

# Hysteresis effects in stereopsis and binocular rivalry

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## Abstract

Neural hysteresis plays a fundamental role in stereopsis and reveals the existence of positive feedback at the cortical level [Wilson, H. R., & Cowan, J. D. (1973). A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. *Kybernetik* 13(2), 55–80]. We measured hysteresis as a function of orientation disparity in tilted gratings in which a transition is perceived between stereopsis and binocular rivalry. The patterns consisted of sinusoidal gratings with orientation disparities ( $0^\circ$ ,  $1^\circ$ ,  $2^\circ$ , ...,  $40^\circ$ ) resulting in various degrees of tilt. A movie of these 41 pattern pairs was shown at a rate of 0.5, 1 or 2 pattern pairs per second, in forward or reverse order. Two transition points were measured: the point at which the single tilted grating appeared to split into two rivalrous gratings ( $T_1$ ), and the point at which two rivalrous gratings appeared to merge into a single tilted grating ( $T_2$ ). The transitions occurred at different orientation disparities ( $T_1 = 25.4^\circ$ ,  $T_2 = 17.0^\circ$ ) which was consistent with hysteresis and far exceeded the difference which could be attributed to reaction time. The results are consistent with a cortical model which includes positive feedback and recurrent inhibition between neural units representing different eyes and orientations.

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## 1. Introduction

In experiments that demonstrate perceptual hysteresis, values of a critical stimulus parameter are gradually increased and decreased. The general finding is that the initial percept persists even though the current value of the parameter might favour the alternative percept. Seminal experiments demonstrating hysteresis in binocular vision were carried out by Fender and Julesz (1967) using binocular retinally stabilized images. They found that when two images were moved apart and then brought back into correspondence, fusion was lost at a very large disparity ( $2^\circ$ ) but re-established at a much smaller disparity (6 min arc). These hysteresis effects could not be explained using eye movements so they necessarily involved neural mecha-

nisms, most likely at the cortical level (Hubel & Wiesel, 1962, 1970).

The hysteresis effects in Fender and Julesz's (1967) study have subsequently been replicated under a wider range of conditions, although the point at which fusion is reestablished is typically larger than 6 min arc (Diner & Fender, 1987; Erkelens, 1988; Hyson, Julesz, & Fender, 1983; Pian-tanida, 1986). Erkelens (1988) found that the hysteresis was caused by a reduction of the fusional range after prolonged viewing of an image in rivalry, and not by an extension of the fusional range during slow incremental changes in disparity.

Hysteresis effects may have also occurred in studies which involved detecting transitions between fusion and binocular rivalry in dynamic random-dot stereograms (Julesz & Tyler, 1976; Tyler & Julesz, 1976, 1978). The stereograms were identical (100% correlation) or uncorrelated (0% correlation), or were complements of each other ( $-100\%$  correlation). Duration thresholds were measured for detecting transitions between these states. It took

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longer to detect decorrelation–correlation (i.e. rivalry–fusion) transitions than to detect correlation–decorrelation (i.e. fusion–rivalry) transitions. These results were explained using a neural model with inhibition between units representing stereopsis and rivalry, with adaptation to the current state of correlation (Julesz & Tyler, 1976; Tyler & Julesz, 1976). These effects could be understood (in part) as a consequence of suppression of fusional mechanisms generated by the state of rivalry (Blake, 1989; Erkelens, 1988; Harrad, McKee, Blake, & Yang, 1994; Tyler, 1991). That is, the decorrelated stimuli generated interocular suppression that slowed the transition to a fused binocular state. These effects could possibly reflect hysteresis in the transitions between stereopsis and rivalry.

In neural network models of stereopsis, hysteresis plays a role in aiding binocular correspondence and in maintaining fusion once correspondence has been established (Kumar, 1996; Marr & Poggio, 1976; Mayhew, Frisby, & Gale, 1977; Pollard, Mayhew, & Frisby, 1985; Prazdny, 1985; Sperling, 1970). In some models hysteresis may facilitate certain depth interpretations or promote the stability of depth organizations (Anderson, 1992; Julesz, 1971, 1974; Julesz & Chang, 1976). This modelling work is consistent with the results of psychophysical studies which investigated hysteresis effects in transitions between layered and volume interpretations of depth in dynamic random-dot stereograms (Anderson, 1992).

Another demonstration of hysteresis in binocular vision involved transitions between the perception of tilted and flat surfaces using stereoscopic grating pairs (Wilson, 1977). As the contrast of one of the gratings was continuously varied in time, the transition occurred at a different point in the sequence for increasing contrast compared to decreasing contrast. The hysteresis contrast loop was modelled using a cortical model with positive feedback between disparity selective cells generated by disinhibition. It is important to study hysteresis as it reveals the existence of *positive* feedback at the cortical level, which may occur through inhibitory interactions. Any comprehensive theory of perception must also account for the dynamical behaviour of the system (Fender & Julesz, 1967; Julesz, 1971; Wilson, 1977; Wilson & Cowan, 1972, 1973).

In general the results of previous experiments are consistent with the hypothesis that the stability of the percept of either fusion or rivalry is the result of inhibition of the alternative percept. Competition between rivalry and fusion may be generated by mutual inhibition between the neural mechanisms underlying these two perceptual states, and positive feedback resulting from disinhibition (Wilson, 1977, 1999). As the term is used here, positive feedback refers to self disinhibition in a cortical network, which can be conceptualized mathematically as the product of two stages of inhibition (Wilson, 1999). In a model of stereopsis and rivalry, one stage of inhibition is necessary to model binocular rivalry, while the second stage is necessary to account for the stability and persistence of one percept relative to another (rivalry versus depth), in transitions

between these two perceptual states (see Section 4 and Fig. 7). Using a model of cortical dynamics based on this framework, we predicted that it should be possible to measure hysteresis as a function of orientation disparity in tilted gratings in which a transition is perceived between stereopsis and binocular rivalry (Wilson, 2007). Movie sequences would be used in which the orientation disparity in the stereoscopic grating pairs is gradually increased or decreased (Fig. 1). Observers would choose the transition point at which: (1) the single tilted grating breaks into two rivalrous gratings; or (2) two rivalrous gratings merge into a single tilted grating. Observers can easily perform this task, since the percept abruptly switches between tilt and rivalry and these two percepts never occur simultaneously (Buckthought & Wilson, 2007).

If the results were consistent with neural hysteresis, we would expect that observers would perceive the transition to occur at a larger orientation disparity if the movie sequence was presented in the forward direction (fusion to rivalry transition), compared to the reverse direction (rivalry to fusion transition). In fact the results of the experiments were consistent with the predicted hysteresis effects. These hysteresis effects were studied using 100% and 25% contrast gratings at three spatial frequencies (1.5, 3 and 6 cpd). The effects of restricting blocks of trials to contain movie sequences running in one direction only (blocked trials), without any waiting time between trials, was also investigated. This manipulation was used to study the possible effects of adaptation of fusion or rivalry mechanisms which may have acted in opposition to hysteresis. Dominance durations and upper fusion limits were also measured with the stimulus patterns used in the hysteresis experiments, to determine whether the perception of depth

