left, right, unsure) using separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by four 60 second trials where each pair of trials was separated by a forced break of a minimum of 10 seconds long.

Rotating Necker cube

This stimulus was similar to the static Necker cube in that each face of the cube was composed of lines that were 0.1 dva wide and the face of the cube was 3 dva wide. The cube was rotated 15 degrees around the x-axis and 15 degrees around the y-axis in the beginning of each trial. During the trials, the angle of rotation around the y-axis changed over time and hence the cube rotated at a speed of 0.25 revolutions per second around the y-axis. The observers were asked to fixate on a round fixation mark at the center of the display (1 cd/m^2; radius 0.2 dva) and to indicate the first rotation direction they perceived as well as any change in this perceived direction (clockwise, counterclockwise, or a non-exclusive mixture of these percepts) using three separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by four 60 second trials where each pair of trials was separated by a forced break of a minimum of 10 seconds long.

Data Analysis

We calculated the percept durations by taking the time interval separating the start of one exclusive percept from the start of the following alternative exclusive percept, hence including any intervening mixture period (i.e., 'start-to-start' durations, Brascamp et al. 2018). The percept durations were subsequently averaged within participants and then log-transformed to convert the right-skewed percept duration distributions to ones that more closely approximate normality.

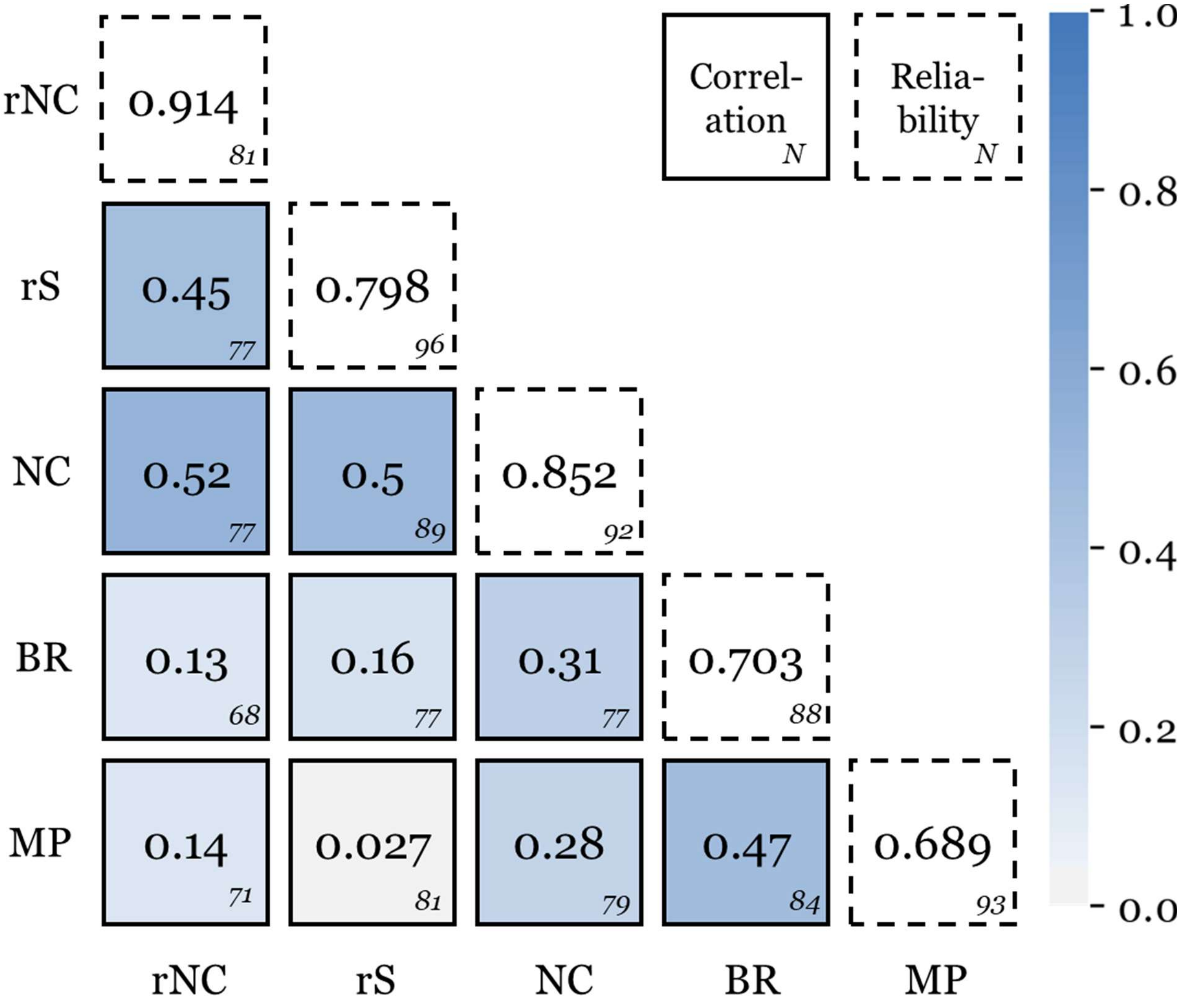
As soon as the data were collected, they were subjected to a preliminary analysis to be sure that there were no issues that would prevent interpretation of our main analyses. The data were excluded if the participant reported fewer than two perceptual alternations for a given paradigm in total. For all paradigms excluding bistable moving plaids, participants were also excluded from analysis if they did not meet the following "balance criterion": the total amount of time one percept was reported needed to be less than three times the total amount of time the other percept was reported (corresponding to a balance between percepts less extreme than 75%/25%). This exclusion criterion was not applied to the bistable moving plaid data because the percepts of the bistable plaid stimulus are inherently asymmetrical. For all the paradigms except binocular rivalry, participants were also excluded if they reported a mixture percept for more than 50% of the viewing time. This cutoff was a little higher, 60%, for binocular rivalry as the tendency to perceive a mixture percept is much higher for binocular rivalry than for the other two paradigms. An additional balance criterion was also applied to all the paradigms such that no more than 50% of reported perceptual transitions were allowed to be return transitions. A return transition is an instance when the participant reports a change in perception from an exclusive percept to a mixture percept and back to the same exclusive percept (Mueller & Blake, 1989).

We further calculated the reliabilities for these bistable perception paradigms by calculating the correlation between two randomly selected, non-overlapping, halves of all collected percept durations for each observer. This value was then corrected using the Spearman-Brown prediction formula. Finally, Pearson correlations were calculated for all combinations of the paradigms.

Results

We first performed preliminary analyses on the data from the bistable perception paradigms by way of sanity check. We analyzed the reliability of each bistable perception paradigm as indicated in our Data Analysis section and found high reliabilities associated with all the paradigms (figure 3). We also investigated whether we could replicate the previously reported across-observer correlation between the average percept duration of binocular rivalry and of bistable moving plaid perception, their correlation with Necker cube, as well as their potential correlations with average percept duration of the rotating sphere and rotating Necker cube. As shown in figure 3, the results from this correlation analysis indicate that the log-transformed percept durations of binocular rivalry and bistable moving plaids were positively correlated ($r(84) = 0.475$; $p < 0.001$; 90% CI [*0.29, 0.63*]). This correlation replicates earlier work. Additionally, a positive correlation of log-transformed percept durations of Necker cube with binocular rivalry ($r(77) = 0.311$; $p = 0.006$; 90% CI [*0.09, 0.5*]) and moving plaids ($r(79) = 0.277$; $p < 0.014$; 90% CI [*0.06, 0.47*]) supports the notion that there is a shared mechanism among these three bistable perception paradigms. While on one hand, there is a positive correlation between the log-transformed percept durations of structure-from-motion and Necker cube ($r(89) = 0.496$; $p < 0.001$;

90% CI [*0.32, 0.64*]), on the other hand, the (log-transformed) percept durations of structure-from-motion did not significantly correlate with those for either binocular rivalry ($r(77) = 0.161$; $p = 0.161$; 90% CI [*-0.07, 0.37*]) or the bistable moving plaids ($r(81) = 0.027$; $p = 0.808$; 90% CI [*-0.19, 0.24*]), which matches the fact that reports of a presence of these correlations in the literature have been less unanimous. In sum, the pattern of correlations discussed so far is consistent with the pattern observed in the literature, with mutual correlations between the three paradigms in the 'cluster of interest' (binocular rivalry, Necker cube and bistable moving plaids), but with the structure-from-motion stimulus correlating only with the Necker cube and not with the remaining two stimuli in that cluster. This brings us to our present question: how does the rotating Necker cube fit into this pattern? The (log-transformed) percept durations for this paradigm are positively correlated with both stationary Necker cube ($r(77) = 0.520$; $p < 0.001$; 90% CI [*0.34, 0.67*]) as well as structure-from-motion ($r(77) = 0.449$; $p < 0.001$; 90% CI [*0.31, 0.65*]) but that it is not significantly correlated with either binocular rivalry ($r(68) = 0.126$; $p = 0.307$; 90% CI [*-0.12, 0.35*]) or bistable moving plaids ($r(71) = 0.138$; $p = 0.252$; 90% CI [*-0.10, 0.36*]). This pattern of correlations seems to support our hypothesis that the presence of rotation in depth could be a factor that influences correlations between different bistable perception paradigms, since there is a positive correlation of the percept durations of Necker cube with binocular rivalry and bistable moving plaids, but this correlation is absent for rotating Necker cube. To test this hypothesis, we calculated Steiger's Z, which provides a test of difference between two correlations that share one variable but not the other. We performed this analysis on the correlation pair of binocular rivalry vs. Necker cube and binocular rivalry vs. rotating Necker cube, and also on the pair of moving plaids vs. Necker cube and moving plaids vs. rotating Necker cube. The results of Steiger's test indicate that the correlation of binocular rivalry with Necker cube is significantly different from that of the correlation between binocular rivalry and rotating Necker cube (Steiger's Z(66) = 2.059, *p*=0.039), thus supporting the idea of an influence of rotation. On the other hand, there is no significant difference in the strengths of correlations of bistable moving plaids with Necker cube and rotating Necker cube (Steiger's Z(68) = 1.227, *p*=0.22).



	rNC	rS	NC	BR	MP
rNC	0.914 81				
rS	0.45 77	0.798 96			
NC	0.52 77	0.5 89	0.852 92		
BR	0.13 68	0.16 77	0.31 77	0.703 88	
MP	0.14 71	0.027 81	0.28 79	0.47 84	0.689 93

Figure 3. Correlation matrix for experiment 1a.

