

Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry

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Abstract

A way to study conscious perception is to expose the visual system to an ambiguous stimulus that instigates bi-stable perception. This provides the opportunity to study neural underpinnings related to the percepts rather than to the stimulus. We have recently developed a slant-rivalry paradigm that has beneficial metrical (quantitative) aspects and that exhibits temporal aspects of perceptual reversals that seemed to be under considerable voluntary control of the observer. Here we examined a range of different aspects of the temporal dynamics of the perceptual reversals of slant rivalry and we compared these with the dynamics of orthogonal grating rivalry, house-face rivalry, and Necker cube rivalry. We found that slant rivalry exhibits a qualitatively similar pattern of dynamics. The drift of the perceptual reversal rate, both across successive experimental repetitions, and across successive 35-s portions of data were similar. The sequential dependence of the durations of perceptual phases, too, revealed very similar patterns. The main quantitative difference, which could make slant rivalry a useful stimulus for future neurophysiological studies, is that the percept durations are relatively long compared to the other rivalry stimuli. In the paper that accompanies this paper [van Ee, R., van Dam, L. C. J., Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research*] we focused on the role of voluntary control in the dynamics of perceptual reversals.

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1. Introduction

A promising way to study visual perception is to expose the visual system to an ambiguous stimulus that generates bi-stable perception. This provides the rare opportunity to study neural states that are related to the percepts rather than to the stimulus (reviews in Blake, 2001; Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Logothetis, 1998; Tong, 2003). To study how bistable percepts are related to the metrical

aspects of the constituting signals, we have recently developed a “*slant rivalry*” paradigm that focuses on depth cue integration in stereoscopic vision (van Ee, van Dam, & Erkelens, 2002). The temporal aspects of perceptual reversals for slant rivalry seemed to be under considerable voluntary control. In the present paper we examine the dynamics of perceptual reversals of slant rivalry and we compare the dynamics with those of perceptual reversals obtained with a number of classical rivalry paradigms. In the paper that accompanies this paper (van Ee, van Dam, & Brouwer, 2005) we will focus on the role of voluntary control in the dynamics.

The rationale of the slant rivalry paradigm is as follows: Each of our eyes views a scene from a slightly different position. The resulting binocular disparities

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enable us to reconstruct the three-dimensional (3D) layout. One can construct stereograms in which the monocular depth reconstruction conflicts with the binocular one. In our studies we focus on surface slant perception: we use stimuli in which monocular perspective and binocular disparity specify opposite slants about the vertical axis. A key benefit of using a slanted surface is that one can transfer the stimulus from unambiguous to ambiguous by just adding a few pixels of disparity. And if this is done by evenly distributing the image transformations (creating the disparity gradient) over the two eye's images, all visual directions of the stimulus parts remain virtually fixed, so that the (spatial) image transformations remain unnoticed by the observer. Fig. 1(a) provides a demonstration of the bi-stability experienced with our slant rivalry stimulus (note the similarity with Ames' famous trapezoid stimulus). Upon inspection, the reader might be able to distinguish the two 3D percepts: one percept in which the grid's perceived slant is near to the disparity-specified slant and the other in which the perceived slant is closer to the perspective-specified slant. The two percepts are never present simultaneously. Although there are fundamental differences between observers in the estimated slant, for the whole spectrum of observers we are able to explain the metrical aspects of the (voluntarily) selected slant on the basis of the likelihoods of both perspective and disparity slant information, combined with prior assumptions about the shape and orientation of objects in the scene (van Ee, Adams, & Mamassian, 2003).

The literature on bi-stability that specifically addresses stereoscopic depth perception is sparse. The literature that comes closest examined reversible perspective (Brewster, 1826; Mach, 1866; Schriever, 1925; Wheatstone, 1838). This literature was forgotten for a while until, recently, the paintings of Patrick Hughes, revived the interest in reversible perspective (see Slyce, 1998 for the paintings). In itself reversible perspective is an interesting phenomenon to study, however, existing studies on it did not focus on its temporal aspects (or on the role of voluntary control).

The paradigms that we studied for comparison with our slant rivalry paradigm include binocular rivalry, namely orthogonal grating rivalry and house-face rivalry, as well as Necker cube rivalry. We studied orthogonal grating rivalry because it has been one of the most widely—and successfully—used stimuli for studying neural correlates of bistable perception (Blake, 1989; Breese, 1899; Logothetis, Leopold, & Sheinberg, 1996; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Wilson, Blake, & Lee, 2001; Wolfe, 1996). House-face rivalry is another form of binocular rivalry that has produced useful results (e.g., Lee & Blake, 2002; Rees, Kreiman, & Koch, 2002; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Finally,

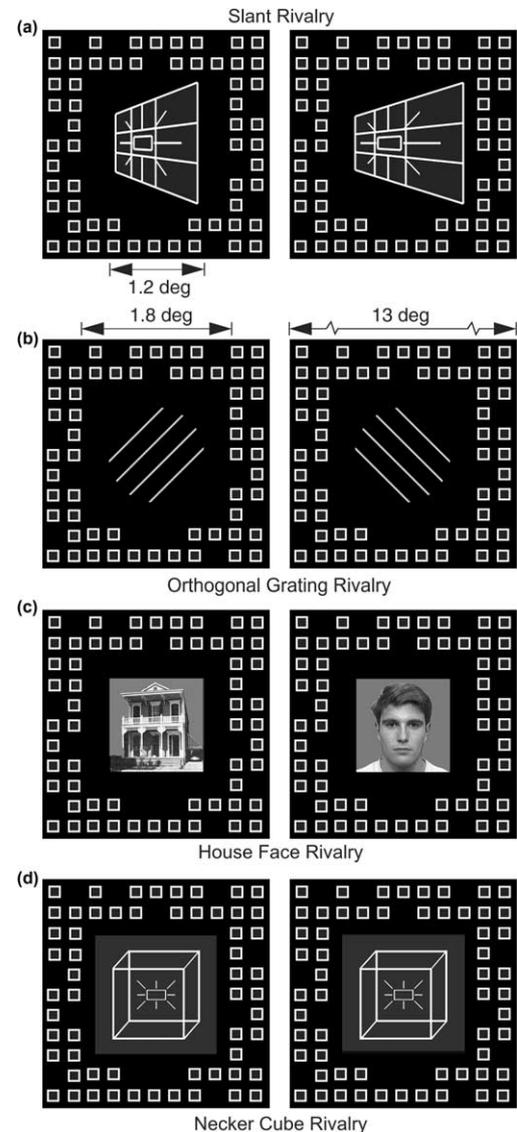


Fig. 1. The four rivalry stimuli studied. Panel a depicts the slant-rivalry stimulus for Expt 1. In this stereogram both linear perspective and binocular disparity specify surface slant about the vertical axis. By horizontally minifying one half-image of the trapezoid, and by magnifying the other half-image we created a disparity gradient. In this depiction, the minification (left panel) and the magnification (right panel) are exaggerated to pronounce the presence of the disparity gradient. In uncrossed fusion of the stereogram (the left eye views the left image and the right eye views the right image) two relatively stable percepts can be distinguished. In the first percept the grid recedes in depth with its left side further away (it is perceived as a slanted rectangle). In the other percept the left side of the grid is closer (it is perceived as a trapezoid with the near-edge shorter than the far-edge). Note that each of the two percepts can be selected and maintained at will in a relatively controlled fashion. More demonstrations can be found on our web page www.phys.uu.nl/~vaneel. Panels b to d depict the rivalrous stimuli for Expt 2: the orthogonal grating, the house-face stimulus, and the Necker cube, respectively. The angular width of the stimuli was fixed at 1.2°. The stimuli were presented within an aperture (1.8° × 1.8°) of a surrounding pattern (13° × 13°) that consisted of small squares. In fact the surrounding pattern consisted of more than the depicted two rows and columns of squares.

