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An International Journal for Functional Aspects of Vision
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Vision Research 63 (2012) 63–68

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Stereopsis and binocular rivalry are based on perceived rather than physical orientations

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ARTICLE INFO

Article history:
Received 23 January 2012
Received in revised form 19 April 2012
Available online 15 May 2012

Keywords:
Binocular vision
Binocular rivalry
Stereopsis
Depth perception
Orientation illusion

ABSTRACT

Binocular rivalry is an intriguing phenomenon: when different images are displayed to the two eyes, perception alternates between these two images. What determines whether two monocular images engage in fusion or in rivalry: the physical difference between these images or the difference between the percepts resulting from the images? We investigated that question by measuring the interocular difference of grid orientation needed to produce a transition from fusion to rivalry and by changing those transitions by means of a superimposed tilt illusion. Fusion was attested by a correct stereoscopic slant perception of the grid. The superimposed tilt illusion was achieved in displaying small segments on the grids. We found that the illusion can change the fusion–rivalry transitions indicating that rivalry and fusion are based on the perceived orientations rather than the displayed ones. In a second experiment, we confirmed that the absence of binocular rivalry resulted in fusion and stereoscopic slant perception. We conclude that the superimposed tilt illusion arises at a level of visual processing prior to those stages mediating binocular rivalry and stereoscopic depth extraction.

1. Introduction

When we look at objects, their visual appearance do not necessarily reflect their exact physical characteristics. This is because visual awareness is the culmination of multiple computational steps involving transformations of the neural representations of the objects' retinal images. Some of those steps entail contrasting operations that embody powerful context effects – one object's appearance is affected by other objects in its vicinity. These contrasting operations are functionally important and integral to normal visual processing, but they can also produce beguiling visual illusions. Consider, for example, the object attribute of color. Patterns of light wavelengths reflected from surfaces are transduced by three pools of cones broadly tuned to three ranges of wavelength (Dartnall, Bowmaker, & Mollon, 1983). In turn, information about surface color is extracted by an initial contrast between these pools (Mollon, 1982) followed by a second contrast that occurs between the chromatic signal at a specific location and the chromatic context around it. Thus, when two physically identical patches are viewed, they can sometimes appear colored differently because of the chromatic induction that has contrasted the color of the patches with the color contexts around the patches. Using chromatic induction, it is also possible to produce two perceptually identical surface colors that, in fact, reflect distinct patterns of wavelength to the eyes, producing startling color illusions (Shevell & Kingdom, 2008). Illusions like this provide a nifty mean for studying stages of processing in vision. Take, for example, the case of two physically identical stimuli that appear different in color because of induction. What happens if those two stimuli are presented one to each eye? Will they fuse (because they match physically) or will they rival (because they are dissimilar perceptually)? The answer is that they engage in binocular rivalry (Andrews & Lotto, 2004; Hong & Shevell, 2008). Conversely, physically different stimuli can fuse if chromatic induction causes them to appear identical. It appears, then, that rivalry and fusion are decided after the level of processing at which chromatic induction transpires. While this question has been answered for color, a similar question remains open for orientation.

Orientation is an important visual attribute that forms the basis for high level visual tasks such as object recognition (Marr, 1982). Oriented contours are extracted by integrating local activity from aligned contrast-computing cells (Hubel & Wiesel, 1962). Orientations at neighboring or superimposed locations are then contrasted. This computation can generate several distinct illusions of tilt. One is a *center–surround contrast*: the orientation of contours within a central patch appear rotated several degrees away from

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http://dx.doi.org/10.1016/j.visres.2012.05.003

their true orientation when the patch is surrounded by an annulus of contours all tilted at an orientation different from the contours in the central patch (Blakemore, Carpenter, & Georgeson, 1970; Julesz & Tyler, 1976). A second illusion is a *superimposed tilt illusion* wherein the two orientations are displayed simultaneously at the same location (Blake, Holopigian, & Jauch, 1985; Gibson & Radner, 1937).