Solid squares represent correlations between paradigms, and broken squares represent reliabilities associated with individual paradigms. rNC = rotating Necker cube; NC = Necker cube; rS = bistable structure-from-motion (rotating sphere); BR = binocular rivalry; MP = bistable moving plaids. The number at the bottom right of each of the squares represents the N for the given paradigm or pair of paradigms. More saturated colors indicate a stronger correlation and less saturated colors indicate a weaker correlation between the different paradigms.

Discussion

In this experiment we successfully replicated the correlations among the three paradigms in the 'cluster of interest' (stationary Necker cube, binocular rivalry and bistable moving plaids) as well as the lack of correlation between the latter two of those paradigms and a structure-from-motion paradigm. When it comes to our newly added stimulus, the rotating Necker cube, this percept durations for this stimulus, like those for the structure-from-motion stimulus, do not correlate with percept durations for either binocular rivalry or bistable moving plaids. This pattern of results suggests that as soon as rotation is added to the Necker cube, it stops being correlated with the two paradigms mentioned earlier. We found a significant difference in the correlations of binocular rivalry with stationary Necker cube and rotating Necker cube but the correlations were not significantly different in case of bistable moving plaids, stationary Necker cube and rotating Necker cube. This pattern of results somewhat supports the rotation hypothesis, but in our next experiment we wanted to test an alternative explanation: that the addition of any motion, and not specifically rotation, could change the perceptual dynamics of the resultant stimulus to the extent that it stops being correlated with other bistable paradigms.

Experiment 1b

In the previous experiment we tested the rotation hypothesis and we found some evidence to suggest that rotation is the factor that leads to the break-down of correlations between the rotating Necker cube and binocular rivalry / bistable moving plaids. However, an alternative explanation for the data pattern is that movement of the cube's contours, rather than rotation in depth specifically, affects the correlation pattern. The rationale underlying this explanation would be that there is evidence that neural adaptation brings about switches in the perception of bistable stimuli (Blake & Wilson, 2011; Tong et al., 2006), and moving the contours of the cube slows the buildup of adaptation in visual neurons that respond only to their preferred stimulus at a certain retinal location. In this follow-up experiment, therefore, we hypothesized that motion, and not specifically rotation, could explain the (lack of) correlations between the various paradigms. In order to test this hypothesis, we designed another stimulus, a sliding Necker cube, which has the same physical structure as that of the stationary Necker cube, but has an additional property of side-to-side motion.

Methods

Participants

We recruited 107 participants, aged between 18 and 25, from the psychology subject pool of Michigan State University. Of these 107 participants, 88 were females and all the participants had normal or corrected-to-normal vision. Similar to the previous experiment, this experiment was conducted over 2 sessions and the task order within each session was fixed but the order of sessions was counterbalanced across participants. The sessions also included other experiments that were unrelated to the present study. One of the sessions comprised binocular rivalry and bistable moving plaids paradigm whereas the other session included structure-form-motion, static Necker cube, rotating Necker cube and sliding Necker cube paradigm. Not all the recruited participants showed up to (all of) the testing sessions and hence data was collected from 93 participants for binocular rivalry and bistable moving plaids, 92 participants for static Necker cube, 91 participants for rotating Necker cube and sliding Necker cube and 90 participants for structure-from-motion stimulus. Some participants were further dropped after the preliminary analysis of the data (see below for the exclusion criteria) and the final sample included 83 participants for binocular rivalry, 88 participants for bistable moving plaids, 82 participants for structure-from-motion, 89 participants for static Necker cube, 66 participants for rotating Necker cube and 76 participants for sliding Necker cube.

Stimulus and Task

This experiment included all the stimuli and tasks from Experiment 1a (binocular rivalry, bistable moving plaids, structure-from-motion, Necker cube and rotating Necker cube) and one additional stimulus that we call sliding Necker cube.

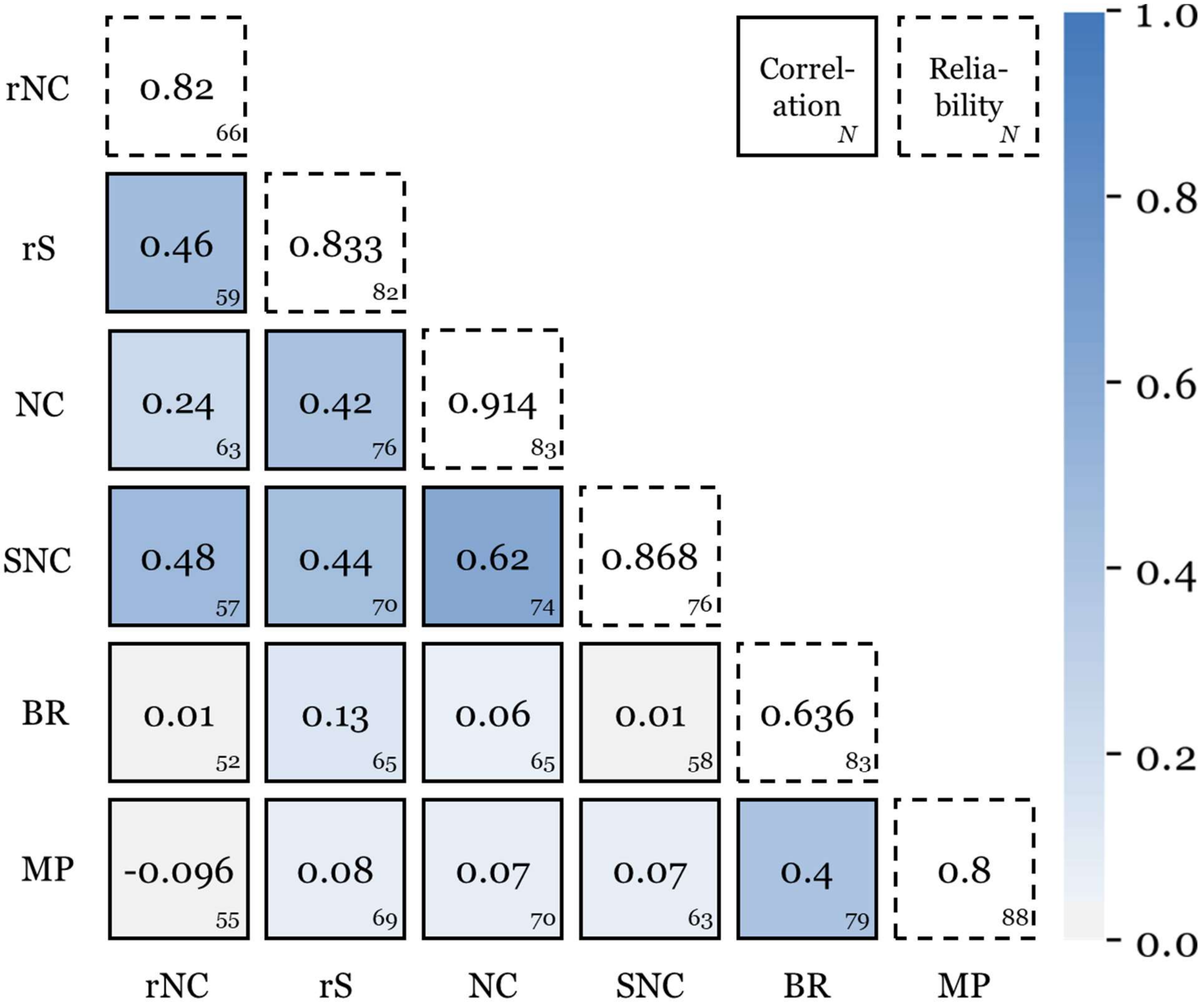
The physical features of this stimulus were same as those of the rotating Necker cube and the static Necker cube. The cube was permanently oriented like the static Necker cube, i.e. rotated 15 degrees around the x-axis and 15 degrees around the y-axis. But in contrast to the static Necker cube, the sliding Necker cube moved on the screen. Its sliding motion was based on the rotating cube used that semester: the sliding cube slid in such a way that the cube's motion trajectory on the screen was identical to the on-screen motion trajectory of one vertical edge of the rotating cube. In other words, the sliding Necker cube, while continuously oriented in the same way, followed the same elliptical on-screen path of motion that any vertical edge of the rotating Necker cube stimulus made as a result of the rotating Necker cube's three-dimensional rotation. Similar to the static Necker cube, the observers were asked to fixate on a round fixation mark at the center of the display (1 cd/m^2; radius 0.2 dva) and to indicate the first direction in which they perceived the cube to be facing towards as well as any change in this perceived direction (left, right, unsure) using separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by four 60 second trials where each pair of trials was separated by a forced break of a minimum of 10 seconds long.

