

Extrinsic factors in the perception of bistable motion stimuli

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Abstract

When viewing a drifting plaid stimulus, perceived motion alternates over time between coherent pattern motion and a transparent impression of the two component gratings. It is known that changing the intrinsic attributes of such patterns (e.g. speed, orientation and spatial frequency of components) can influence percept predominance. Here, we investigate the contribution of extrinsic factors to perception; specifically contextual motion and eye movements. In the first experiment, the percept most similar to the speed and direction of surround motion increased in dominance, implying a tuned integration process. This shift primarily involved an increase in dominance durations of the consistent percept. The second experiment measured eye movements under similar conditions. Saccades were not associated with perceptual transitions, though blink rate increased around the time of a switch. This indicates that saccades do not cause switches, yet saccades in a congruent direction might help to prolong a percept because i) more saccades were directionally congruent with the currently reported percept than expected by chance, and ii) when observers were asked to make deliberate eye movements along one motion axis, this increased percept reports in that direction. Overall, we find evidence that perception of bistable motion can be modulated by information from spatially adjacent regions, and changes to the retinal image caused by blinks and saccades.

Keywords: bistable motion; saccades; contextual modulation; motion integration.

1 Introduction

When two moving gratings are superimposed, they can be perceived as having either transparent motion (the gratings slide across each other) or coherent (pattern) motion. Extended viewing of moving plaid stimuli is often bistable, with awareness alternating between these two percepts over time (von Grunau & Dube, 1993; Hupé & Rubin, 2003). In general, dominance of one or other percept depends on intrinsic properties of the plaid, such as speed, orientation and spatial frequency of the component gratings (Hupé & Rubin, 2003) and the global orientation of the plaid (Hupé & Rubin, 2004). In this paper, we ask to what extent extrinsic factors can affect plaid perception. Specifically, we focus on surround motion and eye movements.

Contextual information can often have a substantial impact on how visual stimuli are interpreted. Surround effects have been reported for orientation judgements

(Georgeson, 1973), perceived brightness/lightness (Adelson, 1993; Anderson & Winawer, 2005) contrast matching (Cannon & Fullenkamp, 1991), detection thresholds (Polat & Sagi, 1993; Petrov, Carandini & McKee, 2005; Meese, Challinor, Summers & Baker, 2009), and motion discrimination (Tadin, Lappin, Gilroy & Blake, 2003) to name but a few. Many perceptual surround effects are attributed to the lateral inhibition between populations of neurones as described in single-cell studies (e.g. Blakemore & Tobin, 1972; Webb, Dhruv, Solomon, Tailby & Lennie, 2005). Bistable stimuli offer a particularly sensitive tool for investigating contextual interactions because although an increase in preference for one stimulus may not affect the initial percept (when the stimulus is first presented), it can produce a substantial change in predominance over extended viewing periods.

Recent work has shown that surrounds which are closely matched to an ambiguous central plaid, but are themselves unambiguously coherent or transparent (owing to moving dots being superimposed on the surround), can affect the percept of the centre (Kozák & Castelo-Branco, 2009). Such surrounds can produce a shift in percept predominance of around 30%. It is not clear whether such plaid surround effects are due to neural interactions between centre and surround representations, or could perhaps be attributed to eye movements. For moving stimuli, it is conceivable that surrounds ‘capture’ eye movements, producing involuntary saccades in the surround direction, which might subsequently bias the observer’s percept of the centre region. Although Kozák and Castelo-Branco (2009) report measuring eye movements, they did so only to confirm that fixation did not stray dramatically from the stimulus centre. Smaller micro-saccades, which may influence perception (Laubrock, Engbert & Kliegl, 2008) were not analysed. Indeed, it has not yet been established whether transitions between transparent and coherent plaid percepts can be initiated by an eye movement in the non-dominant direction.

