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Local Factors Determine the Stabilization of Monocular Ambiguous and Binocular Rivalry Stimuli

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Summary

Perceptual alternation in viewing bistable stimuli can be slowed or halted if the stimuli are presented intermittently [1, 2]. Memory of the recent perceptual experience has been proposed to explain this stabilization effect. But the nature of this "perceptual memory" remains unclear. By using a bistable rotating cylinder and two dichoptically presented orthogonal gratings, we explored the features that are important for the stabilization by changing a particular feature of the stimuli between alternate presentations. For the rotating cylinder, changing its color, rotating speed, size, or its stereo depth had no or minimal effect on the stabilization of its perceived rotation direction. For binocular rivalry, when the two gratings were matched in strength and then swapped between the two eyes synchronously with the intermittent presentation, the percepts were usually stabilized to one eye. In both cases, perceptual stabilization occurred only if the stimuli were presented to the same retinal location. These results suggest that the stabilization of monocular bistable stimuli is likely due to the removal of local adaptation, insensitive to the features that define the object identity. For binocular rivalry, preservation of the direction of interocular suppression rather than memory of the stimulus identity accounts for the stabilization effect.

Results and Discussion

Visual perception is generally accurate and stable. However, when the stimulus provides conflicting or insufficient information, perception can be bistable or even multistable [3, 4]. Studying the visual system's solution when faced with these ambiguous conditions can yield important clues to the underlying mechanisms of visual perception, because one of the major tasks of vision is resolving ambiguous incoming information. Figure 1 illustrates two examples of ambiguous stimuli used in the current study: a bistable rotating cylinder and a pair of stimuli that induce binocular rivalry. The monocular bistable stimulus was an orthographic projection of dots on the surface of a rotating cylinder to a 2D plane and is perceived as a rotating cylinder with ambiguous direction of rotation. This stimulus is composed of two sets of random dots moving in opposite directions within a rectangular area on the computer screen, their speeds following a sinusoidal function. The motion signal generates a vivid impression of a rotating cylinder because of the kinetic depth effect (KDE) [5, 6]. However, because either of the two sets of dots can be perceived as the front or the back surface, the rotation direction is bistable, alternating between two perceived rotating directions every few seconds. It is also possible to perceive two concave or two convex surfaces [3], but that was rarely reported by our observers and does not affect the results of the current study. Also depicted in Figure 1 is an example of binocular rivalry, the alternating perception of each eye's stimulus, which occurs when two different stimuli (e.g., a green radial grating and a red circular grating) are dichoptically presented to the corresponding retinal locations in the two eyes.

Viewing bistable stimuli continuously results in perceptual switches between the two or more interpretations of these stimuli. An important question is what drives these perceptual switches. Neural adaptation of the dominant stimulus or dominant view has been proposed to play an important role in this process [7], but high-level cognitive factors have also been suggested to be important [4, 8, 9]. Interestingly, when the bistable stimuli are presented intermittently, observers experience much fewer or even no alternations of the percept [1, 2]. For the rotating cylinder, observers often see it rotating in the same direction over many presentations. Perception during binocular rivalry can also be stabilized by the intermittent presentation of the stimuli [1]. Why does the visual system prefer the same interpretation when the stimulus is presented intermittently? According to Leopold et al., it is the memory of the recent perceptual history that facilitates the current interpretation [1]. Perceptual memory can include a vast amount of information. If it is perceptual memory that underlies the stabilization, a key question is what kind of information in the perceptual memory is crucial to the stabilization. The mechanisms responsible for monocular bistability and binocular rivalry could be different, although it has been suggested that the two groups of phenomena are similar in some ways [10, 11]. We studied the factors important for perceptual stabilization separately for a bistable KDE stimulus and a pair of binocular-rivalry stimuli.