Data Analysis

Same as Experiment 1a

Results

Similar to the previous experiment, we first performed preliminary analyses on the data from the bistable perception paradigms by way of sanity check. We analyzed the reliability of each bistable perception paradigm as indicated in our Data Analysis section and found high reliabilities associated with all the paradigms (figure 4). We also investigated whether we could replicate the previously reported across-observer correlation between the average percept duration of binocular rivalry and of bistable moving plaid perception, their correlation with Necker cube, as well as their potential correlations with average percept duration of the rotating sphere, rotating Necker cube and sliding Necker cube. As shown in figure 4, the results from this correlation analysis indicate that the log-transformed percept durations of binocular rivalry and bistable moving plaids were positively correlated ($r(79) = 0.399$; $p < 0.001$; 90% CI [*0.20, 0.57*]). This correlation replicates earlier work. We also found a positive correlation between the log-transformed percept durations of stationary Necker cube with log-transformed percept durations of structure-from-motion ($r(76) = 0.421$; $p < 0.001$; 90% CI [*0.22, 0.59*]) and sliding Necker cube ($r(74) = 0.654$; $p < 0.001$; 90% CI [*0.50, 0.77*]). The correlation between the stationary Necker cube and the rotating Necker cube, on the other hand, did not reach statistical significance ($r(63) = 0.237$; $p = 0.061$; 90% CI [-*0.01,* *0.46*]). Similar to the previous experiment, we found several correlations to be absent: between the structure-from-motion stimulus and both binocular rivalry (*r*(65) = 0.126; *p* = 0.318; 90% CI [-*0.12, 0.36*]) and bistable moving plaids (*r*(69) = 0.075; *p* = 0.543; 90% CI [-*0.16, 0.31*]), as well as between the rotating Necker cube and both binocular rivalry (*r*(52) = 0.010; *p* = 0.944; 90% CI [-*0.26, 0.28*]) and bistable moving plaids (*r*(55) = -0.096; *p* = 0.488; 90% CI [-*0.35, 0.17*]). When it comes to our newly added stimulus, the sliding Necker cube, its percept durations, like those for the rotating Necker cube and for the structure-from-motion stimulus, did not correlate with either binocular rivalry (*r*(58) = 0.013; *p* = 0.920; 90% CI [-*0.25, 0.27*]) or bistable moving plaids (*r*(63) = 0.072; *p* = 0.572; 90% CI [-*0.18, 0.31*]). This would appear to support the idea that it is the addition of motion per se, not the addition of rotation, that critically impacts whether percept durations for a bistable figure correlate with those for binocular rivalry and moving plaids. But unfortunately one aspect of the data prevents us from drawing any clear conclusions from this experiment: in this datasete the percept durations of stationary Necker cube did not correlate either with binocular rivalry (*r*(65) = 0.061; *p* = 0.628; 90% CI [-*0.19, 0.30*]) or bistable moving plaids (*r*(70) = 0.071; *p* = 0.558; 90% CI [-*0.17, 0.30*]). This lack of correlation endangers the premise of the study, in that no conclusion can be drawn about the impact of adding movement to the Necker cube, if the stationary Necker cube itself does not correlate with the other paradigms used in this study. For completeness, we calculated Steiger's Z and found that for binocular rivalry the correlation with the stationary Necker cube did not statistically differ from the correlation with the rotating Necker cube (Steiger's Z(50)= 0.876 ; *p*= 0.381). Similarly, the correlation with the the stationary Necker cube did not statistically differ from the correlation with the sliding Necker cube (Steiger's Z(57)= 0.221 ; *p*= 0.825). A similar result was obtained for bistable moving plaids, in that its correlations were not significantly different for the manipulation of rotation (Steiger's Z(53)= 1.047 ; *p*= 0.295) or for sliding motion (Steiger's Z(62)= 0.041 ; *p*= 0.967).



	rNC	rS	NC	SNC	BR	MP
rNC	0.82 66					
rS	0.46 59	0.833 82				
NC	0.24 63	0.42 76	0.914 83			
SNC	0.48 57	0.44 70	0.62 74	0.868 76		
BR	0.01 52	0.13 65	0.06 65	0.01 58	0.636 83	
MP	-0.096 55	0.08 69	0.07 70	0.07 63	0.4 79	0.8 88

Figure 4. Correlation matrix for experiment 1b.

Solid squares represent correlations between paradigms, and broken squares represent reliabilities associated with individual paradigms. rNC = rotating Necker cube; NC = Necker cube; rS = bistable structure-from-motion (rotating sphere); BR = binocular rivalry; MP = bistable moving plaids; SNC = sliding Necker cube. The number at the bottom right of each of the squares represents the N for the given paradigm or pair of paradigms. More saturated colors indicate a stronger correlation and less saturated colors indicate a weaker correlation between the different paradigms.

Discussion

In the present experiment we successfully replicate the correlations between binocular rivalry and bistable moving plaids, along with the correlations among stationary Necker cube, structure-from-motion and rotating Necker cube. The percept durations of the new stimulus, sliding Necker cube, have a positive correlation with stationary Necker cube, structure-from-motion and rotating Necker cube whereas there is a lack of its correlation with both binocular rivalry and bistable moving plaids. Critically, however, we did not find a correlation of stationary Necker cube with either binocular rivalry or bistable moving plaids, which interferes with the objective of this experiment: to test how the addition of motion to the Necker cube affects its correlation with binocular rivalry and bistable moving plaids. It also casts some doubt on the robustness of correlations within the 'cluster of interest' to begin with (i.e. among binocular rivalry, moving plaids and the stationary Necker cube).

The number of observers in this experiment (about 60) is similar to, albeit slightly smaller than, the number in experiment 1a (about 70). The fact that we found a correlation of stationary Necker cube with binocular rivalry and bistable moving plaids in one case but not the other suggests that these correlations are fragile, and not reliably evident with such N-numbers. In a post-hoc analysis we analyzed the data again, now combining the data from experiment 1a and 1b. The results from this analysis (figure 5) do indicate a significant correlation of stationary Necker cube with binocular rivalry ($r(142) = 0.196$; $p = 0.019$; 90% CI [*0.03, 0.35*]) and bistable moving plaids ($r(149) = 0.174$; $p = 0.034$; 90% CI [*0.01, 0.33*]), but the significance level is modest. This is consistent with the idea that these correlations are indeed fragile, and that more data are required to draw a conclusion about these correlations.

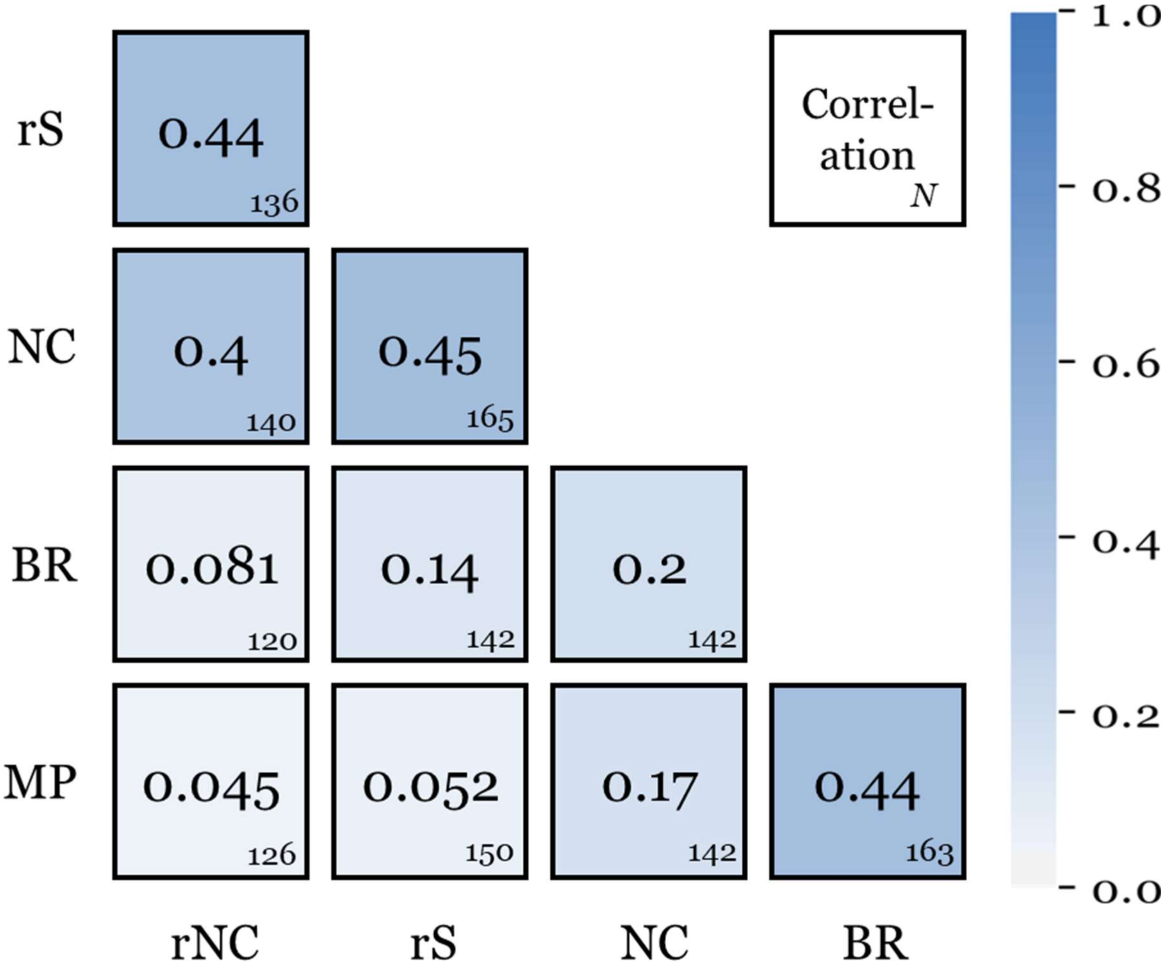


Figure 5. Correlation matrix for experiment 1a and experiment 1b.