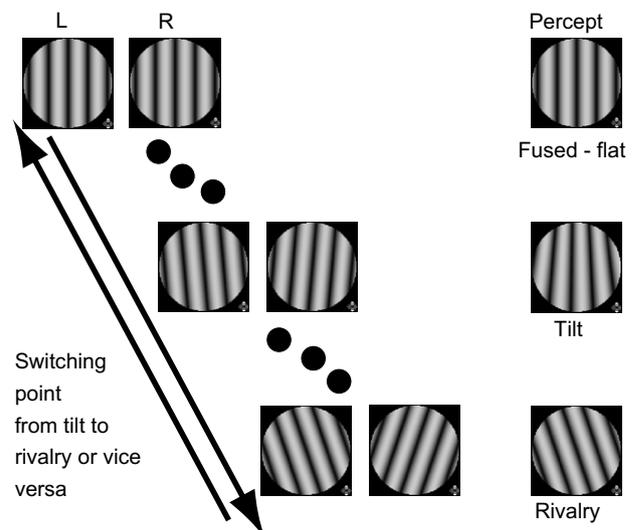


Fig. 1. Procedure. The patterns were sinusoidal gratings with orientation disparities ( $0^\circ, 1^\circ, 2^\circ, \dots, 40^\circ$ ) resulting in various degrees of tilt. A movie sequence of the stereoscopic grating pairs was shown with 0.5, 1 or 2 s frame duration in forward or reverse order. The observer chose the point at which (1) a single grating broke into two rivalrous gratings (increasing orientation trials); or (2) two rivalrous gratings merged into a single tilted grating (decreasing orientation trials).

or rivalry had an effect on the transition points in the hysteresis sequences. Collectively, the results provide evidence that hysteresis plays an important role in stereopsis, a feature which should be incorporated in future modelling efforts.

## 2. General methods

### 2.1. Observers

Two authors (AB, JK) and five naïve observers (TR, SA, SS, JR and YL) participated in all experiments (except where noted otherwise). All had normal or corrected-to-normal vision and stereoacuity thresholds better than 30 s arc, measured using the Titmus stereo test (Stereo Optical Co., Chicago, IL).

### 2.2. Display

All stimuli were presented on a PowerMac G5 Macintosh computer with 800 × 600 resolution, 120 Hz refresh rate and a LaCie Electron 22blue IV 22" video monitor with an 8 bit/pixel grey scale which was gamma-corrected using a colour look-up table. Stimuli were generated and displayed using VPixx software (VPixx Technologies Inc., Longueuil, Canada, www.vpixx.com). CrystalEyes 3 liquid crystal shutter glasses (StereoGraphics Corporation, REAL D Scientific Corp.) were used. The display had a mean luminance of 30 cd/m<sup>2</sup> and peak luminance of 60 cd/m<sup>2</sup>, viewed through the shutter glasses. Viewing distance was set to 114 cm using a chin rest, such that one pixel subtended 1.46 min arc. The stimuli were viewed under dim room illumination.

### 2.3. Stimuli

#### 2.3.1. Sinusoidal gratings

The patterns were sinusoidal gratings with orientation disparities (0°, 1°, 2°, ..., 40°) increased by a fixed increment (1°) in successive pairs. Each of these numbers refers to the total orientation difference between the two eyes (equivalent to ±0°, 0.5°, 1°, ..., 20°). This description in terms of total orientation difference will be used throughout this paper. The movie sequence of the 41 stereoscopic grating pairs was shown with 0.5, 1 or 2 s frame duration, in forward or reverse order, and thus with increasing or decreasing orientation differences. These two types of trials will henceforth be referred to as increasing orientation trials and decreasing orientation trials. Throughout each sequence the gratings were tilted so that either the top or bottom appeared tilted forward (with positive or negative orientation disparities). The starting frame of the sequence was chosen randomly as the first, second, third or fourth grating pair, to prevent observers from using the elapsed time in the sequence to choose the transition point.

The display consisted of the sinusoidal patterns, in a circular patch (3° diameter) at the centre of the screen. The sinusoidal grating stimulus was surrounded by a black rectangle (5° width × 9° height) to aid fixation. The remainder of the screen was at mean luminance.

### 2.4. Procedure

#### 2.4.1. Experimental trials

The observer initiated the start of the movie sequence with a button press. The observer used a button press to indicate the transition point at which:

(1) the single tilted grating broke into two rivalrous gratings (in increasing orientation trials); or (2) two rivalrous gratings merged into a single tilted grating (in decreasing orientation trials). The observer waited 3–5 s before initiating each subsequent experimental trial.

Observers were tested at spatial frequencies of 1.5 cpd (100% and 25% Michelson contrast) and 3 cpd (100% Michelson contrast) for the gratings. Observers AB, TR, SA, SS, JR and YL were also tested at an additional

spatial frequency (6 cpd) at 100% contrast, by doubling the viewing distance with the 3 cpd gratings. Each observer was tested twice with each block of trials in which the spatial frequency, contrast and direction of movie sequence was held constant. Each block of trials consisted of 8 trials corresponding to 8 conditions, presented in random order (4 different starting frames for the sequence, and 2 conditions for gratings with the top or bottom tilted forward). The order in which these blocks of trials was presented was randomized for each observer.

#### 2.4.2. Control experiment 1 (reaction time)

The observer chose the transition point in a movie sequence in which there was an abrupt transition from fusion to rivalry or rivalry to fusion. Eight to ten images with fusion, followed by eight to ten images with rivalry were presented (or alternatively in reverse order). The orientation disparities for the images were selected randomly from appropriate values (fusion: 0°, 1°, 2°, ..., 8°; rivalry: 30°, 31°, 32°, ..., 40°) to give rise to percepts of fusion or rivalry without any ambiguity. At the frame duration of 0.5 s the length of the sequence was randomly chosen to be 8, 8.5, 9, 9.5 or 10 s. At the 1 and 2 s frame durations the lengths of the sequences were twice and four times these values, respectively. Observers were tested at the same spatial frequencies (and contrast values) as in the main experiment.

#### 2.4.3. Control experiment 2

Observers were shown the 41 images (0°, 1°, 2°, ..., 40°) which were used to produce the movie sequences in the main experiment one at a time in randomized order, and asked to judge if there was one fused grating present or two gratings undergoing rivalry. Each image was left on the screen for an unlimited duration, until the observer made the response with a key press. Observers were tested with 1.5 cpd gratings (100% and 25% contrast).

#### 2.4.4. Control experiment 3

Observers were tested in the same way as in the main experiment except that the movie was shown in the forward and reverse directions simultaneously. The forward and reverse sequences were displayed in two circular patches (3° diameter), 4° to the left and right of the screen centre. Observers indicated the transition points for the forward and reverse sequences by pressing two keys. Observers AB, SA, TR and JR were tested in this control experiment (using 1.5 cpd gratings at 100% contrast).

#### 2.4.5. Dominance duration

Dominance durations were measured at a range of orientation disparities (2°, 4°, 6°, ..., 40°). Note that each value is the total orientation difference between the two eyes as in the hysteresis experiments. Observers reported perceptual alternations continuously over 100 s trials. Observers pressed one key when the left grating predominated, or another key when it was not visible. Observers were tested at the same spatial frequencies (and contrast values) as in the main hysteresis experiment, and were tested three times at each condition (i.e. combination of orientation disparity, spatial frequency and contrast).