Rao (1977) reported that center–surround contrast disappears when the surround is suppressed from awareness by a rivalrous high contrast patch, but he provided no quantitative measures of this effect. A few years later, Wade (1980) showed that Rao's report could actually be explained by a 50% interocular transfer of the center–surround repulsion. Wade provided quantitative evidence that the repulsion survives rivalry suppression, suggesting that orientation contrast between center and surround occurs before the level of rivalry suppression. Partial interocular transfer can be interpreted as follows: the repulsion is the sum of two center–surround repulsion effects at monocular and binocular levels. The binocular repulsion does transfer between the eyes while the monocular does not. However, such an interocular transfer was not confirmed in another study (Walker, 1978).

The superimposed tilt illusion has been extensively measured (Gibson & Radner, 1937; O'Toole & Wenderoth, 1977; Over, Broerse, & Crassini, 1972): it leads to a similar repulsion as the center–surround contrast. To the best of our knowledge, it has not been studied in binocular rivalry conditions. The superimposed tilt illusion is very likely related to the Zöllner illusion (Zöllner, 1860). In the Zöllner illusion, the perceived orientation of long lines is influenced by orientation of superimposed short lines (*inducers*, see Fig. 1a). For large angles (50–90°), the superimposed tilt illusion takes the form of a reduction of perceived angles (indirect effect: Gibson & Radner, 1937; O'Toole & Wenderoth, 1977). Lau (1922) and Squires (1956) reported that the orientation deviation produced in the Zöllner illusion could produce stereoscopic depth when orientation is different between eyes. Others have tried but failed to find depth produced from illusory orientation differences in such conditions (Julesz, 1971; Ogle, 1962) but none provided any quantitative measurements. To our knowledge, no other work has attempted to confirm or disconfirm these last reports, so that the level of the superimposed tilt illusion remains unknown.

In addition, there is a lack of data about the nature of the orientations engaged in rivalry: are they oriented like the physical orientations before the occurrence of any contrasts or like the illusory orientations that are generated after those contrasts?

In the present study, both questions were addressed by investigating the transition from fusion/stereopsis to binocular rivalry that occurs when increasingly large orientation disparities are introduced between the two eyes. In our study we measured those transitions under conditions where the orientation difference could be augmented or diminished by the superimposed orientation illusion (based on the Zöllner illusion). Here is our reasoning. When a difference in orientation between monocular grids (orientation disparity) exists (Fig. 1b), observers perceive stereoscopic slant (Fig. 1c). As orientation disparity is increased, fusion fails and the grids engage in rivalry (Fig. 2a). Imagine that grids with the orientation disparity near the transition between fusion and rivalry are displayed and we add short fused lines (inducers) to the grid. If the orientation illusion occurs monocularly, some inducers will increase the orientation disparity of the grids and others will decrease it. If stereopsis and rivalry are based on the illusory orientations, grid orientations could be perceptually changed so that they can now be fused and produce stereoscopic depth, and conversely, they could be pushed into rivalry. Transition points between fusion and rivalry would be shifted by different inducers.

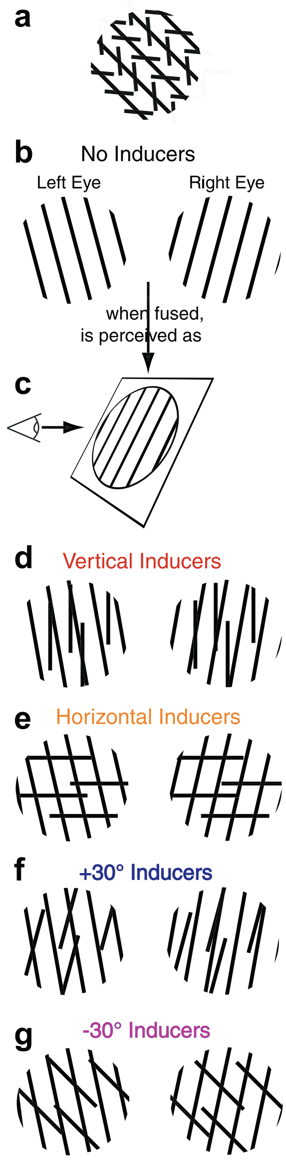

Fig. 1. Stimuli: (a) Zöllner illusion: long lines do not appear parallel although they are parallel. Inducers change the perceived orientations of the long lines; (b) left and right eye images are fused into a slanted surface (c) because of the orientation difference between eyes. Schematics of the left and right eye displays in the conditions with vertical inducers (d), horizontal inducers (e), +30° inducers (f) and −30° inducers (g).