Solid squares represent correlations between paradigms. rNC = rotating Necker cube; NC = Necker cube; rS = bistable structure-from-motion (rotating sphere); BR = binocular rivalry; MP = bistable moving plaids. The number at the bottom right of each of the squares represents the N for the given paradigm or pair of paradigms. More saturated colors indicate a stronger correlation and less saturated colors indicate a weaker correlation between the different paradigms.

Experiment 1c

In order to replicate the findings from experiment 1a and draw a conclusion about the motion hypothesis from experiment 1b, we hosted an online experiment to collect data from a larger sample. In this experiment we included bistable moving plaids, stationary Necker cube, rotating Necker cube and sliding Necker cube. We did not include a binocular rivalry task because of the technical difficulties associated with dichoptic stimulation in online experiments.

Methods

Participants

We recruited a total of 277 participants (54 males) of which 196 completed the online experiment. All the participants reported having normal or corrected-to-normal vision and gave their informed consent prior to testing. They received course credit for their participation in the experiment.

Stimulus and Task

This experiment was hosted online on Pavlovia. The participants were first asked to calibrate their screen so that the stimulus dimensions are appropriate. This was done using the Card task (Li et al., 2020) in which the participants were asked to place a credit card on the screen and adjust the size of the rectangle displayed on the screen to match the size of the credit card in the real word. This procedure allowed us to control the on-screen size of our stimuli. The experiment began after the calibration task was completed and consisted of the following four stimuli.

Bistable moving plaids.

This stimulus consisted of two overlapping square wave gratings oriented at ±26.6 degrees relative to vertical and each grating had 5 cycles. The diameter of the stimulus was 4 cm assuming that the participants calibrated their screens correctly (see above for the card task). The gratings shifted diagonally upward at the speed of 1 period/s. The luminance of the gratings was not controlled as the screens of the participants for this online experiment were not calibrated individually. Nonetheless, the stimulus gave rise to periods when observers perceived a coherent, solid, diamond pattern moving straight upward, as well as periods when they perceived two transparently superimposed gratings moving in two different directions. The task of the participant was to indicate the onset of either of the aforementioned percepts, as well as the onset of mixture percepts, throughout the stimulus presentation using three separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by six 60 second trials where each pair of trials was separated by an optional break.

Necker cube.

This stimulus was similar to the Necker cube stimulus used in experiment 1a and it differed in two aspects. First, the cube was rotated by 15 degrees on both x-axis as well as y-axis and second, the length of a side of the cube was 3 cm (assuming correct calibration procedure using the card task, see above) and each face of the cube was slightly smaller than 3 cm because the rotation of the cube on the axes. The observers were asked to fixate on a round fixation mark at the center of the display and to indicate the first direction in which they perceived the cube to be facing towards as well as any change in this perceived direction (left, right, unsure) using separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by six 60 second trials where each pair of trials was separated by an optional break.

Rotating Necker cube.

This stimulus was same as the rotating Necker cube stimulus used in the previous experiment with two exceptions. First, the length of a side of the cube, like the Necker cube stimulus in this experiment, was fixed at 3 cm and each face of the cube was slightly smaller than 3 cm because the cube was rotated by 15 degrees on the x-axis as well as the y-axis at the beginning of each trial. Second, the cube revolved at a speed of 0.2 revolutions per second around the y-axis. The observers were asked to fixate on a round fixation mark at the center of the display and to indicate the first rotation direction they perceived as well as any change in this perceived direction (clockwise, counterclockwise, or a non-exclusive mixture of these percepts) using three separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by four 60 second trials where each pair of trials was separated by an optional break.

Sliding Necker cube.

This stimulus was same as the sliding Necker cube stimulus used in experiment 1a with two exceptions. First, the length of a side of the cube, like the stationary Necker cube stimulus in this experiment, was fixed at 3 cm and each face of the cube was slightly smaller than 3 cm because the cube was rotated by 15 degrees on the x-axis as well as the y-axis. Second, the cube translated at a speed of 0.2 revolutions per second around the x-axis in the manner that mimicked the elliptical motion (around the x-axis) that any corner of the rotating Necker cube stimulus made. The observers were asked to fixate on a round fixation mark at the center of the display and to indicate the first rotation direction they perceived as well as any change in this perceived direction (clockwise, counterclockwise, or a non-exclusive mixture of these percepts) using three separate keys on the keyboard. Each observer completed one block which consisted of a practice trial of 45 seconds (data not analyzed) in the beginning followed by six 60 second trials where each pair of trials was separated by an optional break.

Data analysis

Same as Experiment 1a.

Results

As in the previous experiments, we first performed preliminary analyses on the data from the bistable perception paradigms by way of sanity check. We analyzed the reliability of each bistable perception paradigm as indicated in our Data Analysis section and found high reliabilities associated with all the paradigms (figure 6). The results indicate that the stationary Necker cube shows a positive correlation, in terms of the percept durations, with the rotating Necker cube ($r(151) = 0.247$; $p = 0.002$), the sliding Necker cube ($r(151) = 0.334$; $p < 0.001$), as well as with bistable moving plaids ($r(151) = 0.283$; $p < 0.001$). To our surprise, however, there is also a positive correlation of bistable moving plaids with rotating Necker cube ($r(151) = 0.231$; $p = 0.004$) and, less compellingly, sliding Necker cube ($r(151) = 0.172$; $p = 0.035$), even though those correlations were absent in Experiments 1a and 1b. One possible explanation is that motion does affect correlations involving the Necker cube, but that those correlations remain significant in Experiment 1c because of the large N-number. Therefore, in order to understand if the correlation between bistable moving plaids and Necker cube in Experiment 1c changed at all as a result of rotation/motion incorporation, we performed Steiger's Z test. The results from Steiger's test indicate that there is no significant difference between the correlation of moving plaids with stationary Necker cube and the correlation of moving plaid with rotating Necker cube (Steiger's $Z(151)= -0.372$; $p= 0.710$), nor is there a significant difference between the correlation of moving plaids with stationary Necker cube and the correlation of moving plaid with sliding Necker cube (Steiger's Z(151)= 0.519 ; *p*=0.604).

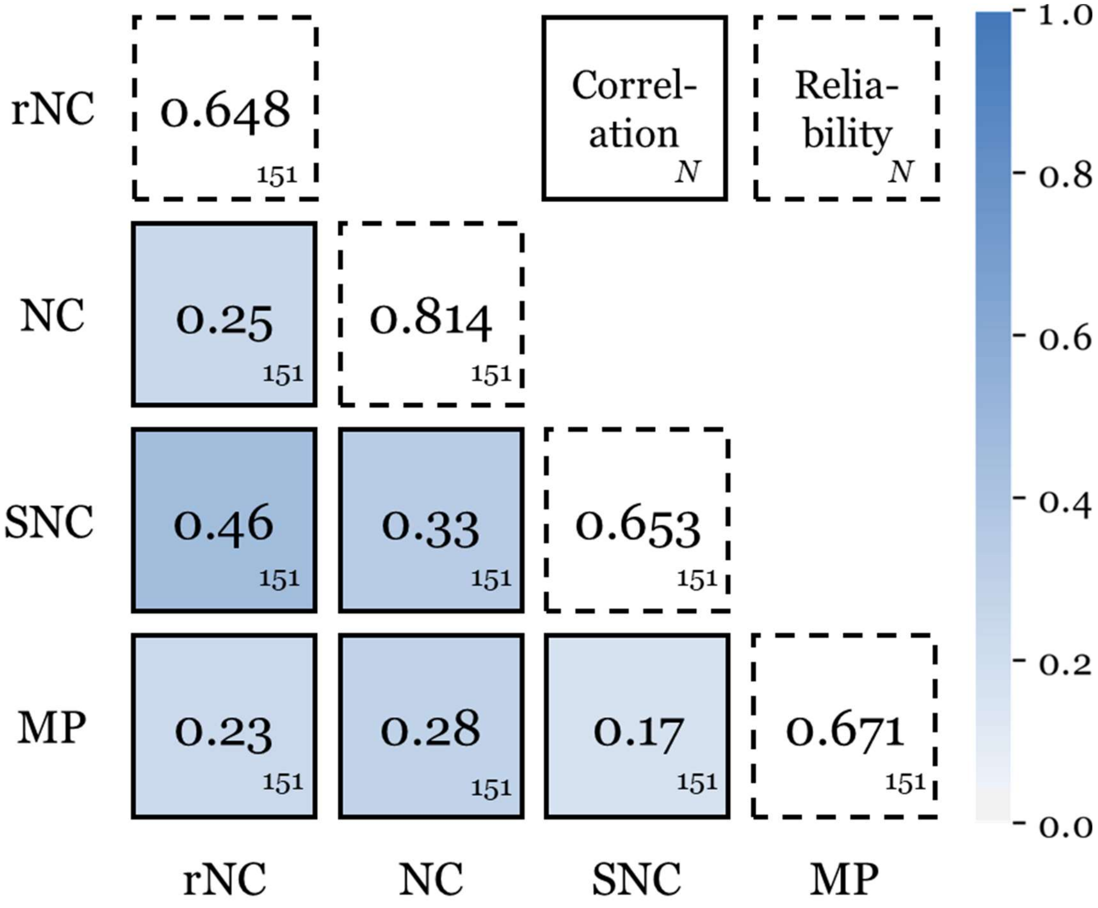


Figure 6. Correlation matrix for experiment 1c.