A further unanswered question is to what extent surround effects depend on the properties of the surround itself. Kozák and Castelo-Branco (2009) used surrounds which were closely matched to one of the centre percepts, in speed, direction, orientation, phase and spatial frequency. Here we remove some

of these correspondences, and focus on two surround dimensions – speed and direction – to investigate how these influence the pattern of dominance during bistable plaid perception.

We conducted two experiments. In the first, observers reported plaid percept as a function of surround speed and direction, for surrounds composed of moving dots. We report behavioural effects sensitive to the speed and direction of the surround. In the second experiment we measured eye movements in conjunction with the reported plaid percept. We ask whether (often involuntary) eye movements can trigger changes in plaid perception, and if surrounds increase such eye movements.

2 Methods

2.1 Stimuli & equipment

Stimuli were plaids, constructed from two rectangular-wave gratings oriented $\pm 15^\circ$ from vertical (see Fig 1, left icon) and subtending 3° . The gratings had a spatial frequency of $1.2c/^\circ$ and a duty cycle of 1/3. They were superimposed, and translated horizontally (in opposite directions) at $1^\circ/sec$. The minimum luminance of the final plaid pattern was equal to the mean luminance of the display. The plaid could be perceived as either a coherent pattern moving upwards at $4^\circ/sec$ or two semi-transparent gratings moving leftwards and rightwards.

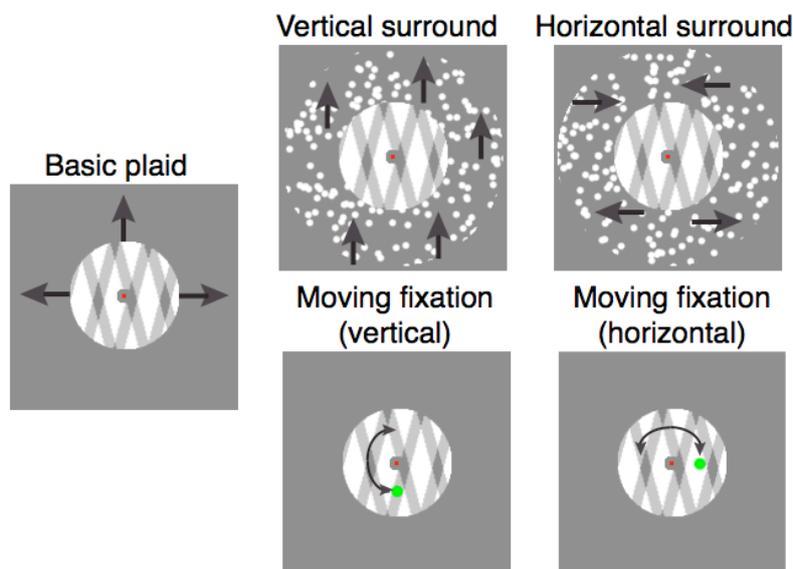


Figure 1: Example plaid stimuli. The basic plaid (far left) could be perceived as moving upwards (top arrow), or as two transparent gratings moving laterally (side arrows). Dots were added to the surround, moving in the directions indicated by the black arrows. In Experiment II only, a green fixation dot changed position from top to bottom or left to right, as indicated by the black curved arrows. No arrows were displayed during the experiment.

In the centre of each plaid was a red fixation dot, surrounded by a small circle of mean luminance (Hupé & Rubin, 2003). Surrounds were composed of white dots (diameter 12 *arc min*, density 6 *dots/°*), distributed in a circular aperture with a diameter of 6°. Surround dots could either move upwards, consistent with the coherent plaid percept, or horizontally (50% left, 50% right) consistent with the transparent percept.

All stimuli were generated in Matlab (The Mathworks Inc.), and displayed using elements of the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peters & Palmer, 2002) toolboxes running on an Apple Macintosh computer. Stimuli were presented on an Iiyama VisionMaster 500 CRT monitor (Experiment I) or a Viewsonic P227f CRT monitor (Experiment II). Eye movements were recorded throughout Experiment II by an EyeLink-1000 eye tracker (SR Research Ltd., Ontario, Canada) controlled by a PC.