#### 2.4.6. Upper limit in orientation disparity for depth perception

Following the hysteresis experiments, tests of depth perception were carried out to determine whether these perceptual measures related to the transitions in the hysteresis sequences. The orientation disparity of the sinusoidal gratings was varied in an adaptive staircase procedure (Taylor & Creelman, 1967) in order to determine the upper limit for depth perception, using a display similar to previous studies (Wilcox & Hess, 1995). The display consisted of three sinusoidal patterns, in circular patches (3° diameter) with one patch at the screen centre, and two other reference stimulus patches centred 4° above and below the screen centre. The two reference sinusoidal grating patches were always displayed at zero disparity and provided a strong fixation plane. The central stimulus was at a variable orientation disparity, which could be positive or negative (i.e. top tilted forward/backwards). The observer reported whether the top was tilted forward or backwards. The upper limit for

depth perception was the orientation disparity at which the observer reported the correct depth perception 75% of the time. Two stimulus durations were used: 180 ms and 1 s. Before and after an experimental trial the screen was blank except for a central Nonius fixation cross ( $0.30 \times 0.25$ ). Observers were tested with 1.5 cpd (100% and 25% contrast) and 6 cpd patterns. Six observers took part in this experiment, including one author (AB).

### 3. Results

Fig. 2 shows the size of the hysteresis effect for 1.5 cpd gratings in different panels for the three frame durations (0.5, 1 and 2 s) of the movie sequence. In each panel, a step function illustrates the transition from fusion to rivalry (solid line) or rivalry to fusion (dashed line) which occurred at a particular orientation difference (degrees). The three columns in the figure show results for (1) one observer (JR) at 100% contrast; (2) the mean from all observers at 100% contrast; and (3) the mean from all observers at 25% contrast.

The hysteresis effects at 100% contrast will be described first, followed by the results at 25% contrast. As shown in Fig. 2 (middle column), the hysteresis effects at 100% contrast, when measured by orientation disparity, were largest at the 0.5 s frame duration corresponding to the fastest movie speed and decreased as frame duration increased. On average, observers chose a transition point of  $23.8^\circ$  (increasing orientation trials) and  $17.1^\circ$  (decreasing orientation trials) at the 0.5 s frame duration. Subtracting these numbers, the magnitude of the hysteresis effect expressed as an orientation difference was equal to  $6.72^\circ$ , corresponding to a timing difference of 3.36 s. Computed in the same way, the size of the hysteresis effect at the 1 s frame duration was equal to  $3.89^\circ$  (a timing difference of 3.89 s). Thus, at both these frame durations observers perceived the transition to occur at a larger orientation disparity when the movie sequence was shown in the forward direction (increasing orientation) compared to the reverse direction (decreasing orientation). There was no hysteresis effect at the 2 s frame

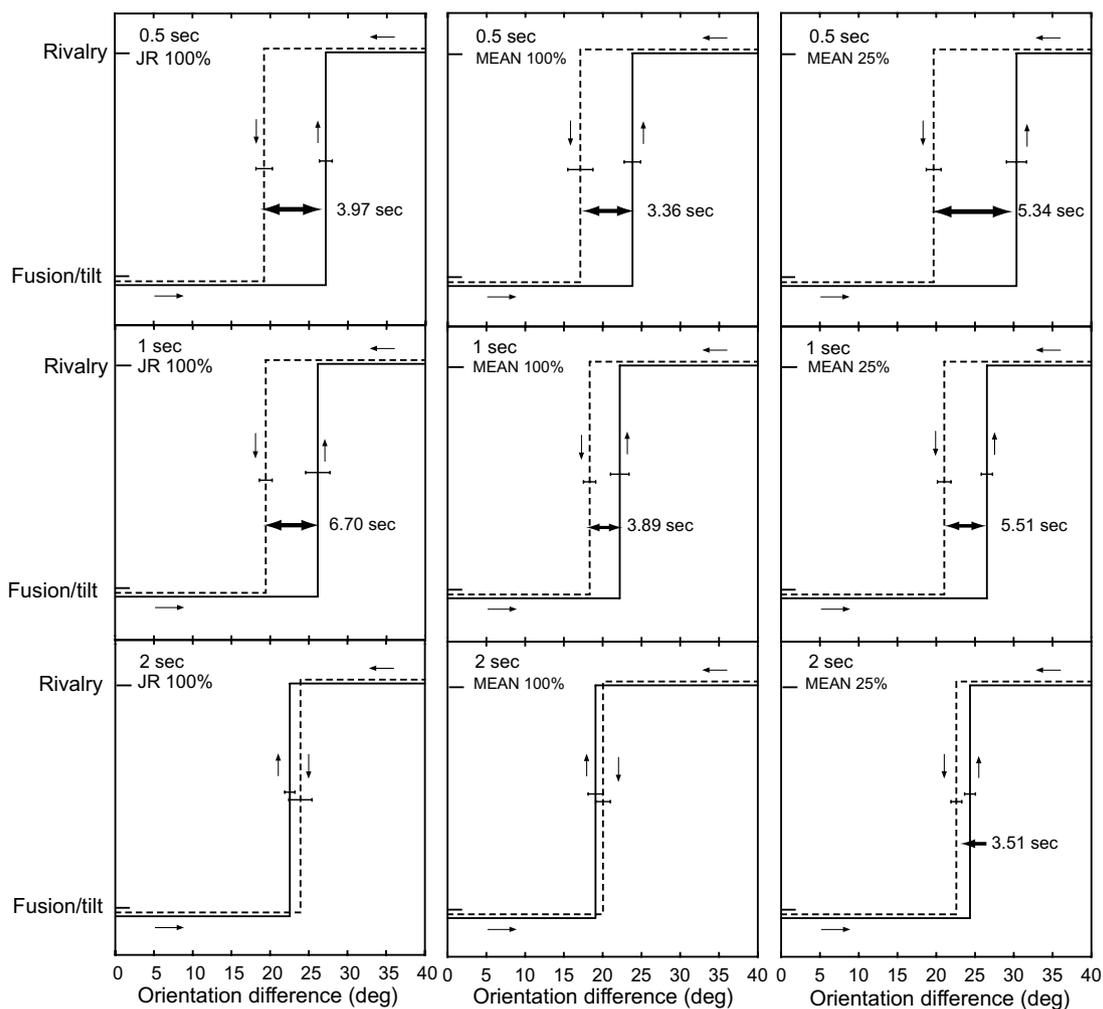


Fig. 2. Hysteresis effects as a function of the frame duration of the movie sequence. In each panel, a step function illustrates the transition from fusion to rivalry (solid line) or rivalry to fusion (dashed line) which occurred at a particular orientation difference (degrees). The left, middle and right columns show results for 1.5 cpd gratings for: (1) one observer (JR) at 100% contrast; (2) the mean from all observers at 100% contrast; and (3) the mean from all observers at 25% contrast. In each column the top, middle and bottom rows show results at the 0.5, 1 and 2 s frame durations. These results are the raw data, without the correction for reaction time. Error bars in this and all subsequent figures are  $\pm 1 SE$ .

duration, as the orientation difference was not significantly different from zero, with a value of  $-1.11^\circ$ . The results for the observer (JR) (first column) show similar trends to the mean, with substantial hysteresis effects at the 0.5 and 1 s frame durations, and no effect at the 2 s frame duration.