Monocular Bistable Rotating Cylinder

A rotating cylinder with ambiguous direction of rotation (Figure 1A) was used here as the bistable stimulus. With

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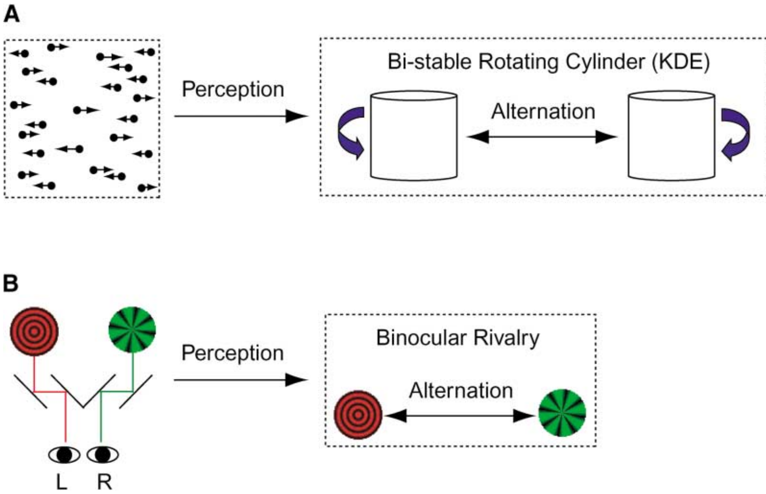

Figure 1. Schematic Depictions of Bistable Stimuli Used in the Current Study

(A) Monocular bistable stimulus. Randomly distributed dots moving within a rectangular area with their speeds following a sinusoidal pattern. Because of the kinetic depth effect, a cylinder can be seen alternating between rotating clockwise and counterclockwise.

(B) Binocular rivalry. The circular and radial gratings are dichoptically presented to the two eyes through a pair of mirror stereoscope. Observers perceive the alternation between these two stimuli.

intermittent presentation, the bistable cylinder was almost always perceived to rotate in the same direction each time it was presented [1]. Apparently some information is maintained across presentations. If this is indeed a form of perceptual memory, what type of information is stored in the perceptual memory? Is the object identity part of this memory? Is it important for the observer to recognize the stimulus as the same stimulus from one presentation to the next? To answer these questions, we changed certain features of the bistable stimulus from one presentation to the next by using the intermittent presentation paradigm (Figure 2). For example, the color of the stimulus varied alternately between red and green in the intermittent presentations. Because the current stimulus does not match the perceptual memory of the previous one in certain dimensions (e.g., color), would the visual system maintain the same interpretation for rotation direction for the bistable stimulus? If the remembered information was the identity of the object, then changing a feature of the cylinder should reduce the preservation of the same rotation direction. We tested which factors were important to the stabilization of the rotation direction. A number of features were changed between alternate presentations to investigate whether the stabilization was affected by the change. The changes included color, size, speed, depth, and spatial location (Figures 2A and 2B).

Our results show that changing color, size, rotation speed, or stereo depth had minimal or no influence on the stabilization of the rotation direction, but changing location significantly reduced stabilization (Figure 2). Furthermore, changing location across the vertical meridian (stimulus projected alternately to the two hemispheres) more severely disrupted stabilization than changing location across the horizontal meridian (stimulus always projected to the same hemisphere). The results are summarized in Figure 2C, which shows the frequency of perceptual switches of rotation direction under the six different test conditions (a frequency of zero means no perceptual switch, i.e., stabilized perception). Apparently, the perceptual memory important to the stabilization of perceived rotation direction is independent of the object identity but, surprisingly, is dependent on the stimulus location.

Binocular Rivalry

With intermittent dichoptic presentation of two different stimuli engaged in binocular rivalry, Leopold and colleagues reported that perception was stabilized to one stimulus [1]. We replicated this observation in the present study (Figure 3Aa). We then tested whether the stabilization effect during intermittent presentation was due to the facilitation of one eye or "perceptual memory" for one stimulus by swapping the two stimuli between the left and right eye in each sequential presentation.