2.2 Procedure

In Experiment I there were eleven conditions – no surround, vertical surround at five speeds, and horizontal surround at five speeds. The surround speeds ranged from 0.5°/sec to 8°/sec in octave steps. In Experiment II there were five conditions – no surround, vertical surround (4°/sec), horizontal surround (1°/sec), vertical induced eye movements, and horizontal induced eye movements. The surround speeds were chosen as the most effective conditions from Experiment I (see below). In the first three conditions observers were instructed to fixate on the red central dot, and in the induced eye movement conditions they tracked a green dot which periodically changed its position once every second, but was always placed 0.75° from fixation in one of the cardinal directions (see Figure 1, lower row).

Stimuli were presented for trials of one minute. Response was via a keyboard (Experiment I) or a two-button mouse (Experiment II). Observers were instructed to press and hold a button corresponding to the ‘coherent’ percept or the ‘transparent’ percept, holding neither button if the percept was mixed or otherwise different. The viewing distance was either 76cm (Experiment I) or 57cm (Experiment II). In Experiment II, the eye-tracker was calibrated at least every five trials, and validated before every trial. Observers completed 15 (Experiment I) or 5 (Experiment

II) trials on each condition. In Experiment II, a baseline measure of eye movement and blink activity was recorded for one minute, during which observers fixated on a red dot in the centre of a mid-grey screen.

Behavioural data were analysed in two ways. The proportion of all ‘coherent’ responses was calculated from the response time course, giving a measure of the relative strength of each percept (periods in which both or neither percept was reported were excluded from this calculation). Also, dominance durations were determined for each one minute trial. Both measures were averaged across trials (both experiments) and across observers (Experiment II). For dominance durations, which typically approximate a lognormal (or gamma) distribution, we used the geometric mean, and excluded the duration of the first percept from each trial (see Hupé & Rubin, 2003). To aid comparison across observers, these data were also normalised to each observer’s geometric mean durations for the no surround condition (Experiment I) or across all conditions (Experiment II). ANOVA assumptions (homogeneity of variances, residual distributions) were valid for all reported statistics.

Eye movement data were analysed by parsing the EyeLink output to determine saccades and blinks with high precision (sample rate of 1000Hz). Saccades were defined as epochs with an acceleration above 8000°/s² and a velocity above 30°/s. This relatively conservative definition was chosen to minimise noise in the data. We analysed eye movement data in Matlab using custom-written software, which allowed us to separate saccades according to direction, and also relate them to percept reports by synchronising with the behavioural data. For rate histograms (see Figures 5-7), we converted saccade, blink and reversal rate data into z-scores to permit averaging across observers (see Einhäuser, Stout, Koch & Carter, 2008).

2.3 Observers

Three observers (including the first author) participated in both experiments, and an additional 9 observers (including the second author) participated in Experiment II only (12 total, 5 male). Observers varied in their level of psychophysical experience, and understanding of the purpose of the experiment. Informed consent was obtained from all observers, and the study was approved