2. Material and methods

2.1. Stimulus and material

Gratings were nearly vertical grids of black lines (width: 0.02°, luminance: 3 cd m^{-2}, spatial frequency: 2 cpd). Luminance of the pattern was spatially shaped by a Gaussian envelope centered on the grating (0.5° at half height). Twenty black segments (inducers) were added to the display in several conditions: their locations were random and their lengths were identical, 0.8°. Stimuli were displayed through a circular aperture of 4.2° with a central red fixation dot: the grating covered the whole area visible through the aperture. Background luminance was 15 cd m^{-2} (line contrast: 0.8). Stimuli were displayed for 2 s (Experiment 1) or 3 s (Experiment 2). Vergence was maintained by a group of small white squares surrounding the stimuli. Dichoptic stimulation was

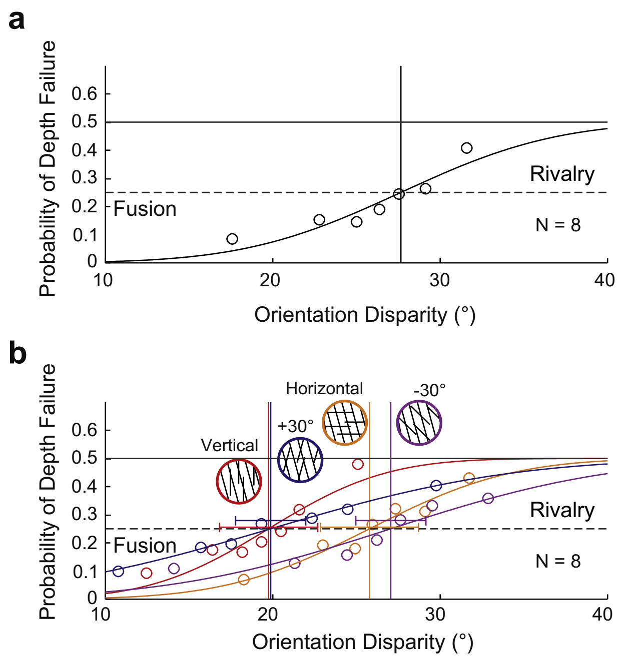

Fig. 2. Experiment 1: (a) Probability of failure in estimating the slant as a function of the interocular difference in grid orientation. It illustrates the transition between fusion (low failure probability) and rivalry (performance at chance) for the *no inducers* condition. The horizontal black solid line indicates depth perception at chance. The horizontal black dashed line indicates the 75% correct performance for depth perception. (b) Probability of failure in estimating the grid slant as a function of the interocular difference in grid orientation. The four conditions are vertical inducers (red), horizontal inducers (orange), +30° (blue) and −30° (purple). Open circles are data from the staircases, averaged between observers and split into 7 bins. Solid curves are maximum likelihood estimates with a cumulative Gaussian curve. Vertical colored solid lines depict transition points for each condition. Error bars are within-subject 95%-confidence intervals (Masson & Loftus, 2003) for the horizontal/vertical inducer comparison and the +30°/−30° comparison.

achieved using a modified Wheatstone stereoscope with a chin rest in a darkened room. Distance between the screen and the observer was 61.5 cm. Stimuli were displayed on a 21-in. CRT monitor at a frame rate of 120 Hz and a resolution of 1280 × 960 pixels. Stimuli were generated with the PsychToolBox library (Brainard, 1997; Pelli, 1997) on a G5 Macintosh computer.

2.2. Observers

Eight observers (one woman, seven men) with normal or corrected vision (Snellen acuity equal or greater than 20/30) participated in the experiment. All observers had normal far acuity, color vision, no lateral or vertical far phoria, no lateral near phoria and far and near stereo perception of less than 25 s of arc. Six of the eight observers were naïve as to the purpose of the experiment.

2.3. Procedure

In Experiment 1, the interocular difference (disparity) of the grid orientations was varied according to a staircase procedure. Grid orientation disparity compatible with fusion usually creates the perception of a surface slanted about the horizontal axis, such that the top of the surface relative to the bottom appears slanted away from the observer ("uphill" slant) or slanted toward the observer ("downhill" slant). Following each presentation, observers reported the direction of that slant (uphill or downhill). The goal of the staircase was to find the orientation disparity for which observers' performance on this 2AFC slant discrimination task was 75% correct (50% was the level of chance): the transition point between fusion and rivalry. The disparity was made larger so long as the observer responded correctly. The staircase core was an adaptive stochastic approximation procedure (Kesten, 1958). For each condition, two independent staircases were run, one starting at 10° of orientation disparity and the other at 30°. All staircases were intermixed between conditions. When the two staircases of a condition did not converge to approximately the same value, they were automatically repeated. Failure of convergence was defined to exist when the distance between converging values was more than three times their average standard deviation (after a maximum likelihood estimation fit with a Gaussian cumulative function).