the third stimulus that we compared with our slant rivalry is the well-known Necker cube rivalry, which is interesting because it is a 3D perceptual rivalry stimulus (e.g., Meredith & Meredith, 1962; Necker, 1832; Washburn, Reagan, & Thurston, 1934).¹ The binocular rivalry paradigms are fundamentally different from slant rivalry and Necker cube rivalry, which concern perceptual rivalry.

To date, the dynamics for slant rivalry have not been described. In this paper we address this basic issue before we embark—in the accompanying paper (van Ee et al., 2005)—on the role of voluntary control in bi-stable perception.

2. Methods

2.1. Experiment 1

2.1.1. Stimuli and apparatus

In experiment 1 we examined the dynamics of the bistability that occurs when linear perspective and binocular disparity specify opposite slants. Fig. 1(a) shows a schematic (not to scale) example of the stimulus. In this depiction, the minification (left panel) and the magnification (right panel) are exaggerated to pronounce the presence of the disparity gradient.² We utilized a conventional red-green anaglyphic technique to present the trapezoid dichoptically. This technique enabled us to produce disparity-specified slant independently of the perspective-specified slant. Note that using this technique the two half-images were superimposed and projected onto corresponding retinal locations, meaning that the vergence eye posture was natural (i.e., not decoupled from the disparity information, as is the case in the schematic free-fusion stereogram of Fig. 1). The width of the trapezoid was 1.2° (before disparity was added to the grid stimulus). By horizontally minifying one half-image of the trapezoid, and by magnifying the other half-image, we

created a disparity gradient that specified a slant of 56° . Note that positive slant angles specify right side far. The disparity was evenly distributed over the two half-images so that the locations (or binocular visual directions) of the trapezoid segments in the fused stereo-image remained fixed. The foreshortening of the trapezoid in Fig. 1(a) (the short height was 0.95° ; the other height was 1.5°) created a monocular perspective cue that specified a slant about the vertical axis of -70° (i.e., left side far). The correct perspective and disparity distortions of the stimuli were generated using OpenGL libraries. The chosen combinations of perspective- and disparity-specified slants ($-70^\circ, 56^\circ$ or $70^\circ, -56^\circ$) were motivated by the reliable bi-stable percepts they evoked in our earlier work (see van Ee et al., 2002 or van Ee et al., 2003 for more details).

Subjects were seated at a viewing distance of 114 cm. The head was stabilized using a chin and forehead rest. The stimuli were viewed on a LaCie monitor ($20^\circ \times 15^\circ$; resolution 1600×1200 pixels). The aperture in which the trapezoid was presented measured $1.8^\circ \times 1.8^\circ$. A surrounding pattern ($13^\circ \times 13^\circ$; only part of it is shown in Fig. 1) consisting of small squares ($0.1^\circ \times 0.1^\circ$) provided a zero-slant reference and prevented depth contrast illusions. Only 80% of these surrounding squares were shown to prevent fixation in the wrong depth plane (wall-paper effect). Subjects were requested to keep their gaze within a central rectangle ($0.6^\circ \times 0.4^\circ$) of a sunburst-like fixation symbol. Line widths for the grid were $1.5'$; those for the background were $0.75'$. The intensities of the red and green half-images were adjusted until they appeared equiluminant when viewed through the red and green filters. The red and green filters were custom-made (using transmission filters provided by Bernell, Belgium) so that their transmission spectra matched the emission spectra of the monitor as well as reasonably possible. Photometric measurements showed that minute amounts of the green and the red light leaked through the red (0.4%) and the green (0.2%) filter, respectively. The room was completely dark, so only the grid and the reference were visible.

2.2. Task

After the subject fixated the sunburst symbol, the stimulus onset was initiated by a mouse click. While keeping their fixation within the sunburst symbol the subjects reported their perceptual reversals using two keyboard keys. One key signalled that the left side was perceived in front, the other key that the right side was perceived in front. Subjects were asked to view the stimulus for 3 min in a natural (or sometimes called “habitual”) way, without attempting to control the reversal rate.

¹ Another successful neurophysiological method is to study the 3D percepts generated by the structure-from-motion of a 2D projection of a transparent, rotating cylinder (or globe) with random dots on it (Blake, Sobel, & Gilroy, 2003; Bradley, Chang, & Andersen, 1998; Parker, Cumming, & Dodd, 1999). For this stimulus one has to make special precautions to prevent multistability (Hol, Koene, & van Ee, 2003).

² The relative size exaggeration in Fig. 1(a) consumed to a considerable extent the gaps between the trapezoid and the background; in the real stimulus this gap was about 0.3° on either side of the trapezoid. This gap in the stimulus is in fact important. By changing this gap one changes the influence of relative disparity on the final percept. If the gap is about zero then the disparity-specified percept will overrule the perspective-specified percept. If the gap becomes large the reverse is the case.

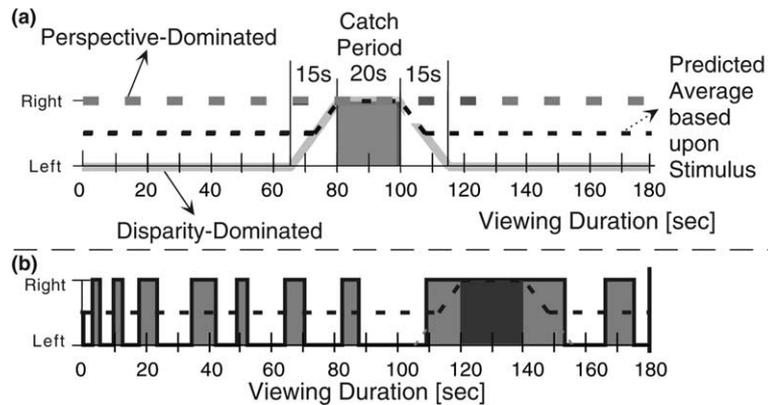


Fig. 2. Catch paradigm and time series of perceptual Reversals. (a) To ensure that the subjects were reporting their perceptual states reliably, rather than pressing keys at random, a catch period was added to all data collection blocks. In this example, the thick grey dashed horizontal line indicates that perspective specified a slant of right side front throughout the stimulus block (which lasted 180 s). The thick grey line indicates that disparity initially specified a slant that was opposite (rivalrous) in sign to the sign of the perspective-specified slant. The rivalrous stimuli were intermixed with periods of non-rivalrous stimuli: during a catch period the disparity specified slant became identical to the perspective-specified slant. The transformation from rivalrous to non-rivalrous stimuli, and vice versa, lasted 15 s. In this example the catch period started at 65 s. The black dashed line indicates the predicted average based upon the stimulus, i.e., independent of perceptual biases. In the absence of biases one expects that, on average, during the rivalrous periods a subject perceives the right side equally long in front as the left side. As indicated, no perceptual reversals are expected to occur during the non-rivalrous periods denoted by the dark grey square. (b) An example of raw data while subject LW viewed the slant rivalry stimulus. The onset of the catch procedure occurred in this example at 105 s. During the non-rivalrous period LW did not experience perceptual reversals.