Binocular rivalry is a competitive process between the two eyes' stimuli. If one stimulus is considerably stronger than the other, then the stronger stimulus is expected to be dominant [12–14] and will be visible during each of the intermittent presentations (i.e., stabilized). However, if the two stimuli are approximately balanced in their strength, then it is unclear whether the stabilization effect observed by Leopold et al. is due to facilitation of one stimulus (as advocated by Leopold et al. [1]) or one eye. Their results could not distinguish between these two possibilities, because one stimulus was always presented to the same one eye and the other stimulus to the other eye in their experiments. In other words, the dominant eye and dominant stimulus always covaried. In our study, we aim to tease these two possibilities apart by swapping the two stimuli between the two eyes during the intermittent presentations (Figure 3Ab). If the perceptual memory of the dominant stimulus underlies the stabilization effect, then observers should see the same stimulus appear over repeated presentations, though coming from each of the two eyes alternately. However, if the stabilization effect is due to the facilitation of one eye, one would expect observers to see the two stimuli alternating, originating from the same eye. Our results show that perception was stabilized to one eye when the stimuli were swapped between the two eyes during binocular rivalry (Figures 3Ab and 3C). Similar results were obtained by Pearson and Clifford [15]. In this case, the so-called perceptual memory for stabilization may be the memory of the eye of origin. Since the eye of origin information is not explicitly represented in perception, this result argues for a simple maintenance of the direction of interocular suppression as the explanation of the stabilization effect during bin-

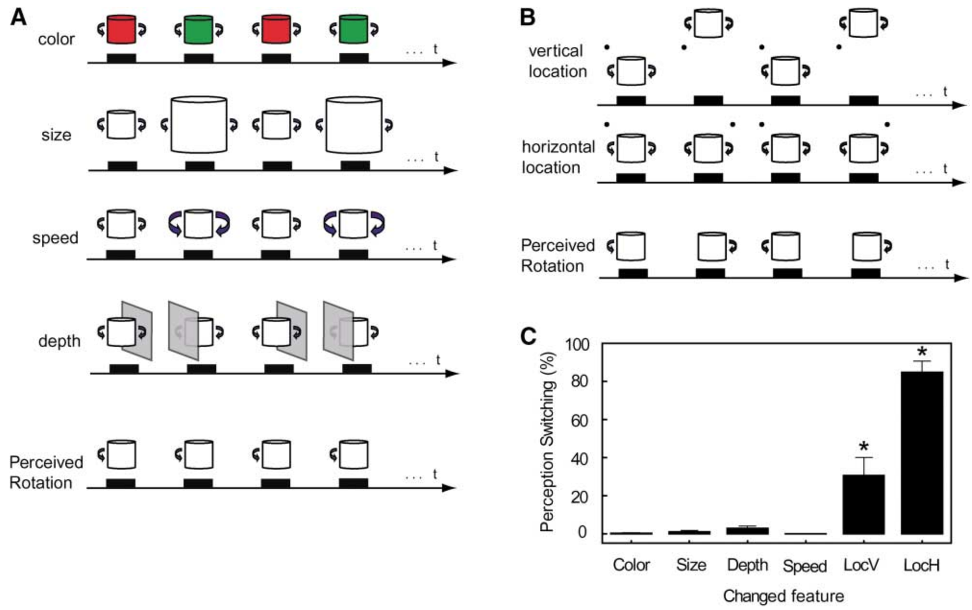

Figure 2. Experimental Conditions and Effects of Feature Change on the Perception of the Bistable Cylinder

(A) Changing a feature: color, size, rotation speed, and depth of the stimulus during the intermittent presentations of the bistable cylinder had minimal or no effect on the stabilization of the cylinder.

(B) Changing the location of the stimulus vertically or horizontally during the intermittent presentations of the bistable cylinder did affect the stabilization of the cylinder.