The hysteresis effects with 1.5 cpd gratings at 25% contrast are also shown in Fig. 2 (third column). The results are the mean from all observers. On average, observers chose a transition point of  $30.4^\circ$  (increasing orientation trials) and  $19.7^\circ$  (decreasing orientation trials) at the 0.5 s frame duration (1.5 cpd). Subtracting these numbers, this was equal to an orientation difference of  $10.7^\circ$  (1.5 cpd), or a timing difference of 5.34 s. Thus, the hysteresis effects were greater at 25% contrast than 100% contrast, for which the comparable value was  $6.72^\circ$ . When the contrast was reduced, the transition point from fusion to rivalry shifted to a larger orientation difference ( $30.4^\circ$  versus  $23.8^\circ$ ), as did the transition from rivalry to fusion ( $19.7^\circ$  versus  $17.1^\circ$ ). Of these two factors, the shift in the transition from fusion to rivalry had a slightly larger impact in increasing the magnitude of the hysteresis effects. However, performing a *t*-test on the differences in the fusion–rivalry and rivalry–fusion transition points as contrast was reduced revealed that these differences were not significant ( $t(6) = 2.03$ ,  $p = .09$ ).

The measures of hysteresis up to this point included the reaction time associated with choosing the transition point in the sequence, which might have added a significant time delay. In order to determine whether reaction time was a significant factor, control experiment 1 was carried out in which the observer was asked to choose the transition point in sequences in which there was an abrupt transition from fusion to rivalry or rivalry to fusion. The reaction times measured for each observer ranged from 322 to 400 ms, with a mean of 383 ms (across all spatial frequencies and values of contrasts used in the hysteresis experiments) and were very similar at all three frame durations.

The hysteresis effects with reaction times subtracted for 1.5 cpd patterns (100% and 25% contrast) been plotted as a

function of frame duration of the sequence in Fig. 3. As described with reference to Fig. 2, the orientation disparity at the transition point when the movie was shown in the reverse direction (decreasing orientation), subtracted from the orientation disparity for the forward direction (increasing orientation) was used to compute the size of the hysteresis effect (i.e. orientation difference in degrees). The left and right panels show data from one observer (JR) and the mean of all observers, respectively. With the magnitude of the hysteresis effect adjusted by subtracting reaction time in both directions of the movie sequence, the size of the effects were  $5.18^\circ$  (1.5 cpd, 100% contrast), and  $9.12^\circ$  (1.5 cpd, 25% contrast) at the 0.5 s frame duration, corresponding to time delays of 2.59 and 4.56 s. Note that the mean orientation difference for the 100% contrast stimulus patterns was negative at the 2 s frame duration ( $-1.75^\circ$ ). This indicated that, on average, observers chose the transition point at a smaller orientation disparity in the increasing orientation trials and a larger orientation disparity in the decreasing orientation trials. However, this value of  $-1.75^\circ$  was not significantly different from zero ( $t(df = 6) = -2.28$ ,  $p > .05$ ). Overall, the results far exceeded the effects which could be attributed to reaction time and thus indicate neural hysteresis. A two-way repeated measures ANOVA indicates that the hysteresis effect was significantly larger at lower contrast ( $f_{(1,6)} = 11.34$ ,  $p = .0034$ ), and there was a significant effect of frame duration ( $f_{(2,12)} = 29.4$ ,  $p < .0001$ ), but the interaction was not significant ( $f_{(2,12)} = 0.864$ ,  $p > .05$ ).

Fig. 4 compares the hysteresis effect with 1.5, 3 and 6 cpd gratings (at 100% contrast) plotted as a function of the frame duration of the movie sequence. The hysteresis effects are shown for seven observers at 1.5 and 3 cpd and six observers at 6 cpd, and the mean of these groups. The measured hysteresis effects vary with spatial frequency and appear to be somewhat larger at 6 cpd. As before, the size of the hysteresis effect has been adjusted for the effects of reaction time. With reaction time subtracted the mean

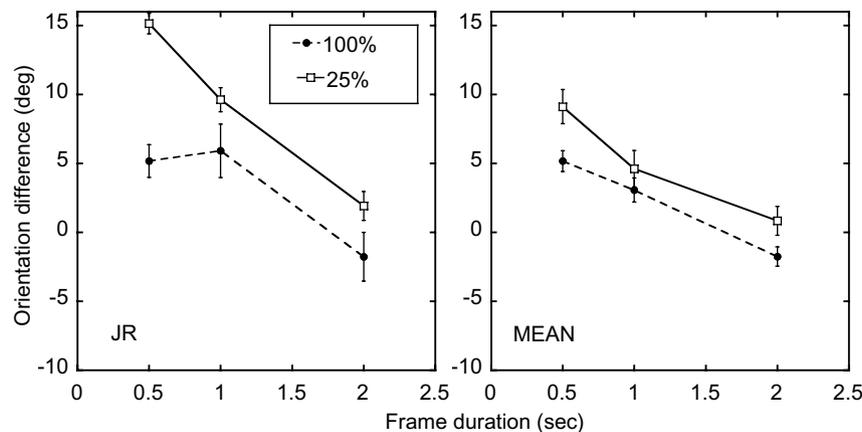


Fig. 3. Hysteresis effects for 1.5 cpd gratings at 100% and 25% contrast as a function of the frame duration of the movie sequence. Results are shown for one observer (JR) and the mean from all observers, in left and right panels. In this and all subsequent figures the size of the hysteresis effect has been adjusted by taking in account the effects of reaction time.

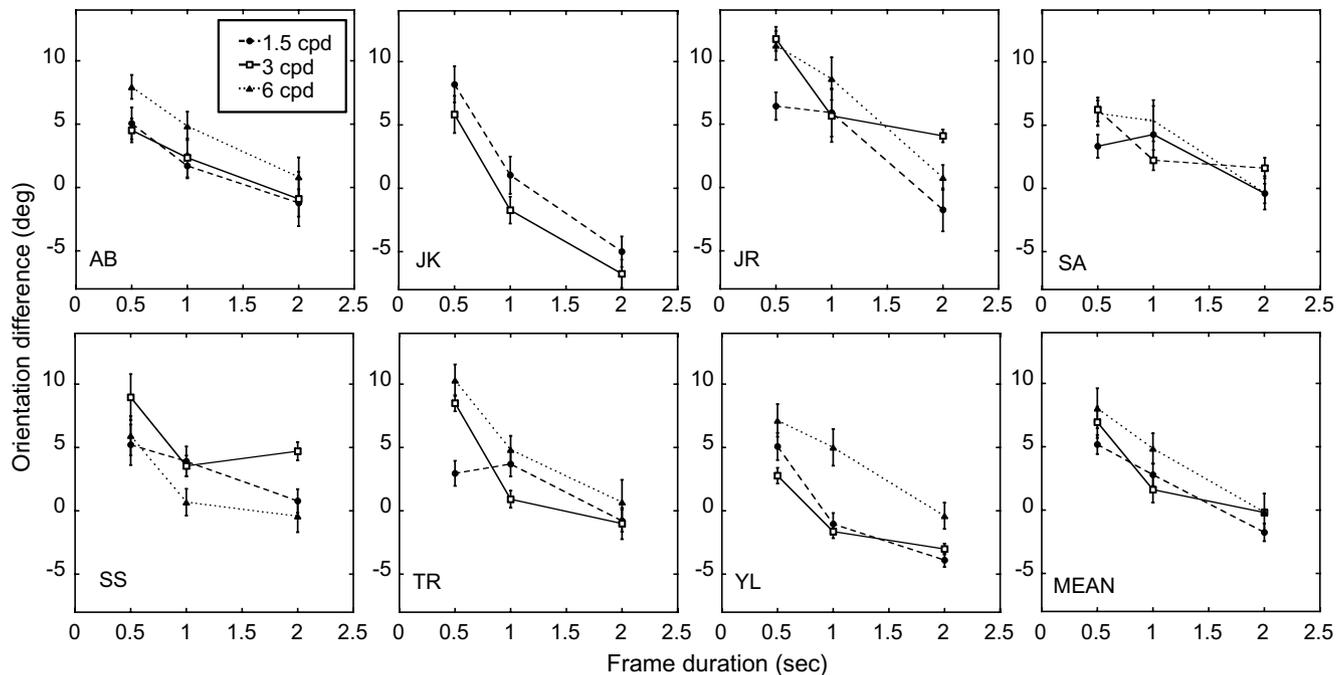


Fig. 4. Hysteresis effects for 1.5, 3 and 6 cpd gratings as a function of the frame duration of the movie sequence. The orientation disparity at the transition point in decreasing orientation trials was subtracted from the orientation disparity at the transition point in increasing orientation trials to compute the hysteresis effect (i.e. orientation difference in degrees). The results for 1.5 and 3 cpd gratings are shown for seven observers while the results for 6 cpd gratings are shown for six observers. The mean of the data from these observers is also shown.