2.3. Procedure

In describing the procedure we distinguish three parts: (1) randomisation, (2) an estimation method for the perceived slant, and (3) a catch period.

Randomisation—It is important to prevent selective biasing for a particular stimulus feature. We therefore presented the magnified trapezoid half-images in both red and green (corresponding to both positive and negative surface slant), and to both the left eye and the right eye. In half of the sessions the subjects wore the red filter over the left eye and the green filter over the right eye. In the other sessions the filters were reversed. We, thus, randomised for the sign of the surface slant as well as for both anaglyph colour, and for left and right eye presentation.

Slant estimation—In order to know whether the subject was able to experience slant rivalry (that is, being able to perceive two significant slants with opposite sign), we asked the subject to estimate the slant that was perceived during the stimulus presentation. We did so after each presentation block. The slant estimation procedure (van Ee & Erkelens, 1996) as we use it for the current stimulus has been previously described in detail (van Ee et al., 2002, 2003). In short, after presentation of the stimulus, three frontoparallel lines were presented on the screen. One of the lines was horizontal and the other two lines could be rotated about their centre. The horizontal line was fixed and represented a top view of the unslanted reference; each of the other lines represented the top-view of the perceived grid for either the left-side-in-front percept or in the right-front

percept. Subjects were instructed to match the angles between the rotatable lines and the horizontal line to the two perceived slants.³

Catch period—To check whether the subjects were reporting their perceptual states reliably, rather than pressing keys at random, the rivalrous stimuli were intermixed with periods of non-rivalrous stimuli that continued for 20 s (see Fig. 2(a)). In such a catch period the disparity specified slant was identical to the perspective-specified slant and no perceptual reversals were expected to occur during that period of non-rivalrous stimuli. The transformation from rivalrous to non-rivalrous stimuli lasted 15 s. This relatively long transformation period was required because the magnification of one of the two half-images had to become a minification, and vice versa for the other half-image. Although, in the fused binocular image the locations of the trapezoid segments were not altered (because the disparity was evenly distributed over the two half-images) a subject might be able to detect the onset of the catch period based on monocular lateral motion caused by a changing magnification. To prevent this from happening we ensured that the monocular lateral motion was below

³ A reasonable objection to this metrical slant estimation method is that it is hard to interpret the data because a slant angle that is estimated to be 35° in one trial might look like 40° in another trial. Previous work has demonstrated, however, that subjects have a relatively constant internal reference and that they do not regard this task as difficult. This estimation method has been used previously for real planes and when subjects wore distorting lenses. In addition, a similar metrical depth estimation method has proven to be useful for volumetric stimuli (van Ee & Anderson, 2001).

threshold (when viewing the images through the red-green filters), and this in turn, determined the 15 s-duration of the transformation. So a catch period lasted 50 s made up of: a slow magnification transformation (15 s), a non-rivalrous stimulation (20 s), and again a slow magnification transformation (15 s) to return to rivalrous stimulation (see Fig. 2(a)). The data collected during the catch period were not used for further data analysis. These data were, however, used to check if the rest of the data could be passed on to the subsequent data analysis: if the performance in the 20s-non-rivalrous period was below 90% we discarded the data of the complete stimulus presentation block and the subject was asked to redo this block. For each condition the catch period could commence at three different times (25, 65 or 105 s) to ensure that the subject was unable to anticipate the onset of the catch period.

Note that, in addition, the procedure also consisted of separate data collection blocks for examination of the role of voluntary control. The data for the voluntary control exertion tasks will be presented in the accompanying paper.

2.4. Subjects

Six subjects with normal or corrected to normal vision participated. Their stereoacuties were lower than 10 arcsec. The subjects participated in a recently developed stereoanomaly test that focuses on the ability to distinguish both crossed and uncrossed disparities of different signs and magnitudes within a range of -1° to 1° , without the possibility that eye movements interfere (van Ee, 2003; van Ee & Richards, 2002). Subjects LW, NK, MS, LD and SV were excellent at distinguishing the different signs and magnitudes for both the crossed and the uncrossed disparities. These subjects were part of a pool of subjects who were routinely involved in an assortment of stereovision experiments of our group. They had, however, never participated in perceptual reversal experiments. The sixth subject, GB, was able to correctly process the crossed disparities, but not the uncrossed disparities.

Prior to participation, the candidates were also tested for consistency in their responses when estimating the slants of both real and dichoptically presented planes. The subjects knew that they were participating in an experiment containing ambiguous (flip) stimuli but they were not informed about the purpose of the experiment. Initially, a seventh subject participated but his data were not used for further analysis because the button presses signalled percept reversal even during the catch period.

2.5. Data analysis

The randomisation and the catch period procedure resulted in 12 data collection blocks (3 catch periods, times 2

surface orientations, times 2 anaglyph colours) per subject. Four subjects repeated the experiment twice, and two subjects (LW and NK) repeated the experiment four times to get a better indication of the variability in performance across experimental repetitions. Thus, given that each data collection block lasted 3 min, in all for Expt 1 we collected data for a total of 288 ($3 \times 12 \times 8$) min.

The collected raw data indicated whether either the left side or the right side of the trapezoidal grid was perceived in front. Because we took into account whether the side that was perceived in front was caused either by disparity-specified or the perspective-specified slant, we further analysed the data in terms of disparity-slant-dominated and perspective-slant-dominated perceptual durations.

Rivalry processes are variable by nature meaning that, on the one hand, one needs to know whether a sufficiently large distribution of perceptual reversals has been collected before one can describe the characteristics of reversal process. On the other hand one should know the role that learning effects play in the data. Therefore, we first examined for each subject the stability of the reversal process across successive experimental repetitions and within each separate 35-s portion of data. Subsequently we determined the percept duration for each subject. Finally we examined the correlation of successive percept durations. We did so by subjecting each separate block of data to a Spearman rank correlation analysis. The Spearman rank correlation technique is a mathematical technique developed to deal with not-normally distributed data. For not-normally distributed data it is not allowed to use standard auto correlation techniques. The Spearman method considers the topology of the data along the relevant axes. It is therefore especially sensitive to drift in the data meaning that a proper analysis requires that only data portions without drift can be considered for the correlation calculations.