(C) Results summary of the bistable-cylinder experiment from seven observers. Features that were changed during the presentation were labeled on the horizontal axis. LocV and LocH stand for changing location in the vertical and horizontal direction, respectively. Frequency of perceptual switches is plotted on the ordinate. Error bars are 1 SE. Only 2D location changes resulted in frequent switches in perceptual state. LocV and LocH both reached statistical significance (indicated by an asterisk). Changing the position horizontally (across the midline) was especially effective in breaking the overall perceptual stabilization, with the possibility that perception was independently stabilized locally.

ocular rivalry. Furthermore, this stabilization effect is retinotopically specific and local in that there was no systematic stabilization across spatial locations (Figures 3B and 3C). Not surprisingly, when one of the two stimuli was stronger (e.g., higher contrast), the observer's perception was stabilized to the stronger stimulus (Figures 3Ac and 3C).

Local Adaptation as the Explanation for Switching

The stabilization effect of both the monocular bistable and binocular-rivalry stimuli is location specific and insensitive to changes in concurrent stimulus features. This finding is consistent with the view that the possible mechanism underlying the stabilization is the removal of local adaptation, as suggested by Blake et al. through a different paradigm [7]. For binocular rivalry, the stabilization effect is specific to the eye rather than to the stimulus, suggesting that what is preserved from presentation to presentation is not the memory or representation of the stimulus, but the direction of interocular suppression between the two eyes. Normally the direction of interocular suppression cannot be maintained for long due to local adaptation of the dominant stimulus.

It is likely that some form of inertia exists in perception, including bistable perception: when the perceptual system reaches an interpretation, it stays with that interpretation, unless another force is strong enough to change that. In the case of bistable perception and binocular rivalry, that other force, we assume, is local adaptation. Indeed, Fang and He recently showed that exposure to a subjectively stabilized, ambiguous, rotating stimulus leads to a perceptual aftereffect—the ambiguous, rotating stimulus was perceived to rotate in the opposite direction [16]. In Leopold et al.'s intermittent presentation paradigm, a possible explanation of the stabilization effect is that local adaptation could not accumulate enough strength to overturn one perception for the other because of the temporal gap. Thus, the perceptual inertia dominates between presentations. Similar reasoning can be applied to the findings of Blake et al. [7]. In their study, the ambiguous stimuli were slowly moved across the retina, which also averts sufficient local adaptation. In both cases, the consequences are the same: stabilization of the percept. In the current study, we provide evidence that the key factor behind the stabilization is not a representation of object features, but something that is local and is likely the removal of local adaptation of the dominant perception (direction of motion in the case of KDE or direction of interocular suppression in the case of binocular rivalry).

Conclusions

For the bistable, rotating cylinder, rotation direction is represented independent of color, size, rotating speed, and depth but specific to its location. For binocular rivalry, aside from the trivial stimulus stabilization when one stimulus is much stronger, perception seems to be stabilized to one eye. This may be the result of the