Observers were tested in two main conditions and three control conditions. In all conditions, inducers, when present, were always displayed identically in the two eyes. The two first conditions contrasted the inducers influence. In the *vertical inducer* condition, inducers were vertical and a shift of perception toward rivalry was expected if orientation illusion occurred. Conversely, in the *horizontal inducer* condition, inducers were horizontal and a smaller shift toward fusion was expected if orientation illusion occurred. In a neutral *no inducer* condition, the absence of inducers allowed us to assess the influence of the inducers themselves, independently of their orientation. Finally, the two last conditions allowed us to test for an alternative hypothesis according to which the more the inducers are oriented like the grid, the more they interfere with fusion. In the +30° condition, inducers were oriented exactly 30° relative to the grid in one eye so that perception was maximally pushed toward rivalry in that eye, and has the same orientation in the other eye. In that other eye, inducers were almost parallel to the grid so that almost no effect was expected for that eye. The expected effect in the +30° condition is then the same as the one expected when inducers are vertical (near doubled in one eye added to near zero in the other). In the −30° condition, inducers were oriented exactly 30° relative to the grid in one eye so that perception was maximally pushed toward fusion in that eye. Thus, inducers were oriented 56° in average relative to the grid in the other eye, so that little effect was expected in that eye. Consequently, the expected effect was the same in the −30° condition and in the horizontal one.

In Experiment 2, the transition point m observed in the *no inducer* condition (Experiment 1) was noted and seven orientation disparities were selected equally distributed between $m - 2$ standard deviations and $m + 2$ standard deviations. Each chosen orientation disparity was administered twenty times with the *no inducer* stimulus and the following task consisting of two parts. First, observers were asked to report whether the stimulus was bistable. If the stimulus was not bistable, they were asked to report the perceived surface slant.

Statistics were ANOVA comparisons. The hypothesis of normality could not be rejected for any sample (Kolmogorov–Smirnov test; $p > 0.27$) and statistics were adjusted for sphericity by the Greenhouse–Geisser coefficient.

3. Results

In Fig. 2, probability of fusion/depth failure is expressed as a function of orientation disparity. The transition point between fusion and rivalry is defined as the orientation disparity for which probability of depth failure is 25% (i.e., at midway between 0% representing fusion and 50% representing chance performance due to too large disparity). Large and consistent differences were found between transition points with vertical and horizontal inducers ($F(1,7) = 10.4$, $p = 0.015$, see Fig. 2b). As expected, the transition point in the vertical inducer condition was smaller than the one in the horizontal inducer condition: we interpret this difference as the influence of the inducers. The vertical inducers pushed the grids toward rivalry and the horizontal toward fusion, in a manner consistent with the orientation illusion they can trigger monocularly.

The transition point in the neutral condition appears larger than in any other inducer condition (Fig. 2a), but the difference from the mean of all other conditions is not statistically significant (only a trend exists: $F(7,1) = 4.3$, $p = 0.077$). This result suggests that inducers may have the general effect of interfering with fusion and more precisely with the resolution of the correspondence problem. If this effect was dependant of the orientation difference between the grid and the inducers (the closer they are, the bigger is the fusion interference), it could explain the difference found between the horizontal and vertical inducer conditions (anti-fusion hypothesis) because the orientation difference between the grid and inducers is much smaller in the vertical than in the horizontal inducer condition. Thus, to test the anti-fusion hypothesis, the two conditions +30° and −30° were designed. As stated in the methods, the expected effect in the +30° condition is the same as in the vertical inducer condition and the expected effect in the −30° condition is the same as in the horizontal inducer condition. However, if we compare between these two conditions the difference between inducer orientation and grid orientation, their difference is much smaller than in the horizontal and vertical inducer conditions.