3. Experiment 2

3.1. Stimuli and apparatus

The purpose of Expt 2 was to compare the perceptual reversal dynamics of slant rivalry with more classical rivalry stimuli. The used apparatus, the procedure, and the data analysis for Expt 2 were identical to those used for Expt 1. The only difference was that we now presented different stimuli within the aperture formed by the background. The stimuli were presented in the same location as the trapezoids so the two (rivaling) half-images were again superimposed on corresponding retinal locations.

The rivalrous stimuli of Expt 2 consisted of (1) orthogonal gratings, (2) house-face stimuli, and (3) the Necker cube. The first two of these stimuli fall in the class of binocular rivalry stimuli. The Necker cube is a

perceptual rivalry stimulus. The stimuli subtended 1.2° , which is the same size as used in Expt 1. This small size was chosen to prevent piecemeal rivalry. For both the orthogonal grating and the house-face stimulus we did not present the relatively complex sunburst-like fixation symbol because we found that this symbol affected the nature of these stimuli. (Note here that it has been reported that fixating a dichoptic symbol interferes with the reversal task (Peterson, 1986).) For these stimuli subjects were requested to keep their gaze within the central region of the image and control eye movement recordings showed that subjects were able to do so.

The orthogonal gratings stimuli consisted of four oblique lines that had perpendicular orientations (45° with the vertical) in the two eyes (Fig. 1(b)). The spatial frequency of the gratings was 3.3 cycles per degree and the contrast of the gratings was 0.8. The house-face stimuli are depicted in Fig. 1(c). The house-face stimuli were identical to those developed by Tong (Tong et al., 1998), which have now been used in several other studies. The contrast of the house-face stimuli was 0.7 to prevent cross talk between the red and the green filter. The Necker cube stimulus is depicted in Fig. 1(d). The contrast of the Necker cube stimulus was 0.8, and although the bistability occurs monocularly we presented the Necker cube in red for one eye and in green to the other eye, so that the stimulus presentation of the other stimuli was resembled.

3.2. Task and procedure

The instructions to the subjects were also identical to those of Expt 1 (except that the slant estimation was omitted). For the orthogonal grating stimulus the subjects were instructed to press one key when they perceived the left obliques (lines under 45° going from top left to bottom right) and to press another key when they perceived the right obliques (going from top right to bottom left). Although the stimuli were chosen to be small in retinal size, in principle it could be the case that there is not always a completely dichotomous reversal. Instead, parts of both patterns could be simultaneously present in different regions of the visual field. Indeed, in our stimulus this happened. This was, however, not experienced as a problem because subjects were instructed to select the dominating pattern in the central area of the patch. It was not difficult for the subjects to disregard the patchiness that occurred outside the central area. The same held for the house-face stimulus. For this stimulus subjects were instructed to press one key when the house was perceived in the central region of the stimulus, and to press another key when the face was perceived. For the Necker cube subjects pressed one key when they perceived the cube as if they viewed it from below and another key when they perceived the cube as if they viewed it from above.

The order in which the subjects did the experiments was as follows: They first participated in a complete experiment for the trapezoid stimulus (six sessions in Expt 1) before they started the orthogonal grating experiment. Again they completed six sessions before they started the house-face experiment and again they completed six house-face sessions before they started the Necker cube experiment. Then a repetition of the four stimuli began. In other words, for each stimulus two complete experiments were conducted. Two subjects (LW and NK) did twice as many sessions to get a better indication of the variability in performance across Expts.

For the orthogonal grating stimulus we randomised for anaglyph colour, for viewing eye, and for the orientation of the oblique lines (left obliques or right obliques) so that we were able to analyse the data in terms of dominance of either the left or the right eye. Thus, left obliques were presented in both red and green (in different data collection blocks) to both the left and the right eye. During the catch period for the orthogonal grating stimulus we used a 15 s transition period to slowly fade the red grating. Then during 20 s the red oblique line pattern was invisible to become slowly visible during another transition period that lasted 15 s. A comparable catch procedure for orthogonal grating stimuli has been used previously (Leopold & Logothetis, 1996). For the house-face stimulus we randomised for anaglyph colour, for viewing eye, and for the presence of the house or the face so that we were able to analyse the data in terms of dominance of either the left or the right eye. For the Necker cube stimulus we only randomised for anaglyph colour and for viewing eye.

3.3. Subjects and data analysis

The six subjects from Expt 1 participated. To compare the subjects' performance across the four stimuli we compared the means of (1) perceptual reversal rate drift across experimental repetitions, (2) reversal rate drift within data blocks, (3) the percept durations as well as (4) correlation coefficients of successive percept durations.

4. Results

For Expt 1 we will first present the data of the individual subjects and then the averaged data of the six subjects. For Expt 2, we will restrict data presentation to the average results across the six subjects. Both for Expt 1, and for Expt 2, it is first demonstrated how (un)stable the data is over time, then we look at the percept duration and finally we consider the correlation of successive percept durations.

4.1. Results of experiment 1

Fig. 2(b) illustrates an example of the raw data of subject LW. LW experienced frequent reversals between perceiving the left side and the right side in front. During the catch period in which the disparity and the perspective specified slant were congruent, he did not experience perceptual reversals.

Fig. 3 examines the statistical behaviour of the percept durations. The graphs correlate the i th duration of a list of perceptual durations that were dominated by disparity-specified slant with the $(i + 1)$ th duration of the same list. The left panel of Fig. 3 shows the data on a time scale up to 10 s, the right panel shows the same data on a larger time scale, demonstrating that the data is not normally distributed.

As noted above, an experiment that concerns a temporally variable process demands a sufficiently large distribution of data to describe the characteristics of the reversal process. However, the danger of collecting a lot of data is that the data varies across data collection series, due to either practice effects or intrinsic changes in the perceptual processing. The left panel of Fig. 4(a) illustrates the subjects' number of reversals per second across 35-s data collection portions. From the slope of these data we calculated the drift in the reversal rate. The right panel shows the subjects' reversal rate drift across the 35-s data portions. There is a consistent decrease of the reversal frequency for the subjects in the course of the experiment. Inspection of the complete set of data revealed that after about 90 s the number of reversals per unit time became stable. Fig. 4(b) depicts the subjects' reversal rate drift across successive experimental repetitions. Interestingly, while across data portions the reversal rate decreases to a considerable amount, across sessions the data is reasonably stable for a process that is variable in nature.

Fig. 5 depicts the subjects' percept durations for the disparity-dominated percept and the perspective-domi-

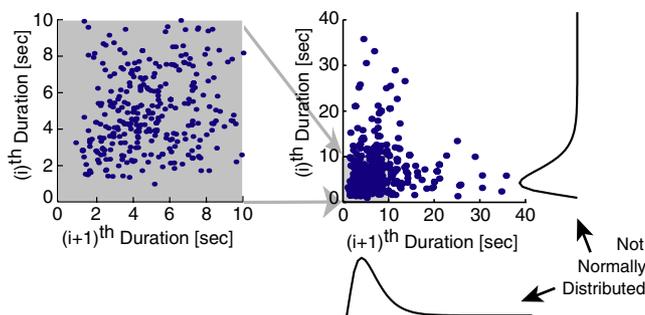


Fig. 3. Distribution of percept durations for slant rivalry. We plotted the i th number in a list of subject LW's disparity-dominated percepts durations versus the $(i + 1)$ th duration of the same list. The left panel portrays a detailed view (0–10 s) of the larger data set that is portrayed in the right panel. This analysis reveals that the durations are, as expected, not normally distributed.