Solid squares represent correlations between paradigms, and broken squares represent reliabilities associated with individual paradigms. rNC = rotating Necker cube; NC = Necker cube; MP = bistable moving plaids; SNC = sliding Necker cube. The number at the bottom right of each of the squares represents the N for the given paradigm or pair of paradigms. More saturated colors indicate a stronger correlation and less saturated colors indicate a weaker correlation between the different paradigms.

Discussion

In this experiment, we found a positive correlation between bistable moving plaids and stationary Necker cube, but we also found a positive correlation between bistable moving plaids and the two moving Necker cube variants. Moreover, the results from the Steiger’s test showed that the addition of neither rotation nor sliding motion affected the Necker cube's correlation with the moving plaid stimulus, in contrast to our finding in Experiment 1a that rotation does reduce this correlation.

Overall discussion of Experiments 1a-1c

The pattern of results across Experiments 1a-1c is somewhat problematic in the context of the original aim of this part of these experiments, which was to examine whether the addition of rotation in depth to a bistable figure interferes with its correlation with binocular rivalry and moving plaids. Across the three experiments we have now found, in one instance, that even a stationary Necker cube did not correlate with those paradigms (Experiment 1b, so in that instance there was no correlation to be affected by motion) and, in another instance, that even a rotating Necker cube did correlate (Experiment 1c) even though earlier it did not (Experiments 1a and 1b). Similarly, in one case (Experiment 1a) we found that the addition of rotation did reduce the correlation between Necker cube and moving plaids (and also binocular rivalry), whereas in another case we found that it did not (Experiment 1c). Based on all results across our experiments as well as earlier work, we suggest that the correlations between binocular rivalry and moving plaids on the one hand, and the Necker cube, its variants, and structure-from-motion stimuli are fragile rather than clearly present or absent in particular cases. This view, if correct, interferes with our original aim of investigating which factors determine whether a correlation with binocular rivalry and moving plaids will be found. For this reason, we do not draw any definite conclusions from this first part of our work. Instead, we will now continue to the second part of our work, which allows us to draw clearer conclusions.

Cortical inhibition and bistable perception

As indicated in the introduction section, in this second experiment we again capitalized on inter-observer variability in the perceptual time course of bistable perception. In this case, we aimed to examine the specific hypothesis that bistable perception critically involves cortical inhibition, so that inter-observer variability in the dynamics of bistable perception may reflect inter-observer variability in cortical inhibition strength.

The two bistable stimuli used in this experiment are binocular rivalry and a bistable moving plaid stimulus. The results from the experiments discussed above, as well as those of earlier studies (refs) indicate that those two paradigms give rise to the most consistent and strong correlation among bistable perception paradigms. In addition, we include a paradigm that does not involve bistable perception, but that is thought to rely on cortical inhibition. If this is true that the correlation in percept dynamics between binocular rivalry and bistable moving plaid perception reflects a shared dependence on cortical inhibition, then one might expect the dynamics of these two bistable perceptual phenomena to show correlations with this third perceptual phenomenon, and one might expect these correlations to (partly) account for the observed relation between binocular rivalry and bistable plaid perception. The inhibition-related phenomenon examined here is surround suppression: a reduction in the apparent contrast of a central stimulus as a result of the presence of a surrounding pattern (Cannon & Fullenkamp, 1993; Chubb et al., 1989; Xing & Heeger, 2000). A reduced perceptual strength of surround suppression has been linked to a reduction in cortical GABA concentrations in the same patient populations also mentioned above in the context of altered binocular rivalry perception (Flevaris & Murray, 2015; Serrano-Pedraza et al., 2014). Additional evidence from a recent study (McKendrick et al., 2019) indicates that there is, indeed, a positive correlation between the perceptual strength of surround suppression and percept durations for binocular rivalry, further encouraging the hypothesis that inhibition could be an underlying factor, perhaps mediated by GABA concentration, that explains the correlation in percept durations between binocular rivalry and bistable plaid perception.

As outlined above, we hypothesize that the correlation between percept durations of binocular rivalry and bistable plaid perception can be accounted for, in part, by across-observer variance in the perceptual strength of center-surround suppression. We test this hypothesis with the help of a test battery which includes binocular rivalry, bistable moving plaids and a (non bistable) center-surround suppression task. Additionally, we include a bistable structure-from-motion stimulus. While correlated perceptual dynamics have been consistently observed for the combination of binocular rivalry and bistable plaid perception (Brascamp et al., 2019; Cao et al., 2018; Sheppard & Pettigrew, 2006), this picture is less consistent for other combinations of bistable stimuli, including the combination of binocular rivalry and bistable structure-from-motion (Brascamp et al., 2018; Cao et al., 2018 show no significant correlation whereas Steinwurzel et al., 2020 show a positive correlation between switch rates in these two paradigms). Adding a structure-from-motion stimulus to our battery, therefore, allowed us to re-examine any correlation with the other bistable phenomena and, if it is observed, to test whether it is (partly) accounted for by variance in the strength of surround suppression.

Methods

Participants

We recruited 217 healthy participants, aged between 18 and 25, from the psychology subject pool of Michigan State University. Of these 217 participants, 113 (34 males) were recruited in one semester and 104 (18 males) in the following semester. The study was conducted over 3 sessions in one semester and over 2 sessions in the other semester (the sessions also included experiments unrelated to the present work; see below). Not all recruited participants showed up to (all of) the testing sessions, and data were collected from a total of 196 participants for binocular rivalry, 195 participants for bistable moving plaids, 192 for structure-from-motion and 196 for the surround-suppression task. For each task some further participants were dropped after preliminary analysis of the data (see below for exclusion criteria). The final sample for which the data were fully analyzed (beyond preliminary analysis; details in the Data Analysis section) consisted of 171 participants for binocular rivalry, 181 participants for bistable moving plaids, 178 participants for structure-from-motion and 151 participants for the surround-suppression task.

The study was approved by the Michigan State University institutional review board and was conducted over the course of two semesters. Written informed consent was obtained from all the participants prior to testing. The testing battery included other tasks not reported here, and this set of tasks differed slightly between the two semesters. The tasks reported here, however, were the same in both cases. Participants fulfilled course requirements through their participation.

Stimulus and Task

Three bistable perception paradigms were used in this experiment including binocular rivalry, bistable moving plaids, and structure-from-motion stimulus. The stimulus specifications for all these bistable paradigms were same as are reported in experiment 1a above.

Center-surround stimulus

This task was derived from (Xing & Heeger, 2000, 2001). It involved a circular central grating disk (spatial frequency of 2 c/d) and a surrounding grating annulus (same spatial frequency; figure 7). The contrast of the surrounding annulus was 0.8 (Michelson) and the contrast of the central disk was 0.2. This type of stimulus usually induces perceptual suppression, in the sense that the contrast of the center is typically underestimated for this type of stimulus. Perceptual suppression in such paradigms is often thought to be associated with cortical inhibition (Angelucci et al., 2017; Flevaris & Murray, 2015; Robertson et al., 2016; Serrano-Pedraza et al., 2014; Spiegel et al., 2019; Tibber et al., 2013; Yoon et al., 2010). Each trial consisted of two center grating disks presented sequentially at fixation for 0.5 seconds each, separated by a 0.3 second blank. The observer was asked to report which of the two gratings had a higher contrast. One of the central disks served as a reference stimulus and was presented without a surround. The contrast of this reference stimulus varied from trial to trial. The other central disk of the trial was the actual test stimulus; it always had the same contrast, and it was accompanied by a surround. The order of the test stimulus and reference stimulus was assigned randomly on each trial. The orientation of both the center gratings and the surround gratings was vertical and there was a 180-degree phase difference between the two gratings at all times. The phase of all gratings shifted by 180 degrees at a rate of 8 times per second during each presentation. The center stimulus had a radius of 1.75 dva, the inner radius of the surround stimulus was identical to the outer radius of the center stimulus, and the outer radius of the surround stimulus was 5 dva. The outermost part of the center stimulus (0.2 dva) was occupied by a raised cosine edge. Similarly, the innermost part (0.2 dva) of the surround stimulus was occupied by such an edge.