With vertical inducers, the difference between inducer orientation and grid orientation was around 20°, using the observed average orientation disparities at the transition points between rivalry and fusion, added between eyes. The same difference was about 154° with horizontal inducers. The difference of these differences is then 134°.

In the +30° condition, the difference between inducers and the grid (added between eyes) was 43°. In the −30° condition, the same difference was 86°. The difference of these differences was then only 43°.

According to the anti-fusion hypothesis, the transition points should be much closer between the +30° and the −30° conditions than between the horizontal and vertical inducer conditions because the differences between conditions of the grid and inducer orientation differences is only 43° for the +30° and −30° conditions vs. 134° with horizontal and vertical inducers. However, the same large difference was found between the +30° and the −30° conditions ($F(1,7) = 32.2$, $p = 0.001$; see Fig. 3) and this difference was not statistically different from the difference between the horizontal and vertical inducer conditions ($F(1,7) = 0.38$, $p > 0.10$).

In the first experiment, we measured only perceived slant and presumed from the absence of slant that rivalry occurred. After the loss of slant perception when orientation disparities are too large, it is still possible that no rivalry occurs. A percept of mixed eye fusion with no depth information would be perceived and rivalry would occur for even larger orientation disparities. We refer to this possibility as the hypothesis of *neither rivalry nor depth*. We tested this hypothesis with Experiment 2. In that experiment, phenomenological perception of rivalry was first reported, and perceived slant was measured when reports indicated an absence of rivalry. If the hypothesis of *neither rivalry nor depth* is correct, there would be orientation disparities for which no rivalry is reported and at the same time, stereoscopic slant perception would be at chance. Fig. 4a plots the proportion of trials where rivalry is reported as a function of orientation disparities. Orientation disparities larger than 30° result in rivalry more than 50% of the time. For those orientation disparities, when no rivalry is reported, slant can be perceived: Fig. 4b plots the proportion of correct responses when slant is reported. Observers are thus able to report the slant of the grid with a low error rate. In summary, observers perceive either stereoscopic slant or rivalry.

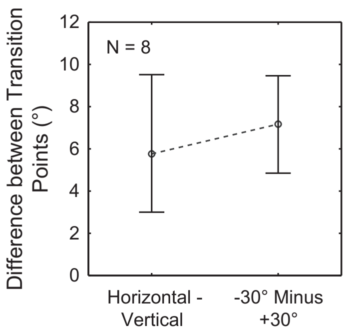

Fig. 3. Average difference between the transition points in the horizontal and vertical inducer conditions and in the +30° and −30° conditions, for all observers. Error bars are bootstrapped 95%-confidence intervals.

4. Discussion

We investigated whether the transition point between stereofusion and rivalry could be changed by induction of illusory shifts in perceived orientation. In Experiment 1, the large difference between horizontal and vertical inducers provided evidence that shifts in this transition point do occur.

The neutral condition (with no inducers) exhibited a transition point similar to those recently reported (Buckthought, Kim, & Wilson, 2008). Introducing inducers tended to prevent fusion of the grids, independently of their orientation. This tendency could vary with the orientation of the inducers and their difference. The same large difference found between the +30° and −30° conditions confirmed that this effect does not vary as a function of the difference in orientation between the inducers and the grid and therefore could not explain the results.

We interpret our results as follows: Each Zöllner-like orientation illusion occurs monocularly, before fusion–stereopsis or rivalry is resolved.

The conclusion about stereopsis comes naturally from the data because depth perception was measured. An additional measure is necessary to strictly extend our findings to the perception of rivalry. In Experiment 2, we confirmed that an absence of rivalry is replaced by slant perception, rather than by fusion with no depth signal. To be rigorous, is it necessary to also show that rivalry and slant perception cannot co-occur? There is strong evidences

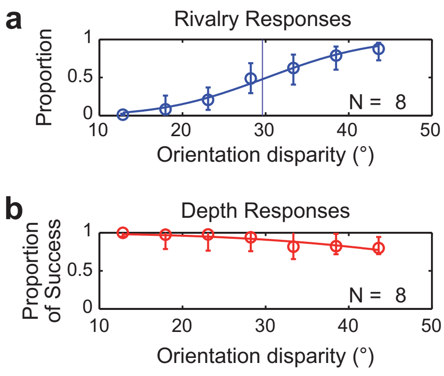

Fig. 4. Experiment 2: Phenomenology; (a) average proportion of rivalry responses among all the responses as a function of orientation disparity, for all observers. Vertical solid line indicates the 50% value. (b) Proportion of successful depth estimation among depth responses as a function of orientation disparity. Error bars are bootstrapped 95%-confidence intervals.