value for the hysteresis effect at 3 cpd, averaged across observers (bottom right panel) was equal to  $6.94^\circ$  at the 0.5 s frame duration, which corresponded to a timing difference of 3.47 s. At the 1 s frame duration the size of the hysteresis effect was  $1.62^\circ$  (a timing difference of 1.62 s), while at the 2 s frame duration the size of the effect was  $-0.18^\circ$ . This latter value is not significantly different from zero. The loss of hysteresis at 2 s may have occurred as a result of adaptation of fusion or rivalry mechanisms. The size of the hysteresis effect at 6 cpd was 8.04, 4.87 and  $-0.16^\circ$  at the 0.5, 1 and 2 s frame durations, respectively. A repeated measures two-way ANOVA performed on the hysteresis data at the three spatial frequencies revealed that both the effect of spatial frequency ( $f_{(2,10)} = 5.67$ ,  $p < .05$ ) and frame duration were significant ( $f_{(2,10)} = 30.48$ ,  $p < .0001$ ), but the interaction was not significant ( $f_{(4,20)} = 2.42$ ,  $p > .05$ ), indicating that the measured size of the effects varied with spatial frequency and frame duration.

Additional tests were performed to measure dominance durations and upper fusion limits in order to determine whether the perception of depth or rivalry had an impact on the transitions in the hysteresis sequences. Fig. 5 shows dominance durations with 1.5 cpd gratings at 100% and 25% contrast, as a function of orientation difference ( $26^\circ$ ,  $28^\circ$ ,  $30^\circ$ , ...,  $40^\circ$ ). There was no rivalry for orientation differences less than  $26^\circ$  (100% contrast) or  $32^\circ$  (25% contrast), so no data points are shown for these values. Thus, rivalry was perceptible at an orientation difference of  $26^\circ$  (100% contrast), but was not perceptible for the

25% contrast gratings until the orientation difference was increased to  $32^\circ$ . It is possible that slower rivalry with the 25% contrast gratings may have had an effect on the perceived transition points in the hysteresis sequences.

The upper limit in orientation disparity supporting depth perception was measured with 1.5 cpd gratings at 100% and 25% contrast. An adaptive staircase procedure was used, in which the orientation disparity of the sinusoidal grating was varied in order to determine the disparity limit, at which the correct depth perception (top tilted forward or back) was reported 75% of the time. These tests were carried out at two stimulus durations. The values at the 180 ms stimulus duration were:  $19.8 \pm 1.3^\circ$  (1.5 cpd, 100% contrast) and  $19.9 \pm 0.47^\circ$  (1.5 cpd, 25% contrast). The values at a duration of 1 s were:  $20.9 \pm 0.55^\circ$  (1.5 cpd, 100% contrast) and  $21.0 \pm 0.39^\circ$  (1.5 cpd, 25% contrast). The upper disparity limit at 25% contrast did not differ from the value at 100% contrast, at either duration (1 s:  $t(df = 5) = -0.658$ ,  $p > .05$ ; 180 ms:  $t(df = 5) = -0.633$ ,  $p > .05$ ). These results are consistent with previous studies showing that fusion limits are independent of contrast (Schor, Heckmann, & Tyler, 1989). Thus, there were no differences in perceived depth for low and high contrast gratings so we would not expect any differences in the transitions in the hysteresis sequences arising from depth perception with these images.

The mean dominance durations were longer with 6 cpd patterns, compared with the 1.5 cpd patterns, in tests carried out with 100% contrast gratings. The mean dominance duration with 1.5 cpd gratings at an orientation difference

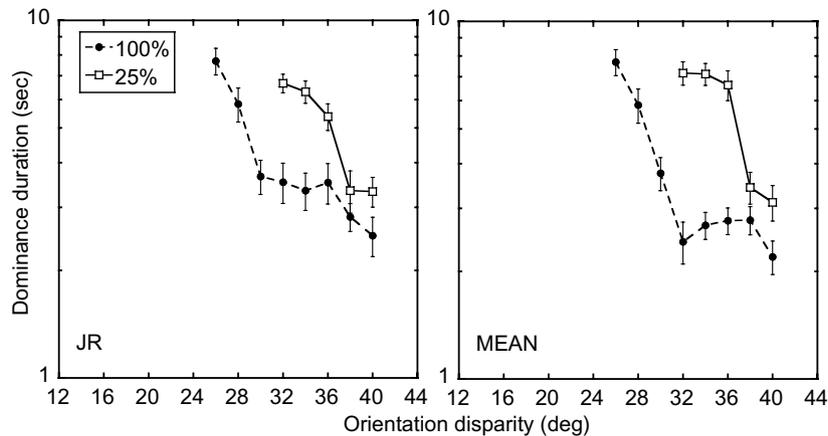


Fig. 5. Dominance durations for 1.5 cpd gratings at 100% (circles) and 25% contrast (squares) as a function of orientation difference (26°, 28°, 30°, ..., 40°). There was no rivalry for orientation differences less than 26° (100% contrast) or 32° (25% contrast) so no data points are plotted. Results are shown for one observer (JR) and the mean from all observers, in left and right panels.

of 26° (i.e. close to the perceived transition point) was 7.69 s. The results of the tests measuring dominance durations with 6 cpd gratings at a range of orientation differences revealed that no rivalry was perceived at this orientation difference (observers perceived a single tilted grating). The orientation difference had to be increased to 32° before rivalry was perceived. The upper limits in orientation disparity at which depth was perceived measured with 6 cpd (100% contrast) patterns were  $19.1 \pm 0.66^\circ$  (1 s duration) and  $18.4 \pm 0.81^\circ$  (180 ms). Depth perception was poorer at 6 cpd compared to 1.5 cpd at both stimulus durations (180 ms:  $t(df=5) = -3.82$ ,  $p < .05$ ; 1 s:  $t(df=5) = -5.50$ ,  $p < .05$ ) but the value at the 1 s duration may be more relevant for the hysteresis experiments as these were carried out with prolonged viewing times. These effects are consistent with studies showing that stereopsis fails at higher spatial frequencies (Schor & Wood, 1983; Smallman & MacLeod, 1994). Thus, as the spatial frequency was increased from 1.5 to 6 cpd, there were some differences in depth perception and rivalry (slower alternations) which may have affected the perceived transitions in the hysteresis sequences.