Each observer ran a single block involving this stimulus, which consisted of 3 interleaved 1-up-1-down staircases during which the reference contrast was varied. For the three staircases the reference contrast started, respectively, at 75%, 100% or 125% of the test contrast for that condition. Each staircase had 40 trials. After each trial, the reference contrast was incremented or decremented (depending on the response) by a set amount. At the beginning of a given staircase this set amount was 50% of the current reference contrast. Every time a reversal occurred within a staircase (i.e., the observer said ‘reference contrast is higher’ on the previous trial and ‘test contrast is higher’ on the current trial, or vice versa) the current percentage amount was multiplied by 0.8, but it was not allowed to drop below 5%. The perceived contrast of the test stimulus was calculated by coding the ‘reference is higher’ and ‘test is higher’ responses as 1 and 0, respectively, and plotting these responses for all trial as a function of the reference contrasts on all those trials. The perceived contrast of the test stimulus was then computed as the mean of a cumulative gaussian fitted to this relationship. Aside from the mean and standard deviation there was a third free parameter (a 'lapse rate' parameter) that we used for fitting the cumulative gaussian. This parameter scaled the vertical range of the function so that it could be smaller than the usual range of 0 to 1. This was done keeping in mind that motor errors or attention lapses may prevent the curve from spanning the full range from 0 to 1, as those might cause a non-zero error rate even on trials where the difference in contrast between the test stimulus and the reference stimulus is easy to perceive.

Each observer had 10 practice trials before the beginning of the experiment block. Observers were asked to fixate at a black round fixation point (radius 0.5 degrees) throughout the stimulus presentation periods and the inter-stimulus intervals. They had to report which contrast (first or second stimulus) appeared higher using two keys on the keyboard.

Figure 7. Center-surround suppression stimulus.

This is a schematic representation of the center-surround test stimulus. The participants were asked to compare the contrast of the central part of this stimulus (while ignoring the surround grating) with the reference stimulus which did not have a surround. The contrast of the central area of test stimulus kept constant at 0.2 whereas the surround had a contrast of 0.8. The contrast of the reference stimulus was varied on each trial.

Data analysis

For the three bistable perception paradigms, the data analysis was same as is reported in the data analysis section of Experiment 1a. For the center-surround suppression task we applied an exclusion criterion based on the slope of the psychometric curve that relates the probability of a 'reference contrast higher' response to the physical contrast of the reference stimulus. A shallow slope here indicates that a participant's responses regarding the reference contrast show little dependence on the physical value of that contrast, suggesting that the participant did not follow the instructions. Because curve slope in this case depended on the combination of two parameters (both the standard deviation and the lapse rate) we quantified slope as the difference in the curve's vertical position between the two horizontal points located at 5% contrast to the right of the curve mean and 5% contrast to the left of the curve mean. Participants whose average curve slope across this 10% contrast interval was less than 2 were excluded from the main analysis (25 participants were excluded as a result of this criterion). In other words, only the participants who had at least a 20% change in their probability of judging the reference contrast as higher than the test contrast across this range of reference contrast values around the curve mean were included for further analysis. Additionally, we excluded a handful of participants whose curve slopes indicated they were judging the reference contrast, yet for whom the curve mean (i.e. the reference contrast value that perceptually matches the test contrast) was unusually high. In particular, whereas the test contrast was 0.2, a few observers had curve means that were closer to the contrast of the surround of the test stimulus, which was 0.8. We suspect that those participants misunderstood the task and compared the contrast of the reference grating with the contrast of the surround grating instead of that of the center, test, grating. 4 participants were excluded on these grounds, all of whom had curve means higher than 0.65.

In order to compute the reliability of the center-surround suppression strength, we calculated the correlation between the odd and the even trials of each condition and then again used the Spearman-Brown prediction formula to extrapolate the observed correlation coefficient to the one predicted for twice the amount of data.

Finally, Pearson correlations were calculated for all combinations of the paradigms. In addition, a mediation analysis was carried out to determine if surround suppression could be the mediating factor that explains the correlation between binocular rivalry and bistable moving plaids. In other words, this latter analysis tested whether between-observer variability in surround suppression strength was correlated with between-observer variability that is shared between the binocular rivalry paradigm and the bistable moving plaids paradigm.

Results

We first performed preliminary analyses on the data from the bistable perception paradigms by way of sanity check. We analyzed the reliability of each bistable perception paradigm as indicated in our Data Analysis section and found high reliabilities associated with all the paradigms (figure 8). We also investigated whether we could replicate the previously reported across-observer correlation between the average percept duration of binocular rivalry and of bistable moving plaid perception, as well as their potential correlations with average percept duration of the rotating sphere. As shown in figure 8, the results from this correlation analysis indicate that the log-transformed percept durations of binocular rivalry and bistable moving plaids were positively correlated ($r(163) = 0.445$; $p < 0.001$; 90% CI [*0.32, 0.57*]). This correlation replicates earlier work and supports the notion that there is a shared mechanism between these two bistable perception paradigms. The (log-transformed) percept durations of the bistable structure-from-motion stimulus, on the other hand, did not significantly correlate with those for either binocular rivalry ($r(142) = 0.14$; $p = 0.095$; 90% CI [*-0.02, 0.30*]) or the bistable moving plaids ($r(150) = 0.052$; $p = 0.526$; 90% CI [*-0.11, 0.21*]), which matches the fact that reports of a presence of these correlations in the literature have been less unanimous.

Before continuing on to the main analyses, we also performed preliminary analyses of the center-surround data to evaluate their robustness. First, we calculated the reliability for the center-surround paradigm, as we did for the bistability paradigms, and indeed we found this paradigm to be associated with high reliability, as indicated in Figure 8. Next, given that a center-surround stimulus like ours typically results in perceptual suppression, we expected that same general pattern in our data. Indeed, the perceived contrast for the center stimulus ($M(151) = 0.178$, $SD = 0.08$) was significantly lower than its physical contrast of 0.2 ($t(151) = -3.342$, $p = .001$). This argues in favor of the, for our purposes, critical presence of perceptual suppression in our center-surround paradigm.

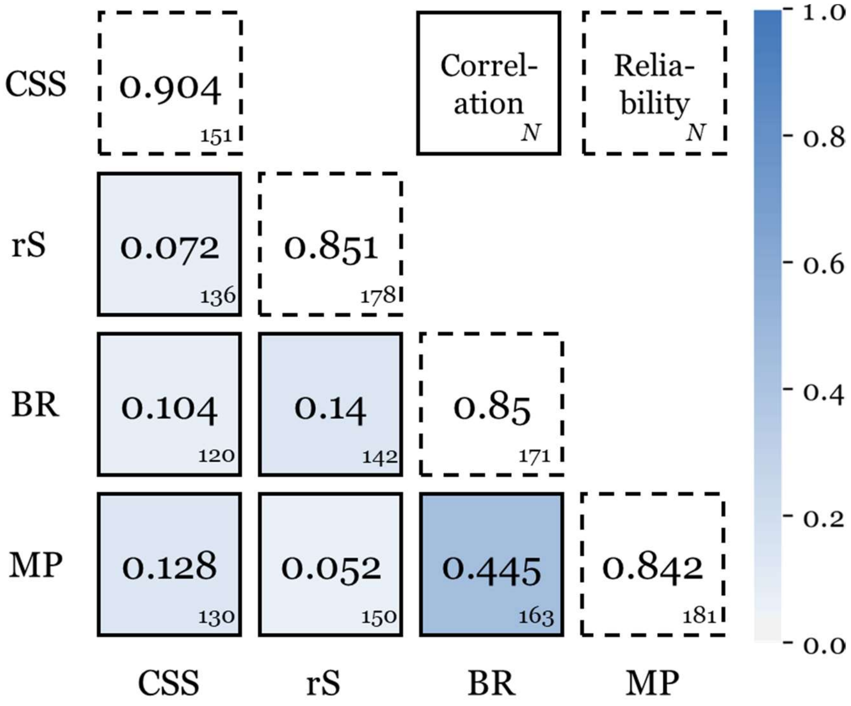


Figure 8. Correlation matrix for all stimuli in the current study.

Solid squares represent correlations and broken squares represent the reliabilities associated with the given paradigm. BR: binocular rivalry, MP: bi-stable moving plaids, rS: bi-stable structure-from-motion stimulus, CSS: center-surround suppression stimulus. More saturated colors indicate a stronger correlation and less saturated colors indicate a weaker correlation between the different paradigms.

Together, these results provide the necessary preconditions for our main analysis of correlations involving both bistable perception and surround suppression, and the good match with existing literature instills confidence in the sanity of our data.

As stated in our Introduction section we hypothesized that the correlation between perceptual switch rates in binocular rivalry and bistable plaid perception could be accounted for, in part, by variance in the perceptual strength of center-surround suppression. Such a data pattern would support the notion that cortical inhibition, as indexed by center-surround suppression, is a factor that underlies the correlated percept durations of binocular rivalry and the bistable moving plaid stimulus. To test our hypothesis, we first analyzed the correlations between percept durations for each bistable perception condition individually on the one hand, and the strength of center-surround suppression on the other, all using the Pearson correlation coefficient. The analysis revealed that there was no significant correlation between the (log-transformed) percept durations of binocular rivalry and surround suppression strength ($r(120) = 0.104$, $p = 0.259$; 90% CI [*-0.07, 0.28*]), shown in figure 8. Similarly, for the log-transformed average percept durations for the bistable moving plaid the correlation with surround suppression strength was not significant ($r(130) = 0.128$, $p = 0.147$; 90% CI [*-0.04, 0.30*]). We also found no significant correlation between structure-from-motion percept duration (log-transformed) and perceived contrast in the surround suppression condition ($r(136) = 0.072$, $p = 0.403$; 90% CI [*-0.10, 0.24*]). The correlations among all paradigms are tabulated in Table 1, which also indicates the reliabilities of each of the paradigms.