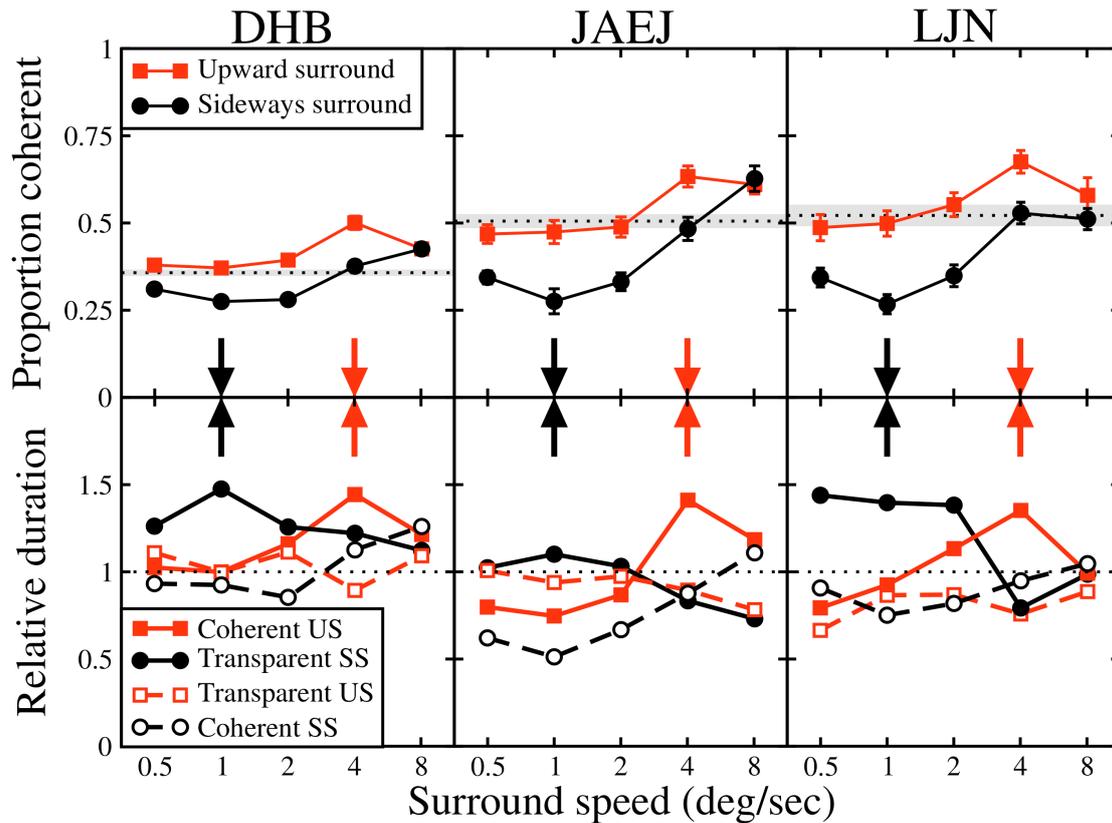


Figure 2: Results of Experiment I for three observers (columns). Upper row gives the proportion of trial time in which the coherent percept was reported, as a function of surround speed, for both vertically (red squares) and horizontally (black circles) translating surrounds. The dashed line indicates the proportion coherent with no surround. Lower row shows dominance durations, normalized to the appropriate values with no surround, to aid comparison across observers. Arrows indicate the physical speeds of the coherent (red) and transparent (black) plaid percepts. Error bars and shaded regions denote ± 1 SE of the mean, and in many cases are smaller than symbols. Note that references to colour apply to the electronic version of the article.

by the Ethics committee of the School of Psychology, University of Southampton.

3 Results - Experiment I

The results of Experiment I are shown in Figure 2. The upper row gives the proportion of ‘coherent’ responses as a function of surround speed. For all observers, the greatest fraction of coherent percepts was reported when the surround moved upwards (red squares) at 4°/sec. This is also the speed and direction of the coherent motion itself, as indicated by the red arrows. The smallest fraction of coherent percepts (and therefore the largest fraction of transparent percepts) occurred when the surround moved sideways (black circles) at 1°/sec – the closest value to the speed and direction of the transparent component motion (black arrows). A highly significant effect of surround condition was revealed by ANOVA across observers ($F_{10,22}=5.59$, $p<0.001$, $h_p^2 = 0.72$), with each individual observer ANOVA also significant (all $F_{10,154}>11$, all $p<<0.001$, all $h_p^2 > 0.42$). Paired t-tests confirmed that conditions where

the speed and direction of the surround were consistent with the coherent or transparent percept always differed significantly from the (no surround) baseline (all $p<0.01$).