One aspect of the data concerns the comparison between the upper fusion limits for depth perception, and the transition orientation disparity in the rivalry–fusion sequence. The upper fusion limits measured at the 1 s stimulus duration (20.9° at 1.5 cpd; 19.1° at 6 cpd) were larger than the orientation disparities (17.9° at 1.5 cpd; 17.7° at 6 cpd, values corrected for reaction time) in transitions from rivalry to fusion, which is expected based upon the effects of hysteresis. Similarly, the upper fusion limit for 1.5 cpd, 25% contrast gratings (21.0°) (1 s duration) also was larger than the orientation disparity (20.5°) in the rivalry–fusion transition. However, these differences were not statistically significant (6 cpd, 100% contrast:  $t(df=5) = -1.71$ ,  $p > .05$ ; 1.5 cpd, 100% contrast:  $t(df=5) = -0.658$ ,  $p > .05$ ; 1.5 cpd, 25% contrast:  $t(df=5) = -1.21$ ,  $p > .05$ ).

The hysteresis effects should be compared with the results of control experiment 2, in which the images used

to make up the movie sequence were presented individually and observers were asked to judge if one fused grating or two rivalrous gratings were present. The psychometric functions obtained in this experiment had a slightly different transition point, or point of highest uncertainty, for each observer. The psychometric function for each observer was fit to a Weibull function (Quick, 1974; Weibull, 1951) to obtain this transition point. The averages of these values across observers for the 1.5 cpd gratings were equal to 21.2° (100% contrast) and 27.2° (25% contrast). These values fell in between the two transition points for fusion to rivalry, and rivalry to fusion (23.0° > 21.2° > 17.9° at 100% contrast; 29.6° > 27.2° > 20.5° at 25% contrast). Performing paired *t*-tests revealed that at 100% contrast the shift of the transition in both directions was statistically significant (rivalry–fusion:  $t(df=6) = 3.08$ ,  $p < .05$ ; fusion–rivalry:  $t(df=6) = -3.17$ ,  $p < .05$ ). At 25% contrast the shift of the transition was statistically significant for the rivalry–fusion sequence ( $t(df=6) = 10.3$ ,  $p < .05$ ) but not the fusion–rivalry sequence ( $t(df=6) = -2.01$ ,  $p = .09$ ). Thus, there was a tendency for the hysteresis effects to shift the transition from fusion to rivalry to larger orientation disparities, and also shift the transition from rivalry to fusion to smaller orientation disparities.

One possible alternative explanation for the results in the main experiment was that the effects could have been a consequence of torsional eye movements rather than neural hysteresis per se. We were particularly concerned about torsional eye movements (and not other types of eye movements) because these were most likely to have produced different effects in the forward and reverse direction sequences (Banks, Hooge, & Backus, 2001). In order to rule out the effects of torsional eye movements, control experiment 3 was carried out, in which observers chose the transition point as the movie was shown in forward and reverse directions simultaneously (using 1.5 cpd gratings at 100% contrast). The results of this control experiment did not differ from the results in the main experiment. The mean hysteresis effect at 1.5 cpd from

the four observers was equal to  $5.76 \pm 0.69^\circ$  and  $5.11 \pm 1.1^\circ$  at the 0.5 and 1 s frame durations, respectively. No hysteresis occurred at the 2 s frame duration, as the orientation difference was not significantly different from zero ( $-0.164 \pm 0.13^\circ$ ). These values have not been corrected for reaction time; with the reaction time adjustment the values are:  $4.23^\circ$  (0.5 s),  $4.34^\circ$  (1 s), and  $-0.547^\circ$  (2 s). A two-way repeated measures ANOVA showed that the differences between the control experiment and the main experiment were not significant ( $f_{(1,3)} = 0.208$ ,  $p = .664$ ), although the effect of frame duration was significant ( $f_{(2,6)} = 41.7$ ,  $p < .0001$ ). The interaction was not significant ( $f_{(2,6)} = 0.104$ ,  $p > .05$ ). Thus, the hysteresis effects in the main experiment could not be attributed to torsional eye movements (Banks et al., 2001).

### 3.1. Mixed versus blocked trials

The hysteresis effects, measured by orientation difference, were largest at the fastest movie speed and decreased as movie speed decreased. These effects could have been due to adaptation (Blakemore & Campbell, 1969; Pantle & Sekuler, 1969) which would have acted in opposition to the hysteresis effects. In this section the same movie sequences were used which provided evidence for hysteresis effects in the first experiment. However, we were interested in investigating whether it makes any difference if we restrict the direction with which the change can occur, and present the experimental trials without any resting time between the trials. In this new procedure, each trial followed immediately after the preceding one (as described above, the resting period in the main experiment was 3–5 s). In one set of trials, forward direction (increasing orientation) trials were segregated from and presented in separate blocks from reverse direction (decreasing orientation) trials. The results from these two blocked trial conditions are compared with a third condition in which increasing and decreasing orientation trials are randomly mixed (mixed trials).

The purpose of these manipulations was to investigate the potential effects of adaptation of (1) fusion and (2) rivalry mechanisms, which are maximized in the blocked trials (as follows). In the increasing orientation trials, as fusion sequences are presented more frequently, relatively stronger effects of adaptation of fusion mechanisms may occur, which would shift the transition to smaller orientation disparities. In the decreasing orientation trials, rivalry sequences are presented more frequently and so relatively stronger effects of adaptation of rivalry mechanisms may occur, which would shift the transition to larger orientation disparities. In the mixed trials, there should be no differential adaptation of the fusion and rivalry mechanisms, so any effects of adaptation should be reduced. Hence any effects of adaptation of either rivalry or fusion mechanisms would result in reduced hysteresis effects in the blocked trials, compared to the mixed trials.

#### 3.1.1. Methods

The same procedure was used as in the first experiment, with 1.5 cpd 100% contrast gratings. The three conditions (increasing orientation blocked, decreasing orientation blocked and mixed) were tested on different days. In all cases only gratings with the bottom tilted forward were used. Observers AB, JR, SA and YL participated in this experiment.

#### 3.1.2. Results

Hysteresis effects for the mixed and blocked trials for 1.5 cpd patterns have been plotted as a function of frame duration in Fig. 6. The magnitude of the hysteresis effects for the blocked trials was computed using the transition points in the increasing orientation blocked trials and decreasing orientation blocked trials. The magnitude of the hysteresis effects for mixed trials was  $7.25 \pm 0.75^\circ$ , or  $5.72^\circ$  with the reaction time adjustment. This replicates the hysteresis effects obtained in the main experiment ( $5.18^\circ$ , adjusted for reaction time). Performing a repeated measures two-way ANOVA revealed that these differences were not significant ( $f_{(1,3)} = 3.57$ ,  $p = .09$ ), although the

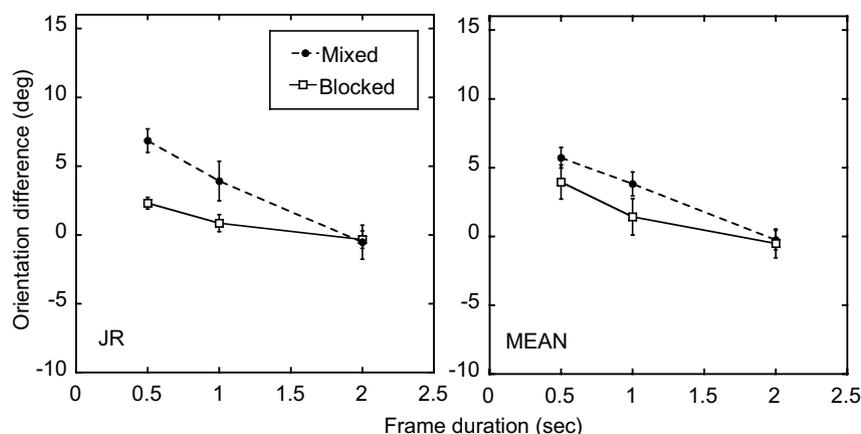


Fig. 6. Hysteresis effect for mixed and blocked trials as a function of the frame duration of the movie sequence (100% contrast, 1.5 cpd gratings). Data is shown for one observer (JR) and the mean from four observers, in left and right panels.

effect of frame duration was significant ( $f_{(2,6)} = 36.9$ ,  $p < .0001$ ). The interaction was not significant ( $f_{(2,6)} = 0.134$ ,  $p > .05$ ).