The lack of significant correlations in our data between center-surround suppression strength and the percept durations for binocular rivalry or bistable moving plaids argues against the idea that the observed correlation between the latter two variables can be explained by the former variable. Still, to formally test this notion we performed a mediation analysis on our data. Here we treated (log-transformed) average percept durations for binocular rivalry and for bistable moving plaids as the independent variable and dependent variable, respectively, while treating center-surround suppression strength as the mediator. This analysis, in other words, tests whether inter-observer differences in the binocular rivalry data are predictive of inter-observer differences in the bistable moving plaid data, and whether any of that predictiveness is captured by inter-observer differences in the center-surround data. Consistent with the simple correlation analyses reported above, the total effect was strong and significant (coefficient = 0.576; $p < 0.001$). This number quantifies the overall relation between the independent variable and dependent variable, irrespective of the mediator. Also consistent with those correlation analyses, the standardized regression coefficients for binocular rivalry percept durations versus surround suppression strength, and for bistable moving plaid percept durations versus surround suppression strength were not significant (coefficient = -0.065; $p = 0.272$, and coefficient = 0.297; $p = 0.108$, respectively, shown in figure 9). The key question, then, is whether any part of the total effect reflects an indirect effect involving the mediator, i.e., the center-surround data. Instead, the indirect effect had a coefficient of 0.013 and was statistically not significant ($p = 0.528$ and 90% CI [*0.005, 0.105*]), and the overall effect was essentially completely due to a direct effect not involving the mediator (coefficient = 0.563, $p < 0.001$, shown in figure 9). Thus, the results from this mediation analysis, along with the above-reported correlation results, indicate that variance in center-surround suppression strength cannot explain the correlation between the dynamics of binocular rivalry and of bistable plaid perception.

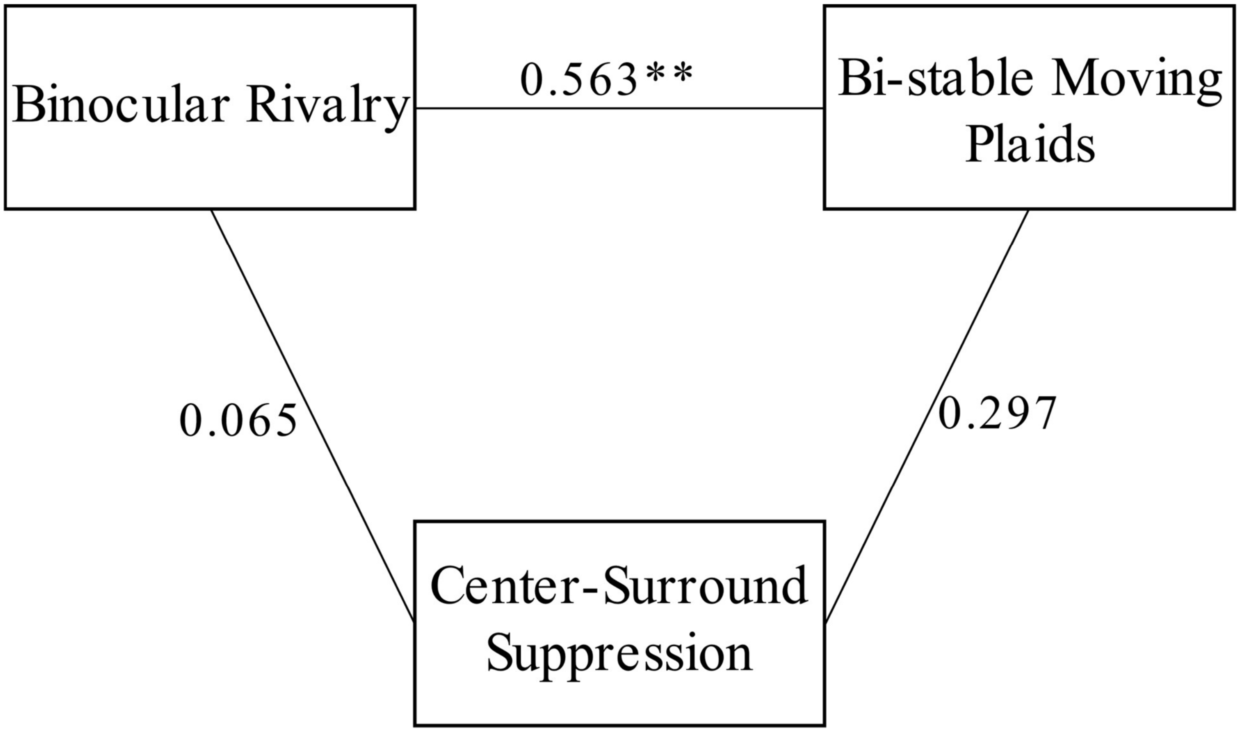


Figure 9. Mediation analysis.

Here we treated (log-transformed) average percept durations for binocular rivalry and for bistable moving plaids as the independent variable and dependent variable, respectively, while treating center-surround suppression strength as the mediator. We observed a significant direct effect and an indirect effect that was small and not significant, indicating that across-observer variance in center-surround suppression strength cannot explain the correlation between the dynamics of binocular rivalry and bistable plaid perception.

Discussion

In this experiment we successfully replicated the correlation in average percept duration between binocular rivalry and bistable moving plaids. This correlation indicates that there is an overlap between the mechanisms that drive perception in these two paradigms. The lack of correlation between percept durations in these paradigms and various other bistable perception paradigms (Brascamp et al., 2018; Cao et al., 2018; Gallagher & Arnold, 2014), including structure-from-motion in the present study, argues against a global shared mechanism such as degree of attention to the task (although see Pastukhov et al., 2019). We hypothesized that the strength of cortical inhibition could be the common underlying factor that accounts for the correlated perceptual dynamics of binocular rivalry and bistable moving plaids. We assessed the perceptual strength of center-surround suppression as an index for cortical inhibition. Although our analyses indicated that our measures of perceptual bistability and of center-surround suppression were reliable, we did not find a correlation between the two types of measures. The lack of correlations of the percept durations of binocular rivalry and bistable moving plaid perception with the strength of center-surround suppression, along with the lack of an indirect effect in the mediation analysis, do not support the idea of cortical inhibition as a shared factor that can explain the correlated dynamics of binocular rivalry and bistable moving plaid perception.

Although we observed significant surround suppression, the magnitude of this suppression does not quite match the magnitude of this variable as observed in some other studies. We used our data to calculate the suppression ratio, which is defined as the matching contrast divided by the test contrast. A ratio of 1 indicates veridical perception whereas suppression and facilitation are indicated by values of less than 1 and more than 1, respectively. The suppression ratio in our study was found to be 0.89. This indicates much weaker suppression than what Xing & Heeger (2001) found in a seminal study, as they reported a suppression ratio between 0.5 and 0.6 for an identical stimulus. One possible reason for the lower degree of suppression in our study relates to the fact that our observers were 151 untrained undergraduate students who completed a battery of many different types of experiments, whereas only 2 participants (one of them being an author) were included in the Xing & Heeger (2001) study, and both collected data across a large number of conditions. It is possible, therefore, that the difference in suppression ratio indicates a relatively large amount of noise in our data, stemming from a relative lack of expertise and/or motivation, on average, in our participant sample. Consistent with this notion are the findings from another study (Karas & McKendrick, 2015) that involved 30 participants. Both this sample size and the amount of data per participant suggest a level of expertise on the part of the participants that is intermediate between the levels in our own study and in the one by Xing & Heeger (2001). Consistent with an account in terms of expertise (and perhaps motivation), the suppression ratios in that study are consistently higher (indicating weaker suppression) than those from Xing & Heeger (2001) across a range of conditions, although still somewhat lower than ours in a condition that matches our own (between approximately 0.7 and 0.75). In sum, the evidence from this study reinforces the notion that our participants' relative lack of expertise might explain the relatively weak surround suppression in our study. This raises the possibility that, whereas we did not find any correlation between surround suppression strength and bistable perception dynamics, such a correlation may have been observed if only we had observed stronger surround suppression. To examine this idea, we further analyzed the data by dividing our sample into two halves based on the participants' performance on the center-surround suppression task, such that one half consisted of the top 50% of participants who show the strongest center-surround suppression, and the other half consisted of the remaining participants. Unsurprisingly, for the group with strong center-surround suppression the perceived contrast of the center stimulus reduced from *M*(151) = 0.178, *SD* = 0.08 to *M*(75) = 0.133, *SD* = 0.028, thereby improving the suppression ratio to 0.67; comparable to the values observed in the two studies mentioned above. More interestingly, the correlation between binocular rivalry and moving plaids also becomes stronger for this group, going from $r(163) = 0.445$, $p < 0.001$, 90% CI [*0.32, 0.57*] to $r(58) = 0.582$, $p < 0.001$, 90% CI [*0.49, 0.84*]. This reinforces the idea that, by selecting this half of the observers we are focusing on participants with relatively noise-free data. In agreement with this observation, the remaining 50% of observers, the ones with weak center-surround suppression, show a weaker, but still significant, correlation between the perceptual dynamics of binocular rivalry and bistable moving plaid ($r(57) = 0.383$, $p = 0.003$, 90% CI [*0.14, 0.67*]), and for the center-surround suppression task these remaining observers also have an inter-observer spread in matching contrast that is larger than the corresponding value for the entire group of observers ($M(74) = 0.254$, $SD = 0.14$, versus $M(151) = 0.178$, $SD = 0.08$ for the entire group), even though this subset has been specifically selected for having similar matching contrasts (i.e. the 50% least suppressed matching contrasts). In other words, the remaining 50% of observers who are weeded out by focusing on the 50% who have strong center-surround suppression, show all signs of having relatively noisy data. Now the critical question becomes, if we focus on the 50% of observers who have strong surround suppression and whose data suggest a relative lack of noise as compared to the rest of our sample, do we observe a correlation between center-surround suppression strength and bistable perception dynamics? The answer is no. Those correlations remain weak and statistically non-significant for the 50% of the observers who have strong surround suppression (center-surround suppression versus binocular rivalry: $r(59) = -0.078$, $p= 0.558$, 90% CI [-*0.33, 0.18*]; versus bistable moving plaids: $r(64) = -0.025$, $p= 0.847$, 90% CI [-*0.27, 0.22*]; and versus structure-from-motion: $r(64) = -0.039$, $p= 0.76$, 90% CI [-*0.29, 0.21*]). Therefore, it would be reasonable to conclude that the lower strength of suppression in our study does not explain the lack of correlation of center-surround suppression strength with perception in our bistable perception paradigms.