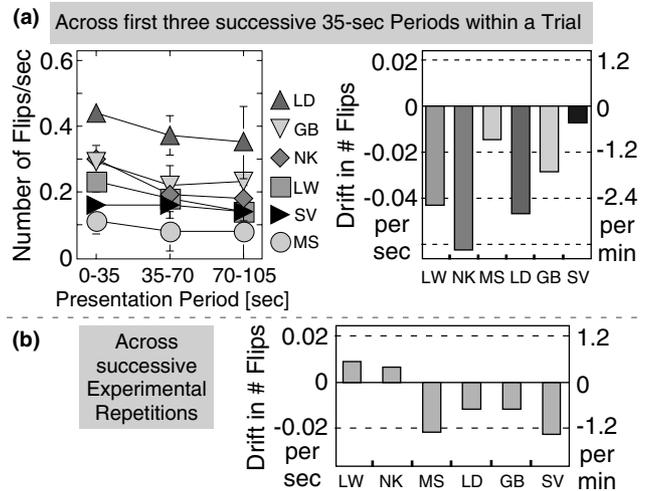


Fig. 4. Flip rate drift during the experiment for slant rivalry. (a) The left panel shows that the number of perceptual reversals per second decreases in the course of the experiment. The slopes of the data in the left panel correspond to the drift in the flip rate across successive 35-s portions of the data blocks. The right panel depicts the drift. (b) The drift in the perceptual reversal rate across repetitions of the experiment. Although the data seem to be unstable across 35-s portions, across repetitions of the experiment the data are reasonably stable.

nated percept, respectively. On average the disparity-dominated percept durations are slightly longer than the perspective-dominated percept durations. There is considerable variation across subjects, just as has been reported previously for other paradigms (Aafjes, Huetting, & Visser, 1966; Bruner, Postman, & Mosteller, 1950; Frederiksen & Guilford, 1934; Sadler & Mefferd, 1970). However, as we will see in the accompanying paper once we consider the role of voluntary control, all subjects reveal similar trends in their data.

Fig. 6 portrays the Spearman correlation coefficients for the six subjects. As noted above, the advantage of the Spearman rank correlation coefficient is that it has been developed for not-normally distributed data. This

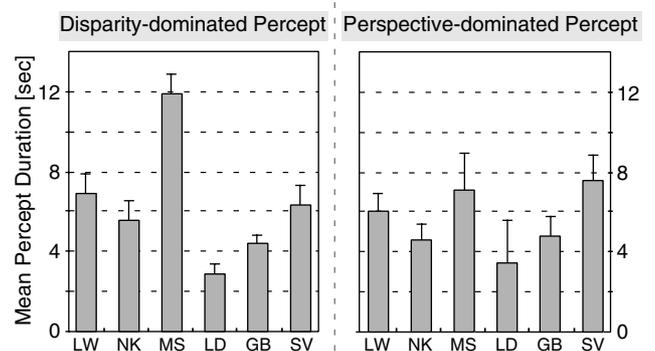


Fig. 5. Duration of perceptual dominance for slant rivalry. The disparity-dominated (left) and the perspective-dominated (right) percept durations illustrate that there is considerable variation across subjects. Error bars represent standard deviations.

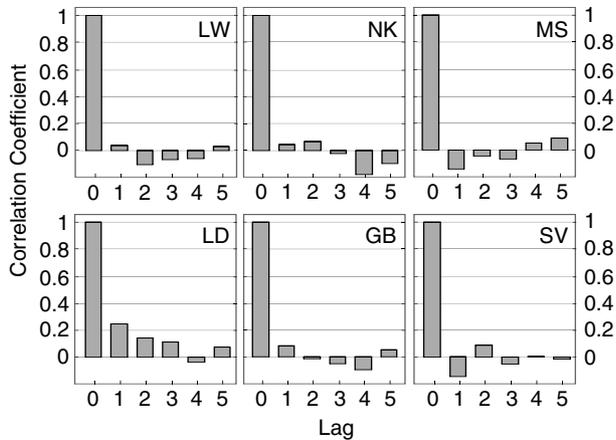


Fig. 6. Sequential correlation of successive percept durations for slant rivalry. We used the Spearman rank correlation method to determine the correlation coefficients of the successive disparity-dominated percept durations for slant rivalry. We minimized the influence of drift on this determination by averaging the coefficients across all available small (35 s) portions of data. The correlation coefficients at lag zero represent the autocorrelation coefficient. The coefficient at lag five has been obtained by shifting the list of successive percept durations over five durations. The six subjects show a similar pattern of correlation coefficients across lag zero to lag five. For increasing lags the correlation coefficients decrease consistently.

comes with the drawback that the coefficient is especially sensitive to drift in the data. We minimized the influence of drift on the determination of the coefficients by averaging the correlation coefficients across all available small (35 s) portions of data. The correlation coefficients at lag 0 represent the autocorrelation coefficient. The coefficient at lag 5 has been obtained by shifting the list of successive percept durations over five durations. When the lag increases the correlation coefficients decrease consistently. The correlation coefficients for the six subjects are similar across lag 0 to lag 5. Only the disparity-dominated percept durations are presented. The correlation for the successive perspective-dominated percept durations as well as for both the perspective-dominated durations and the disparity-dominated percept durations were very similar.

After the stimulus presentation we asked the subject to estimate the slant that was perceived during the stimulus presentation. The reported slants resembled those reported previously (van Ee et al., 2002; van Ee et al., 2003). On average, across the six subjects the estimated slants, and their standard deviations, for the two presented combinations ($-70^\circ, 56^\circ$) and ($70^\circ, -56^\circ$) of perspective- and disparity-specified slants were ($-50 \pm 7^\circ, 39 \pm 9^\circ$) and ($51 \pm 8^\circ, 37 \pm 8^\circ$), respectively. An analysis for each individual data block revealed that the subjects were able to perceive bi-stability for all slant stimuli presented.

The left most bars in Fig. 7(a) and (b) illustrate the mean reversal rate drift across successive experimental repetitions, and across 35-s portions, respectively.

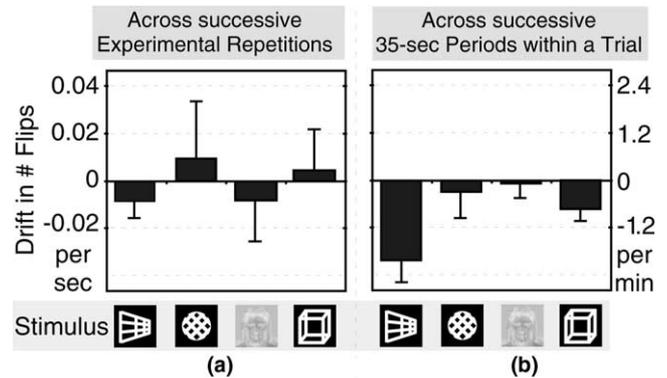


Fig. 7. Mean flip rate drift for the four stimuli. The icons specify the stimuli for which the data is being presented. (a) The mean data of the six subjects show that the drift across the experimental repetitions is not significantly different from zero for all stimuli. (b) The drift across 35-s portions of the data blocks. The flip rate for all stimuli is larger at the start of a trial than during the course of the experiment. Error bars represent standard errors across the six subjects.