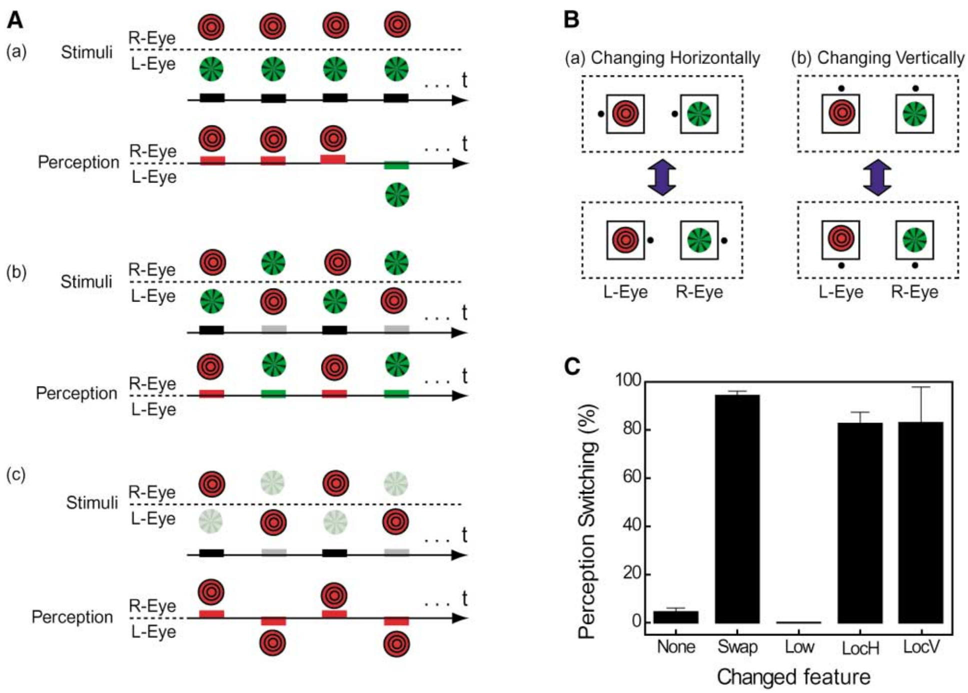

Figure 3. Schematic Depiction of Experimental Conditions and Results in the Binocular Rivalry Experiment

(A) During intermittent binocular rivalry, (a) the observer's perception was stabilized as shown by the very few alternations experienced. (b) If the stimuli were swapped between the two eyes, the observers perceived the alternating stimuli of one eye instead of a constant stimulus; (c) if one of the two rivaling stimuli was much stronger than the other, the observers often perceived the stronger one.

(B) Changing the locations of the stimuli in both eyes horizontally (a) and vertically (b) during the intermittent presentations affected the stabilization of binocular rivalry.

(C) Result summary on the binocular rivalry experiments. Abbreviations: none, no swapping of stimuli between the two eyes, such as depicted in (Aa); swap, the stimuli were swapped between the two eyes (e.g., [Ab]); low, one of the two stimuli was much stronger that the other (e.g., [Ac]); LocH, changing locations horizontally (e.g., [Ba]); and LocV, changing locations vertically (e.g., [Bb]). Frequency of perceptual switches is plotted on the ordinate. Error bars are 1 SE.

maintained interocular suppression due to the reduction of local adaptation. The underlying mechanisms for stabilization of bistable stimuli are location or eye specific, suggesting that what is "remembered" from one presentation to the next may not be high-level object information.

Experimental Procedures

Observers

Ten right-handed observers (three for the rotating cylinder experiments, three for the binocular-rivalry experiments, four for both experiments, including the two authors; four males and six females, ages between 22–38) participated in this study. All observers had normal or corrected-to-normal visual acuity. No formal stereo test was administered, but all observers could see images in random-dot stereograms. The experiments were performed under the approval of the University of Minnesota human subjects review committee. Except for the two authors, all participants received monetary compensation for their time.

Apparatus

Stimuli were generated with Vision Shell software (http://www.visionshell.com/) running on a PowerPC Macintosh computer. A Sony 17seII monitor was used to present the stimuli. In the binocular-rivalry experiments and the changing-depth experiment for the rotating cylinder, observers viewed the image on the left half of the screen with their left eyes and the right half with right eyes through a mirror stereoscope. In all rotating-cylinder and binocular-rivalry experimental conditions, the observers' head and eye positions were fixed with a chin rest. Their responses were recorded through keyboard presses.

Stimuli

The stimulus for the rotating-cylinder experiments was composed of 200 random white dots moving in opposite directions within a rectangular area on a black computer screen. Dot speed varied as a sinusoidal function of the horizontal position, conforming to a 2D projection of dots on a transparent cylinder rotating at a rate of one revolution every 2.8 s. The stimulus is usually perceived as a bistable cylinder rotating in one of the two directions for several seconds and then alternating to the other. The diameter of each dot was 0.06°. The rectangular area was $3.0° \times 3.0°$, and a fixation point was placed at the center of the cylinder. In the changing color experiment, the color of the dots varied between red and green alternatively.