The present study relies on the assumption that center-surround suppression is a good behavioral index of cortical inhibition. Whereas our data provide a clear indication that the strength of center-surround suppression – a behavioral index – does not explain substantial variance in the dynamics of bistable perception, we can be less certain about the strength of cortical inhibition – a neural measure. To what extent does center-surround suppression serve as a reliable index for cortical inhibition? There have been numerous studies that explored this idea. Indirect evidence for the validity of various forms of center-surround suppression as an index of cortical inhibition comes from work involving special populations. For example, in their study involving older adults, Pitchaimuthu et al., (2017) not only report that the concentration of GABA is elevated in the visual cortex of older adults, but also that this higher concentration of GABA was associated with reduced motion suppression indices. Multiple other studies have linked disorders like schizophrenia and ASD to cortical excitatory- inhibitory imbalance and have also reported that these populations perform differently to various perceptual surround suppression paradigms as compared to the healthy population, although it should be noted that there are a number of center-surround paradigms that were used in these studies (Flevaris & Murray, 2015; Robertson et al., 2016; Serrano-Pedraza et al., 2014; Spiegel et al., 2019; Tibber et al., 2013; Yoon et al., 2010). In addition, numerous neurophysiological studies, as reported in Angelucci et al., (2017), have proposed that neural inhibition is involved in center-surround suppression although they suggest that suppression can also result from other factors, including increased bottom-up inhibitory input and decreased excitatory inputs in the local recurrent connections in the visual cortex. In sum, there is good evidence of a relation between perceptual center-surround suppression and cortical inhibition. So, in that light a lack of correlation, in the present work, between inter-individual differences in center-surround suppression strength and in measures of bistable perception, really would argue against a key role of cortical inhibition in driving inter-individual differences in bistable perception.

How do our results compare to existing work that explores the relationship between the dynamics of bistable perception and the strength of cortical inhibition? Various studies on disorders like schizophrenia and ASD have linked disturbances in the excitatory-inhibitory balance in visual cortex with altered dynamics of bistable perception (Robertson et al., 2016; Spiegel et al., 2019; Yoon et al., 2010). Additionally, a study on older adults has reported a modest correlation between the concentration of GABA in visual cortex and perceptual dynamics of binocular rivalry (Pitchaimuthu et al., 2017). On the other hand, a study investigating the excitatory-inhibitory neurochemicals in migraineurs and healthy controls found no overall correlation between the concentration GABA in visual cortex and perceptual dynamics of binocular rivalry (Chan et al., 2019). There are also two behavioral studies, unrelated to disorders, that report an across-observer correlation between binocular rivalry percept durations and the strength of center-surround suppression (Steinwurzel et al., 2020; McKendrick et al., 2019), in contrast to our present findings. Steinwurzel et al. used a tilt illusion, rather than a contrast illusion, to index center-surround suppression, providing one potential explanation for the difference in results. McKendrick et al. (2019) did use a contrast illusion like ours as their measure of center-surround suppression, but it should be mentioned that theirs was a preliminary study. Specifics of experimental paradigm aside, both Steinwurzel et al. (2020) and McKendrick et al. (2019) interpreted their results in terms of the role of cortical inhibition in binocular rivalry. In the face of the combined evidence from all available studies, as well as the intuitive appeal of the notion that cortical inhibition is involved in perceptual suppression, it would not be warranted to use our results as a basis to strongly oppose that notion. However, our results do argue against the idea that inter-observer variability in the strength of cortical inhibition, to the extent that it is expressed in the perceptual strength of center-surround suppression, can account for inter-observer variability in the dynamics of bistable perception.

There are several possible explanations as to why we did not replicate the previous findings of an inter-observer correlation between binocular rivalry measures and surround suppression measures. As already briefly mentioned above, there are differences in the particulars of the stimuli and the paradigms used in the earlier studies (Steinwurzel et al., 2020; McKendrick et al., 2019) as compared to our study. Aside from stimulus differences, it is possible that the correlations between binocular rivalry perception and center-surround suppression that were reported in previous work were false positives, or that the lack of any such correlation in our present work amounts to a false negative. Therefore, it is relevant to compare indices of statistical power between studies: the number of participants in our study (i.e. 120 included for both binocular rivalry and center-surround suppression, after applying exclusion criteria) is considerably larger than the numbers from the previous studies (50 and 57 for Steinwurzel et al. and McKendrick et al., respectively). When it comes to the total duration of viewing, which in the Steinwurzel et al., (2020) study was also reported, our binocular rivalry task consisted of 6 trials that lasted for a combined duration of 4 minutes per observer (excluding the mimic condition) as compared to 2 trials lasting for a combined duration of 6 minutes for Steinwurzel et al (2020), suggesting that per-observer estimates of percept duration were slightly more reliable in that existing study.

What can be concluded about the relationship between the dynamics of structure-from-motion perception with the dynamics of both binocular rivalry and bistable moving plaid perception? Our data shed some light on a potential correlation between the percept durations of binocular rivalry and structure-from-motion, which has been reported by one previous study

(Steinwurzel et al., 2020), but which was not observed by others (Brascamp et al., 2018; Cao et al., 2018). Our data from both the experiments here are consistent with the idea that there might be fragile correlation between perception of the structure-from-motion stimulus and that of both binocular rivalry and bistable moving plaids since we find a correlation in some cases and no correlation in others. In the above we reported that there is no correlation between structure-from-motion and either binocular rivalry or bistable moving plaids, which is true when using the Pearson correlation coefficient, as we had set out to do at the start. An exploratory analysis using Spearman correlation coefficients instead, however, indicates a weak correlation between the (log-transformed) percept durations of structure-from-motion perception and binocular rivalry ($\rho(142) = 0.213$, $p = 0.011$) although not between structure-from-motion perception and bistable moving plaids ($\rho(150) = 0.095$, $p = 0.247$). Additionally, when we analyzed the data by dividing our sample into two halves based on the participants' performance on the center-surround suppression task, as described above, we found that the Spearman correlations with structure-from-motion became statistically significant for both binocular rivalry ($\rho(52)= 0.358$, $p = 0.009$) and bistable moving plaids ($\rho(56)= 0.263$, $p = 0.05$), although Pearson correlations remained non-significant. In light of this ambiguity in our own data, as well as the conflicting results in the literature, it seems plausible that there is some correlation between the percept durations during structure-from-motion perception and those during binocular rivalry or bistable moving plaid perception, but that it is not sufficiently strong to be observed consistently.

General discussion

As mentioned in the Introduction section, this work is partly inspired by previous work that showed correlations between distinct bistable stimuli in terms of the temporal dynamics of the perception they elicit. Such correlations can be informative as to what drives those dynamics. Our present findings add to the body of work showing that some bistable stimuli do correlate in that regard, whereas others seem not to. Across the available papers, the most consistently reported correlation seems to be the one between the percept durations of binocular rivalry and those of bistable moving plaids (Brascamp et al., 2019; Cao et al., 2018; Sheppard & Pettigrew, 2006), and our present results provide further confidence that that correlation is robust. Correlations involving other bistable stimuli are often fragile which is especially observed in the case of structure-from-motion stimulus as well as rotating Necker cube stimulus. From the perspective that between-paradigm correlations may inform about underlying mechanisms, the notion that correlations are strong between only some bistable perception paradigms yet weak or absent between others, renders the more consistent correlations all the more interesting: apparently they do not reflect non-specific factors that influence perceptual bistability across the board. Our results however do not support the notion that the correlation between binocular rivalry and bistable moving plaids is related to variability in cortical inhibition. Since there is a robust correlation between binocular rivalry and bistable moving plaids, future research should focus on what the mechanism underlying these bistable paradigms could be.

In sum, our findings add to the body of work that delineates which bistable perception paradigms do correlate with each other in terms of perceptual dynamics and which do not, and our findings do not provide support for the idea that those correlations that do exist, reflect inter-observer variability in the strength of cortical inhibition.

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