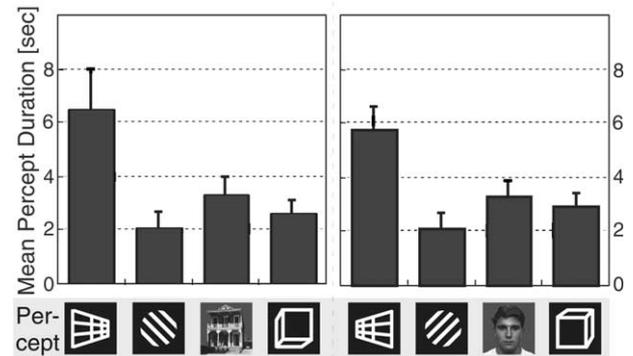


Fig. 8. Mean percept durations for the four rivalry stimuli. The percepts for which we plotted the durations are specified by the icons. The icon for slant rivalry indicates disparity domination in the left panel and perspective domination in the right panel. Error bars represent standard errors across the six subjects. For slant rivalry the mean percept duration is relatively long, for grating rivalry it is relatively short.

Whenever a data collection series starts, the reversal rate is larger than during the course of the series. Fig. 8 (left bar in both panels) presents both the mean disparity-dominated (left panel) and the mean perspective-dominated (right panel) percept durations across the six subjects. Fig. 9(a) portrays the mean Spearman rank correlation coefficients across the six subjects. Only the disparity-dominated percept durations are presented; the data for the perspective-dominated percept durations are similar. We will now compare these data with the data produced by a number of classical rivalry paradigms.

4.2. Results of experiment 2

To compare the dynamics for the slant rivalry paradigm with other paradigms, we performed the

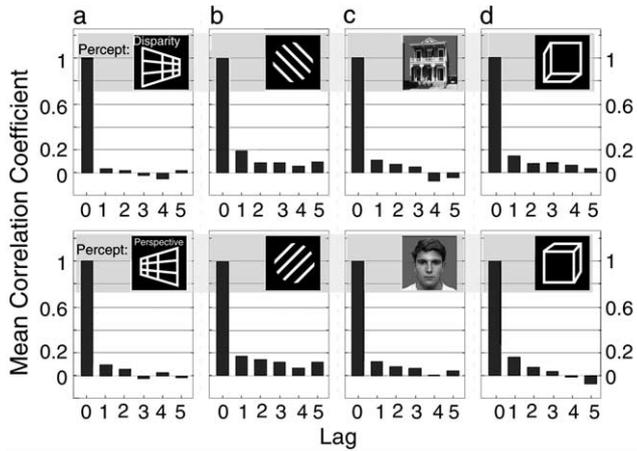


Fig. 9. Sequential correlation of successive percept durations for the four rivalry stimuli. The mean Spearman rank correlation coefficients across the six subjects for (a) the slant rivalry stimulus, (b) the orthogonal grating stimulus, (c) the house-face stimulus, and (d) the Necker cube stimulus. The icons specify the percept examined. The correlation coefficients at lag zero represent the autocorrelation coefficient. For increasing lags the correlation coefficients decrease consistently. A similar pattern of correlation coefficients emerged for the four rivalry stimuli. We minimized the influence of drift by averaging the coefficients across all available small (35 s) portions of data.

above-described analyses for the orthogonal grating stimulus, the house-face stimulus, and the Necker cube. Fig. 7 shows the mean reversal rate drifts. The left panel illustrates that the reversal rate drift across successive experimental repetitions is not significantly different from zero. The right panel illustrates the reversal rate drift across successive 35-s portions. Whenever a data collection series starts the reversal rate is larger than during the course of the series. In agreement, a negative drift in the reversal rate has been reported previously for a grating stimulus (Lehky, 1995) and a horizontal-vertical line stimulus (Cogan & Goldstein, 1967). Fig. 8 compares the mean percept durations for the orthogonal grating rivalry, the house-face rivalry, and the Necker cube rivalry. For the orthogonal grating percept duration we found 2.1 s, which compares well with the values reported in the literature that range from 1.8 to 2.4 s (Alexander, 1951; Cogan & Goldstein, 1967; Lack, 1969; Lehky, 1995; Logothetis et al., 1996; Meredith & Meredith, 1962; Ross & Ma-Wyatt, 2003). For the house-face percept durations we found 3.3 s. In support, Tong reported that the durations for his subjects ranged between 2.5 and 5.5 s (Tong et al., 1998). For the Necker cube percept durations we found 2.7 s. The literature reports durations in the range between 2.0 and 3.2 s (Babich & Standing, 1981; Peterson & Hochberg, 1983; Ross & Ma-Wyatt, 2003). Note that the alternative percept durations for the orthogonal grating stimulus, the house-face stimulus, and the Necker cube stimulus are almost identical. Fig. 9(b)–(d) present the correlation

coefficients for the orthogonal grating, the house-face, and the Necker cube stimulus, respectively. For all paradigms the correlation of the previous percept duration with the next (lag 1) is positive. The correlation coefficients for the four paradigms are qualitatively similar.

5. Discussion

The comparison of the four examined rivalry stimuli revealed qualitative similarities concerning the data patterns for the temporal dynamics across the different experimental manipulations. The drift of the perceptual reversal rate across successive experimental repetitions was not significantly different from zero for the four rivalry paradigms. For the drift across successive 35-s portions of data there were differences: The drift for slant rivalry was much larger than the drift for the other three paradigms, possibly reflecting a contribution of the cognitive aspect of the perspective cue (perspective is only informative once an assumption about the projected shape has been made). The Spearman rank correlation analysis revealed very similar sequential duration correlations across the four paradigms. Finally, concerning the percept durations slant rivalry exhibits long durations relative to the other paradigms.

The qualitative similarities of the dynamics for the different rivalry paradigms have been interpreted previously as being consistent with an underlying mechanism that, at least, shares some common parts (see also Leopold & Logothetis, 1999; Logothetis et al., 1996; McDougall, 1906; Pettigrew, 2001; Walker, 1975). However, the details of an underlying mechanism have not yet been resolved (Blake & Logothetis, 2002; Tong, 2001). In this respect it is important to note that Wilson reported evidence that binocular rivalry involves multiple distinct stages (Wilson, 2003). Instead of looking at the qualitative similarities across the different ambiguous stimuli one could also look at the quantitative differences⁴ and interpret the data as representing different mechanisms. Our described experiment focuses on a comparison of the dynamics of slant rivalry with the classical rivalry paradigms and was not primarily designed to address the issue of underlying mechanisms. In any case, although on an operational level the temporal dynamics of the different ambiguous stimuli are clearly different, it cannot be ruled out that there is a, more evolutionary primitive, underlying bistable oscillator process (Pettigrew, 2001) that mediates, at least, some part of the reversal process. In the accompanying paper we will see

⁴ After completion of this paper we learned about a recent useful paper (Meng & Tong, *in press*) that focused on the differences in data produced by three rivalry paradigms: grating, house-face and Necker cube.

that the influence of voluntary control across the four paradigms also reveals qualitatively similar results.