in favor of the main theory, according to which fusion has to occur to allow the disparity extraction and does not co-occur with rivalry (Blake, 1989; Blake & Boothroyd, 1985; Julesz & Tyler, 1976). A few studies have tried to challenge that view in showing, for example, that color rivalry (Treisman, 1962), illusory contour rivalry (Hong & Shevell, 2008) and stereopsis can co-occur or occur on different spatial frequency channels (Blakemore, 1970; Tyler & Sutter, 1979) but not on the same channels (Buckthought, Kim, & Wilson, 2008; Julesz & Miller, 1975). However, it has never been seriously demonstrated in spite of many attempts that normal contour rivalry (that we used here in our experiments) and stereopsis could happen jointly in the same spatial frequency channel.

Can the results be the consequence of the phenomenon called depth contrast, which is a repulsion between stereo-defined objects (Ogle, 1946): A line or a slanted surface defined in depth by the stereo cue has been found to be repulsed away from another surface at the same location that is slanted approximately the same way. In our experiments, when the grid as well as the inducers are fused, two planes exist, one fronto-parallel (inducers) and one slanted (the grid). It is likely that observers experience these planes with a slightly different slant so that their slants are actually repulsed from one another. However, there would be no difference between vertically oriented and horizontally oriented inducers: they generate the same fronto-parallel surface that triggers the same 3D plane repulsion.

What do we know about the neural bases of the Zöllner illusion? Several different hypotheses have been offered, all of which point to neural events transpiring early in visual processing. According to one view, the illusion results from inhibitory interactions between orientation columns (Blakemore, Carpenter, & Georgeson, 1970); physiological evidence for such interactions in V1 has been reported (Bosking et al., 1997; Kisvarday et al., 1997). According to a second hypothesis, the Zöllner illusion is caused by spatial filtering that produces distortions in the response peaks within orientation-tuned neural mechanisms (Morgan & Casco, 1990). This account has the virtue of linking the Zöllner illusion to the less-well known Judd illusion involving misperception of line length (Judd, 1899). There are characteristics of those illusions, however, that pose problems for the spatial filtering account (Earle & Maskell, 1995; Pastore, 1971).

Whatever the neural causes for the Zöllner illusion, our results indicate that those causes transpire prior to the site at which binocular rivalry suppression is triggered. In agreement with our conclusion, Julesz (1971) found that the Zöllner illusion was the only one among many other illusions that did not occur in exclusively cyclopean conditions (i.e., when the whole figure is depicted from binocular disparities in random stereograms). In this respect, the Zöllner illusion appears to differ from the illusory shift in perceived direction of motion that can occur when viewing two superimposed arrays of dots moving in different directions, i.e., the motion repulsion illusion (Marshak & Sekuler, 1979). When the two arrays of dots are viewed dichoptically (i.e., dots moving in one direction are presented to one eye and dots moving in the other direction are presented to the other eye, thus producing the stimulus conditions for binocular rivalry), motion repulsion is abolished (Chen, Matthews, & Qian, 2001). This observation suggests that motion repulsion arises from neural events transpiring after the suppression site of motion binocular rivalry. Is there some reason that orientation repulsion and motion repulsion arise at different stages of processing? Perhaps in the case of orientation, monocular repulsion between superimposed orientations contributes to our rather good resolution of stereoscopic slant (Gillam & Rogers, 1991), by exaggerating disparities in the orientation domain. In motion perception, there is no evidence that interocular differences in motion directions are involved in stereopsis, so sharpening of direction information is of no functional use prior to binocular combination.

In conclusion, we demonstrated that whether rivalry or stereopsis occurs depends on the illusory orientations rather than on the actual, displayed orientations.

Acknowledgments

This work was supported by a grant from the French Ministère de l'Enseignement Supérieur et de la Recherche, by a travel grant from Université Paris Descartes, by a grant from the National Institutes of Health (EY13358) and by the WCU program through the National Research Foundation of Korea funded by the Ministry of Education, Science and Technology (R32-10142).

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