Inspection of the lower row of Figure 2 reveals a similar pattern for dominance durations. With the upward moving surround, coherent durations were longest at 4°/sec (filled red squares), and with the sideways surround, transparent durations were longest around 1°/sec (filled black circles). Interestingly, we see here that the change in the proportion of coherent responses is driven primarily by an *increase* in durations of the percept consistent with the surround, rather than a *decrease* in the durations of the inconsistent percept (although there are some decreases, e.g. JAEJ at 1°/sec for the coherent sideways surround). This is very different from the traditional Levelt-type relationship, whereby increasing the strength of one percept shortens durations for the other percept (Levelt, 1966). Such behaviour has been reported previously for surround influences on binocular rivalry (Carter et al., 2004) and we replicate the finding here for

bistable plaid motion. A note of caution however: it is difficult to disentangle facilitation of one percept by a surround from suppression of the other percept (often both may occur; see Baker & Graf, 2008). This is because the surround necessarily affects the entire stimulus, unlike in Levelt's (1966) binocular rivalry experiments where features (i.e. luminance or contrast) of the individual rivalling stimuli can be manipulated independently.

The above results indicate that the effects of a moving context on bistable plaid motion perception are dependent on the speed and direction of the surround motion. The maximal effect size and direction is comparable in magnitude to that reported by Kozák and Castelo-Branco (2009) using surrounds matched in speed, direction and luminance profile. This suggests that surround effects are tuned to speed and direction, yet may not rely heavily on continuous contours between centre and surround. However, one possible explanation for these findings is that motion in the surround might influence eye movements, which in turn affect the observer's percept. This could occur either by prolonging percepts consistent with the surround direction, or initiating switches away from an inconsistent percept. Experiment II addresses this by

measuring eye movements during stimulus presentation.

4 Results – Experiment II

4.1 Behavioural data

Observer responses during the eye movement experiment are summarised in Figure 3, averaged over 12 observers. Here, we replicate the main findings from Experiment I; surround motion favours percepts along the consistent axis (orange bars). This is apparent both for proportion of coherent responses (left panel) and dominance durations (right panel). ANOVAs for both variables (proportion coherent and dominance durations) showed significant main effects of condition (for details see Supplementary Materials). Once again, the modulation occurred primarily by lengthening the dominance durations in the consistent direction (right panel). We find a similar pattern of results when observers were instructed to make eye movements to follow a moving fixation dot (the induced eye movements condition, green bars). Here, eye movements along the coherent (vertical) axis increased the reported coherent percept, and vice versa.

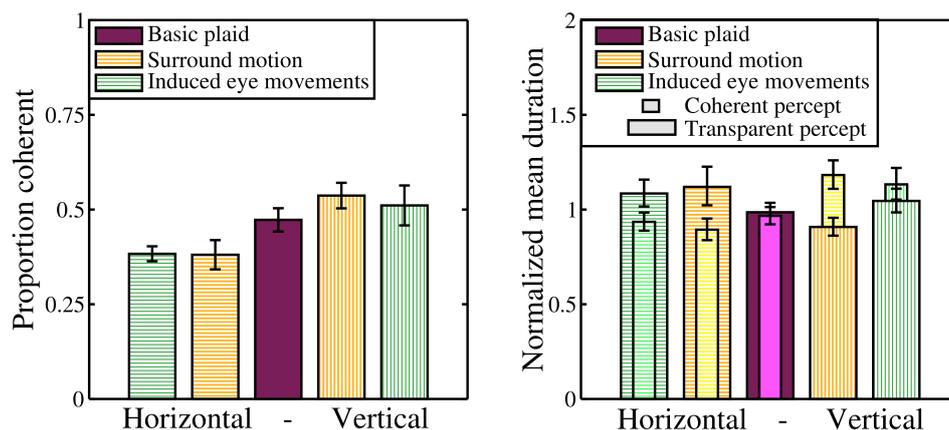


Figure 3: Behavioural data for Experiment II, averaged over 12 observers. The left panel shows the proportion of time the coherent percept was reported across five conditions. The right panel shows normalized mean durations for the coherent (narrow bars) and transparent (wide bars) percepts. In both panels, the middle bars (purple) are for the plaid with central fixation and no surround. Orange bars denote the surround conditions, with motion direction given along the x-axis. The outer green bars are for the induced eye movement condition. Error bars give ± 1 SE across observers. Note that references to colour apply to the electronic version of the article.