What causes the perceptual reversals? Necker's explanation for perceptual reversals is of historical interest: "at the time the change took place, a particular sensation was felt in the eye, which proved to me that it was an optical, and not merely as I had at first thought a mental, operation which was performed" (Necker, 1832). By "sensation" he probably meant a sensation associated with a lenticular accommodation. Another optical explanation concerns heat of the eyeball. But it has been reported that: "the hypothesis linking reversal rate to a direct effect of heat on the eye ball is not supported by the evidence" (Heath, Ehrlich, & Orbach, 1963). Other early explanations based upon peripheral physiological factors include the work of Wallin who argued that reversals are caused by "certain disturbances in the peripheral organ and certain bodily cycles, notably the blood pressure rhythm, possibly the respiration rhythm, and possibly the cortical cell fluctuations" (Wallin, 1910). We have extensively studied the role of both eye movements and blinks while subjects experience bi-stability for our grid stimuli. Our analyses included micro saccades. The cardinal conclusion for the current paper is that (micro)saccades, blinks and vergence in depth are not essential to reverse from one percept to the other (although they obviously can help). Other studies in which different ambiguous stimuli were presented as afterimages, or stabilized on the retina (Blake, Fox, & McIntyre, 1971), or studies that presented multiple ambiguous stimuli in the visual field, have reported a similar conclusion (review in Leopold & Logothetis, 1999). Intriguingly, we found that saccades and blinks are inhibited while perceptual reversals are occurring. An analysis of the eye movement data will be presented elsewhere (for an abstract version: van Dam & van Ee, 2003).

It has been stated frequently that spontaneous events cause the perceptual reversals. An alternative to such a model is a reciprocal-inhibition model in which perceptual adaptation initiates perceptual reversals. There are, however, a variety of experimental facts that speak against perceptual adaptation as the cause for reversals (review in Leopold & Logothetis, 1999). For example, such models predict a correlation between the period in which a percept is suppressed and the following period in which it is dominant, and this pattern is not observed (see also Horlitz & O'Leary, 1993; Sadler & Mefferd, 1970; Taylor & Aldridge, 1974). Adaptation may, however, play a more indirect role on a lower level (e.g., Blake et al., 2003; Laing & Chow, 2002). It could be the case that "the individual cells are susceptible to satiation, and that a majority decision device has evolved which provides the perceived world with the stability it might otherwise lack" (Taylor & Aldridge, 1974; see also Walker, 1975). In this view the "majority deci-

sion device" would then be subjected to reversals. Whether it is the case for slant rivalry that either spontaneous events, or a competition process cause the reversals goes beyond the scope of the current work.

We used the Spearman rank correlation method to calculate the correlation between sequential perceptual durations. In the literature different measures for correlation occur. First, it is frequently not clear how the correlation coefficients were determined and whether it has been taken into account that one deals with not normally distributed data (Fig. 3). Second, as evidence for sequential independence quite often the Lathrop coefficient is used. However, Lathrop developed the coefficient for normally distributed data (Lathrop, 1966, p. 121). Third, the gamma-shape of the perceptual duration distribution (Fig. 3) is frequently taken as evidence for the sequential independence of percept durations. Although it is true that some stochastic processes produce Gamma distributions (for the special case of a Poisson process that directly underlies the reversal frequency, see Levelt, 1967), the inverse, namely that a Gamma-like distribution is necessarily produced by a stochastic process, is not correct. A full analysis of the distributions that underlie the found perceptual durations in our experiment will be presented elsewhere (Brascamp, van den Berg, & van Ee, in press). For the current paper it is noteworthy that for all tested stimuli the correlation of the previous percept duration with the next (lag 1) was often positive. For both the orthogonal grating stimulus and the Necker cube stimulus we even found a correlation coefficient as large as almost 0.2.⁵ It is beyond the scope of the present paper to speculate whether this implies that the pattern of responses for the perceptual reversal process is not completely memoryless.

In conclusion, we compared the dynamics of slant rivalry with those of orthogonal grating rivalry, house-face rivalry, and Necker cube rivalry, revealing that slant rivalry exhibits a qualitatively similar pattern of dynamics: The drift of the perceptual reversal rate, both across successive experimental repetitions, and across successive 35-s portions of data were similar. The sequential dependence of the durations of perceptual phases, too, revealed very similar patterns. The main quantitative difference, which could make slant rivalry a useful stimulus for future physiological studies, is that the percept durations are relatively long compared to the other rivalry paradigms. In the companion paper (van Ee et al., 2005) we examined the influence of volun-

⁵ This compares well with previous studies that reported 0.18 (Walker, 1975) and 0.19 (Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972) albeit these coefficients were not obtained with the Spearman method. It has been reported that these correlations between successive intervals may be due to neural chaos (Laing & Chow, 2002).

tary control on the dynamics of perceptual reversal for the four above-used rivalry stimuli.