However, when the increasing orientation and decreasing orientation trials were presented in separate blocks, the hysteresis effects were reduced ( $5.48 \pm 0.90^\circ$  or  $3.95^\circ$  with the reaction time adjustment). Analysis with a repeated measures two-way ANOVA revealed that the differences between the main experiment and the blocked trials were not significant ( $f_{(1,3)} = 0.218$ ,  $p = .65$ ), although the effect of frame duration was significant ( $f_{(2,6)} = 30.0$ ,  $p < .05$ ). The interaction was not significant ( $f_{(2,6)} = 1.49$ ,  $p > .05$ ). However, when a similar analysis was carried out comparing the results from the blocked and mixed trials, the differences were significant (blocked versus mixed:  $f_{(1,3)} = 15.9$ ,  $p = .003$ ; frame duration:  $f_{(2,6)} = 25.2$ ,  $p < .05$ ; interaction:  $f_{(2,6)} = 0.99$ ,  $p > .05$ ), suggesting an effect of adaptation in the blocked trials.

Although there was some tendency towards a reduction of the hysteresis effects with the blocked design, hysteresis effects were still present at the fastest movie speed, even in these trials designed to maximize the effects of adaptation. Thus, the effects of adaptation were not a significant factor at this movie speed in the main experiment.

#### 4. Discussion

Our results provide strong evidence for hysteresis between stereopsis and rivalry. In transitions between stereopsis and rivalry, observers perceived the transition to occur at larger orientation differences when the movie sequence was shown in the forward direction (increasing orientation) compared to the reverse direction (decreasing orientation). The hysteresis effects decreased as the movie was shown at slower speeds. The hysteresis time delays lasted several seconds and far exceeded reaction times, which were less than half a second.

One of the predicted effects of hysteresis is that the perception of depth or rivalry may persist to larger or smaller (respectively) orientation disparities, when presented in the movie sequence. Hence it was important to perform a comparison of the perception of depth or rivalry in the movie sequences with some measure of perception outside of the sequences. Thus, in control experiment 2 the perception of depth or rivalry was determined for individual images used to make up the sequences. The transition points obtained in the control experiment fell in between the transitions from the hysteresis experiments for fusion to rivalry, and rivalry to fusion. There was a tendency for the hysteresis effects to shift the fusion–rivalry and rivalry–fusion transitions, to larger and smaller orientation differences, respectively. Not only did the perception of rivalry delay the onset of depth perception, but also the symmetrical effect occurred, namely depth delayed rivalry (these effects were statistically significant for the 1.5 cpd, 100% contrast gratings).

Additional tests were carried out to determine whether the hysteresis effects correlated with other perceptual measures. Specifically, measurements of dominance durations and fusion limits were obtained to study whether the perception of depth or rivalry may have affected the perceived transitions in the sequences. Although there may not be strong theoretical reasons why the effects of contrast and spatial frequency should affect hysteresis, there still will be effects on the transitions which may have an impact the measured size of the effects. For example, with 1.5 cpd gratings, as contrast is dropped from 100% to 25%, depth perception is largely unaffected, while rivalry becomes slower. This had the effect of shifting the perceived depth–rivalry transition towards larger orientation disparities. It appears that the rivalry–depth transition was not shifted to the same extent (although these differences were not statistically significant), and this had an effect on the measured hysteresis effect size (Fig. 2). The statistical analysis showed that the size of the hysteresis effect was larger at 25% contrast. A similar point can be made with regards to the effects of increasing spatial frequency from 1.5 to 6 cpd; in this case, rivalry is slower and depth perception is poorer. The statistical analysis showed that hysteresis did indeed vary with spatial frequency.

Generally all of the results of the experiments, including the effects of contrast and spatial frequency, can be explained within the framework of a model of depth and rivalry, as outlined in the Introduction. In a model of rivalry, the effects of contrast and spatial frequency would be evidenced in the alternation rates of neurons representing rivalry, which are affected by physiological variables, such as the strength of self-adaptation or inhibition, and recurrent excitation (Wilson, 2007), but it is not likely that hysteresis occurs through these basic rivalry mechanisms. A model including physiological variables to describe these effects of contrast and spatial frequency would predict that the transition points would occur at the same orientation disparity for all frame durations of the sequences. The explanation for the dependence of hysteresis effects on contrast and spatial frequency may be that slower rivalry or poorer depth perception may have added an extra delay to response times, increasing the size of the measured hysteresis effect.

The most important result confirming the effects of hysteresis was that at all values of contrast and spatial frequency the difference in orientation disparity for the transitions in the fusion–rivalry and rivalry–fusion sequences were largest at the 0.5 s frame duration, and decreased as frame duration was increased. An explanation involving hysteresis in a model of depth and rivalry is necessary to explain these results. A model of hysteresis would have to be based upon existing models of rivalry but include additional mechanisms in order to explain all of the effects in the data, including the dependence on spatial frequency, contrast and frame duration.

Two types of adaptation may have acted in opposition to the hysteresis effects, adaptation of fusion (Blakemore & Campbell, 1969; Pantle & Sekuler, 1969) and adaptation of rivalry mechanisms (Wilson, 1999, 2003, 2007), which will be described in turn. The first possibility was that adaptation of fusion mechanisms occurred, which could result in disparity specific elevations in thresholds (Blakemore & Hague, 1972; Felton, Richards, & Smith, 1972), and may reduce or even eliminate completely the sensation of depth (Beverley & Regan, 1973). The effect of this adaptation, however, could only have been to *reduce* the hysteresis effects. This is because adaptation selectively reduces the sensitivity of the visual system to gratings at the particular depth, which corresponds to a particular orientation disparity in the present study. Hysteresis, on the other hand, depends on the stability of one depth percept relative to another. The presentation time required to obtain hysteresis effects had to be long enough for depth perception, but short enough that adaptation did not eliminate the effects. Stereoscopic acuity increases over periods of 0.5–1.0 s (McKee, Levi, & Bowne, 1990; Ogle & Weil, 1958; Watt, 1987). Adaptation produced by changing orientation disparity too slowly would be expected to reduce the hysteresis effects.

The second type of adaptation which may have occurred was adaptation of rivalry mechanisms, as a result of prolonged viewing of gratings undergoing rivalry (Wilson, 1999, 2003, 2007). Based on modelling work, an increase in slow spike rate adaptation would be expected to increase rivalry rates (Wilson, 1999, 2003, 2007). Consequently observers would respond earlier in the movie sequence as the orientation disparity was decreased. Here again, the effects of adaptation of rivalry mechanisms could only have reduced the magnitude of the hysteresis effects. However, it should be pointed out that although adaptation to rivalry could potentially increase rivalry rates, it has been determined empirically that rivalry slows down in the time scale of the hysteresis sequences used in the present experiments (Lehky, 1995; van Ee, 2005).