The stimuli for the binocular rivalry experiments were a red (CIE $x = 0.61$, $y = 0.35$) circular sine-wave grating and a green (CIE $x = 0.28$, $y = 0.59$) radial sine-wave grating. One was presented on the left part of the screen and the other on the right. This pair of stimuli was selected because they gave relatively clean and crisp rivalry, with minimum mixture status. The diameters of the gratings were 0.7°. The red circular grating had three, cycles and the green radial grating had eight cycles. The mean luminance of both gratings was set at 15 cd/m^2 and their contrast at 0.99. The stimuli were presented on a gray background with a luminance also set at 15 cd/m^2. A fixation point was placed at the center of each grating. A black square frame surrounding each grating was used to help keep the two eyes' stimuli aligned.

Experimental Conditions

Monocular Bistable Stimulus

Five conditions were tested in this study. Changes were made in: (1) color. The color of the dots alternated between red and green (Figure 2Aa). (2) Size. The size of the cylinder alternated between the standard size and twice the standard size (Figure 2Ab). (3) Speed. The rotating speed of the cylinder alternated between the standard speed and twice the standard speed (Figure 2Ac). (4) Stereo depth. Two rotating cylinders, one on the left part of the screen and the other on the right, were viewed through the stereoscope with disparity information. The magnitude of the stereoscopic disparity was 0.19°. A white square frame surrounding each cylinder was used to align them. A fixation point was placed on the intersection of two diagonal lines in the frame. The cylinder alternated between depth planes in front of and behind the fixation plane (Figure 2Ad). (5) Location. The cylinder size was modified to $1.5° \times 1.5°$ and placed at a distance of 2.8° from the center of the cylinder to the fixation point. It alternated vertically between the first and fourth quadrants or horizontally between the third and fourth quadrants (Figure 2B).

Binocular Rivalry

Four conditions were tested in this study. (1) Replicating the basic finding of Leopold et al. [1] on binocular rivalry. (2) Stimuli swapped between eyes. The red and green gratings were swapped between the two eyes in each intermittent presentation. Both gratings were set at full contrast to test eye stabilization. (Figure 3A). (3) Biased stimuli. Similar to the condition above, but the red grating was at full contrast and the green grating at 0.10 contrast to test stimulus stabilization. (4) Location change. The two gratings were presented alternately between two locations, either shifting horizontally or vertically, as shown in Figure 3B. The distance between the center of the grating and the fixation point was 1.4°.

Procedure

Each observer was first positioned on the chin rest and then was asked to fixate on the fixation point. For the rotating-cylinder experiments, because each observer potentially has a biased initial direction of rotation and to avoid observers' always stabilizing to the biased direction, the cylinder was presented continuously first and observers had the control of when to start the intermittent presentation. In half of the trials, they were instructed to start (by pressing the space bar) the intermittent presentation when the cylinder was perceived to rotate in one direction and in the other half of the trials when the cylinder was perceived in the opposite direction. Once the intermittent presentation began, the cylinder was presented on the screen for 1 s and then turned off for 2 s repeatedly in a 2 min trial. Each observer performed two to four trials for each experimental condition, and the order in which the trials were encountered was randomized across the observers. The observers were instructed to report their perceived rotation direction each time the cylinder was displayed. They pressed the space bar for the rotation leftward and the "0" key for the rotation rightward.

In the changing-depth condition of the rotating cylinder, the mirrors of the stereoscope were adjusted so that the fixation points and the frames presented to the two eyes were precisely fused, and the cylinder appeared at a different stereoscopic depth from that of the fixation plane. A similar adjustment was done in the binocular rivalry experiments so that the two gratings were perfectly aligned. During binocular rivalry, the gratings were presented for 0.5 s and then disappeared for 2 s repeatedly in a 2 min trial. The observers were required to press the space bar when they saw the green grating and the "0" key when they saw the red grating.

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