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References

- Aafjes, M., Hueting, J. E., & Visser, P. (1966). Individual and interindividual differences in binocular retinal rivalry in man. *Psychophysiology*, 3, 18–22.
- Alexander, L. T. (1951). The influence of figure-ground relationships in binocular rivalry. *Journal of Experimental Psychology*, 41, 376–381.
- Babich, S., & Standing, L. (1981). Satiation effects with reversible figures. *Perceptual and Motor Skills*, 52, 203–210.
- Blake, R., Fox, R., & McIntyre, C. (1971). Stochastic properties of stabilized-image binocular rivalry alternations. *Journal of Experimental Psychology*, 88, 327–332.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96, 145–167.
- Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain and Mind*, 2, 5–38.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3, 1–11.
- Blake, R., Sobel, K. V., & Gilroy, L. A. (2003). Visual motion retards alternations between conflicting perceptual interpretations. *Neuron*, 39, 869–878.
- Borsellino, A., De Marco, A., Allazetta, A., Rinesi, A., & Bartolini, B. (1972). Reversal time distribution in the perception of visual ambiguous stimuli. *Kybernetik*, 10, 139–144.
- Bradley, D. C., Chang, G. C., & Andersen, R. A. (1998). Encoding of three-dimensional structure-from-motion by primate area MT neurons. *Nature*, 392, 714–717.
- Brascamp, J. W., van den Berg, A. V., & van Ee, R. (in press). Shared neural circuitry for switching between perceptual states and ocular motor states? *Journal of Vision*.
- Breese, B. B. (1899). On inhibition. *Psychological Monographs*, 3, 1–65.
- Brewster, D. (1826). On the optical illusion of the conversion of Cameos into Intaglios, and of Intaglios into Cameos with an account of other analogous phenomena. *Edinburgh Journal of Science*, 4, 99–108.
- Bruner, J. S., Postman, L., & Mosteller, F. (1950). A note on the measurement of reversals of perspective. *Psychometrika*, 15, 63–72.
- Cogan, R., & Goldstein, A. G. (1967). The stability of binocular rivalry during spaced and massed viewing. *Perception & Psychophysics*, 2, 171–174.
- Frederiksen, N. O., & Guilford, J. P. (1934). Personality traits and fluctuations of the outline cube. *American Journal of Psychology*, 46, 470–474.
- Heath, H. A., Ehrlich, D., & Orbach, J. (1963). Reversibility of the Necker cube: II Effect of various activating conditions. *Perceptual Motor Skills*, 17, 539–546.
- Hol, K., Koene, A., & van Ee, R. (2003). Attention-biased multi-stable surface perception in three-dimensional structure-from-motion. *Journal of Vision*, 3, 486–498.
- Horlitz, K. L., & O'Leary, A. (1993). Satiation or availability? Effects of attention, memory, and imagery on the perception of ambiguous figures. *Perception & Psychophysics*, 53, 668–681.
- Lack, L. C. (1969). The effect of practice on binocular rivalry control. *Perception & Psychophysics*, 6, 397–400.
- Laing, C. R., & Chow, C. C. (2002). A Spiking Neuron Model for Binocular Rivalry. *Journal of Computational Neuroscience*, 12, 39–53.
- Lathrop, R. G. (1966). First-order response dependencies at a different brightness threshold. *Journal of Experimental Psychology*, 72, 120–124.
- Lee, S., & Blake, R. (2002). V1 activity is reduced during binocular rivalry. *Journal of Vision*, 2, 618–626.
- Lehky, S. R. (1995). Binocular rivalry is not chaotic. *Proceedings of the Royal Society of London B*, 259, 71–76.
- Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, 379, 549–553.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, 3, 254–264.
- Levelt, W. J. M. (1967). Note on the distribution of dominance times in binocular rivalry. *British Journal of Psychology*, 58, 143–145.
- Logothetis, N. K. (1998). Single units and conscious vision. *Proceedings of the Royal Society of London B*, 353, 1801–1818.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature*, 380, 621–624.
- Mach, E. (1866). Über die physiologische Wirkung räumlich verteilter Lichtreize. *Sitzungsberichte der Wiener Akademie*, 54, 3.
- McDougall, W. (1906). Physiological factors of the attention process (IV). *Mind*, 15, 329–359.
- Meng, M., & Tong, F. (in press). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision*.
- Meredith, G. M., & Meredith, C. G. W. (1962). Effect of instructional conditions on rate of binocular rivalry. *Perceptual and Motor Skills*, 15, 655–664.
- Necker, L. A. (1832). Observations on some remarkable optical phenomena seen in Switzerland; and on an optical phenomenon which occurs on viewing a figure of a crystal or geometical solid. *London and Edinburgh Philosophical Magazine and Journal of Science*, 1, 329–337.
- Parker, A. J., Cumming, B. G., & Dodd, J. V. (1999). Binocular neurons and the perception of depth. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 263–277). Cambridge: MIT Press.
- Peterson, M. A. (1986). Illusory concomitant motion in ambiguous stereograms: Evidence for nonstimulus contributions to perceptual organization. *Journal of Experimental Psychology: Human perception and performance*, 12, 50–60.
- Peterson, M. A., & Hochberg, J. (1983). Opposed-set measurement procedure: A quantitative analysis of the role of local cues and intention in form perception. *Journal of Experimental Psychology: Human perception and performance*, 9, 183–193.
- Pettigrew, J. (2001). Searching for the switch: Neural bases for perceptual rivalry alternations. *Brain and Mind*, 2, 85–118.
- Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience*, 3, 1153–1159.
- Rees, G., Kreiman, G., & Koch, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, 3, 261–270.
- Ross, J., & Ma-Wyatt, A. (2003). Saccades actively maintain perceptual continuity. *Nature Neuroscience*, 7, 65–69.

- Sadler, T. G., & Mefferd, R. B. (1970). Fluctuations of perceptual organization and orientation. *Perceptual and Motor Skills*, *31*, 739–749.
- Schriever, W. (1925). Experimentelle Studien über stereoskopisches Sehen. *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, *96*, 113–170.
- Slyce, J. (1998). *Patrick Hughes: Perverspective*. London: Momentum.
- Taylor, M. M., & Aldridge, K. D. (1974). Stochastic processes in reversing figure perception. *Perception & Psychophysics*, *16*, 9–25.
- Tong, F. (2001). Competing theories of binocular rivalry: A possible resolution. *Brain Mind*, *2*, 55–83.
- Tong, F. (2003). Primary visual cortex and visual awareness. *Nature Neuroscience*, *4*, 219–229.
- Tong, F., & Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, *411*, 195–199.
- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*, 753–759.
- van Dam, L. C. J., & van Ee, R. (2003). Bistability in stereoscopically perceived slant about a horizontal axis. *Journal of Vision*, *3*, 467.
- van Ee, R. (2003). Correlation between stereoanomaly and perceived depth when disparity and motion interact in binocular matching. *Perception*, *32*, 67–84.
- van Ee, R., & Anderson, B. L. (2001). Motion direction, speed, and orientation in binocular matching. *Nature*, *410*, 690–694.
- van Ee, R., Adams, W. J., & Mamassian, P. (2003). Bayesian modelling of perceived slant in bi-stable stereoscopic perception. *Journal of the Optical Society of America*, *20*, 1398–1406.
- van Ee, R., & Erkelens, C. J. (1996). Temporal aspects of binocular slant perception. *Vision Research*, *36*, 43–51.
- van Ee, R., & Richards, W. (2002). A planar and a volumetric test for stereoanomaly. *Perception*, *31*, 51–64.
- van Ee, R., van Dam, L. C. J., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research*, doi:10.1016/j.visres.2004.07.030.
- van Ee, R., van Dam, L. C. J., & Erkelens, C. J. (2002). Bi-stability in perceived slant when binocular disparity and monocular perspective specify different slants. *Journal of Vision*, *2*, 597–607.
- Walker, P. (1975). Stochastic properties of binocular rivalry alternations. *Perception & Psychophysics*, *18*, 467–473.
- Wallin, J. E. W. (1910). Satiation effects with reversible figures. *Journal of Philosophy*, *7*, 33–38.
- Washburn, M., Reagan, C., & Thurston, E. (1934). The comparative controllability of the fluctuations of simple and complex ambiguous perspective figures. *American Journal of Psychology*, *46*, 636–638.
- Wheatstone, C. (1838). Contributions to the physiology of vision – Part the first; On some remarkable and hitherto unobserved phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, *128*, 371–394.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Science*, *100*, 14499–14503.
- Wilson, H. R., Blake, R., & Lee, S. (2001). Dynamics of travelling waves in visual perception. *Nature*, *412*, 907–910.
- Wolfe, J. M. (1996). Resolving visual ambiguity. *Nature*, *380*, 587–588.