In the main experiment, a frame duration of 0.5 s was optimal for obtaining consistent hysteresis effects, while longer frame durations (1 or 2 s) were suboptimal. The comparison between the mixed and blocked trial conditions indicated that the effects of hysteresis were reduced with the repeated presentation of similar sequences. However, hysteresis effects were still present at the fastest movie speed, even in these blocked trials designed to maximize the effects of adaptation of fusion or rivalry mechanisms, as outlined above. This meant the effects of adaptation were probably not an important factor at the fastest movie speed in the main experiment, but may have been important at the slower speeds (Wilson, 2007).

Hysteresis was also likely reduced at the slowest movie speed because the slower rate of change provided more opportunity for the occurrence of noise-induced spontaneous changes during the forward and reverse sequences (Wilson, 1999). Such spontaneous changes would work in

opposition to the tendency of the percept to persist, despite changes in the stimulus which would usually favour the opposite percept.

Additional controls were necessary to provide further evidence that a model involving hysteresis at the cortical level is necessary to account for the results. In particular, control experiment 3 was important in showing that similar hysteresis effects could be obtained in a version of the experiment in which the movie was shown in the forward and reverse direction simultaneously. Thus, the hysteresis effects were not due to torsion or other eye movements, as there was no pattern of eye movements which could have altered the orientation disparities and aided the fusional or rivalry process (Banks et al., 2001).

A possible mechanism explaining the hysteresis effects involves inhibition between mechanisms for stereopsis and rivalry, which fits with psychophysical findings that depth and rivalry do not coexist at the same time in the same spatial location and in the same spatial frequency band (Blake, Yang, & Wilson, 1991; Buckthought & Wilson, 2007; Julesz & Miller, 1975). The stability of the percept of either fusion or rivalry is the result of inhibition of the alternative percept. A number of previous studies have shown evidence for inhibitory interactions between depth and rivalry (e.g. Blake et al., 1991; Harrad et al., 1994). However, it is possible to have a neural network representing depth and rivalry with mutual inhibitory interactions between these two states, without any hysteresis in the system. The results of previous studies involving depth–rivalry and rivalry–depth transitions were interpreted without explicitly including hysteresis effects in modelling work or without using models based upon neurophysiology (Erkelenz, 1988; Julesz & Tyler, 1976; Tyler & Julesz, 1976, 1978). For the sake of parsimony it would be useful to reconcile these previous results under a more comprehensive model. Earlier studies placed the emphasis on hysteresis of fusional mechanisms but did not study any effects involving the dynamics of rivalry. The present work makes an important contribution as it uses a psychophysical method to show effects involving cortical dynamics, which cannot be attributed to any particular pattern of eye movements, and provides a major example of positive feedback in visual perception. There were only two possible perceptual states (i.e. depth or rivalry) in the present experiments, and there was no evidence for a third state. This differs from some other experiments which reported hysteresis in transitions involving three perceptual states, for example in apparent motion with bistable motion quartets (Hock, Bukowski, Nichols, Huisman, & Rivera, 2005).

Thus, the hysteresis effects in the present experiments can be explained with a cortical model including positive feedback arising from recurrent inhibition between neural units representing different eyes and grating orientations, as illustrated in Fig. 7 (Wilson, 2007). The existence of two inhibitory populations provides for positive feedback via disinhibition. The existence of positive feedback in the network is crucial, as it is a necessary condition for

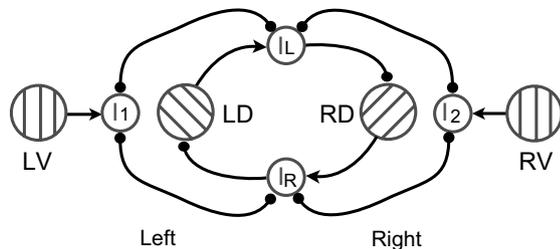


Fig. 7. Fusion and rivalry hysteresis model. Monocular left and right eye neurons (LD, RD) are selective for diagonal gratings (diagonal hatching). Monocular left and right eye neurons (LV, RV) are selective for vertical orientations (vertical hatching). Inhibition is generated with inhibitory interneurons  $I_1$ ,  $I_2$ ,  $I_L$  and  $I_R$ . Rivalry occurs when only LD and RD are stimulated. When LV and RV are stimulated, fusion results and rivalry is suppressed via inhibition of ( $I_L$ ,  $I_R$ ) by ( $I_1$ ,  $I_2$ ). Mutual inhibition between ( $I_1$ ,  $I_2$ ) and ( $I_L$ ,  $I_R$ ) has the effect of stabilizing the rivalry (fusion) state once fusion (rivalry) is initiated. Thus, the model explains the hysteresis effects with positive feedback arising from mutual inhibition between different eyes and orientations via disinhibitory circuits (see text).

the existence of hysteresis effects (Wilson, 1977; Wilson & Cowan, 1972, 1973). The neural units represent populations of monocular cortical neurons which represent visual stimuli within a small region of visual space (Hubel & Wiesel, 1962, 1970). This is a simplified model, which emphasizes the major connections for clarity (Wilson, 2007).

The model contains left and right monocular units tuned to vertical (LV and RV) and diagonally selective neurons tuned to  $+20^\circ$  (RD) and  $-20^\circ$  (LD) to represent the orientation range used in our experiments. When only LD and RD are stimulated, rivalry alternations ensue generated by the inhibitory interneurons  $I_L$  and  $I_R$ . This is a basic minimal rivalry network (Wilson, 2007). Conversely, when vertical gratings are presented to both eyes so that LV and RV are stimulated, fusion results, and any possible rivalry is suppressed via inhibition of  $I_L$  and  $I_R$  by  $I_1$  and  $I_2$ . Thus, this network can generate either fusion or rivalry depending on the nature of stimulation. Competition between rivalry and fusion is generated by mutual inhibition between ( $I_L$ ,  $I_R$ ) and ( $I_1$ ,  $I_2$ ). This mutual inhibition has the effect of stabilizing the rivalry state relative to the fusion state once rivalry is initiated, but it will also stabilize fusion relative to rivalry once fusion is initiated. Thus, a stimulus that sweeps back and forth between vertical in both eyes and opposite diagonals in both eyes will generate hysteresis in the switching points between rivalry and fusion. A simulation of this network shows that it can accurately replicate the hysteresis data reported above (manuscript in preparation).

Stereopsis is only one of a large number of domains of perception with demonstrable hysteresis effects. For example, hysteresis has been studied in apparent motion with bistable motion quartets (Hock, Kelso, & Schoner, 1993; Williams, Phillips, & Sekuler, 1986), motion coherence in random-dot cinematograms (Chang & Julesz, 1984), face categorization (Kim, 2002), 3-D surfaces from optic flow (Atchley, Andersen, & Wuestefeld, 1998), perception of man–woman reversible figures (Chialvo & Apkarian,

1993; Fisher, 1967), object and face recognition (Sadr, 2003) and visual letter recognition (Kleinschmidt, Buechel, Hutton, Friston, & Frackowiak, 2002). In all of these domains it is advantageous for a particular percept to persist despite changes in a stimulus parameter which would usually favour the alternative percept. In stereopsis there are particular difficulties associated with maintaining or establishing fusion, given the correspondence problem. It may not be advantageous to precisely track changes in the image, which would result in abrupt switches between fusion and rivalry and considerable visual discomfort. Thus, hysteresis may play a role in aiding binocular correspondence and in maintaining fusion once correspondence has been established.

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