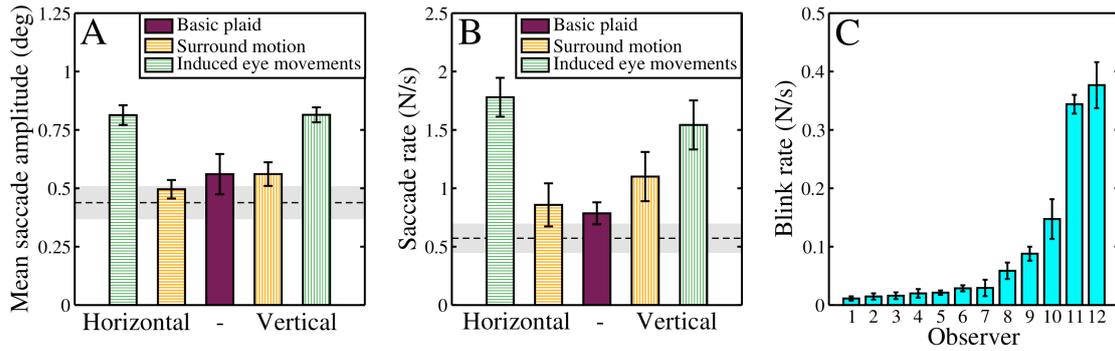


Figure 4: General eye movement statistics. A) Mean saccade amplitudes in six conditions. The horizontal dashed line is for the fixation-only baseline condition. B) Saccade rate, in a similar format to panel A. Data in both panels are averaged across observers, with error bars and shaded regions giving ± 1 SE of the mean across observers ($n=12$). C) Blink rate per observer, averaged over trials (collapsed across all conditions).

4.2 Eye movement data

General eye movement statistics are summarised in Figure 4. Note that in the central three conditions depicted in Figure 4A (Basic plaid and two surround motion conditions), observers were asked to fixate on a central target. For these conditions, we term any eye movements ‘involuntary saccades’. The mean amplitude of these involuntary eye movements was around 0.5° in these conditions (three inner bars), and also for the baseline fixation with no stimulus (dashed horizontal line). Saccades were larger (Fig 4A) and more frequent (Fig 4B) in the conditions where observers tracked a moving fixation target (outer green bars) than when they fixated centrally (central 3 bars and dashed line). Observer blink rates showed no dependence on condition, but were distributed over a wide range (Fig 4C). We discuss the relationship between blink behaviour and perceptual transitions below.

A more detailed analysis of eye movement behaviour is shown in Figure 5. Histograms give the saccade rate in terms of orientation (left column) and amplitude (middle column). These were normalized (z-scores) and averaged across observers, with the shaded regions indicating ± 1 SE. The amplitude data

are divided into horizontal and vertical bins based on the orientation of each eye movement (partitioned about the oblique axes). The rightmost column gives density distributions of eye position. Each row represents a different condition; the middle row is for the basic plaid condition, the second and fourth rows are for the horizontal and vertical surrounds (respectively) and the first and final rows are for the induced eye movement conditions.

The important aspects of these data are as follows. The plaid alone (middle row) elicited the greatest number of involuntary saccades in the cardinal directions, particularly horizontal movements ($\pm 90^\circ$). Adding a surround increased eye movements in the surround direction, but did not make them appreciably larger (rows 2 & 4). Instructing observers to follow a moving fixation point greatly increased the proportion of saccades in the appropriate direction, and made those eye movements substantially larger (top and bottom rows). However, as noted above, behavioural data were similar in conditions with involuntary and induced fixations. The density distributions in the right hand column indicate that observers were good at maintaining fixation within the area of the stimulus (green circles), and were not fixating in the surround region.

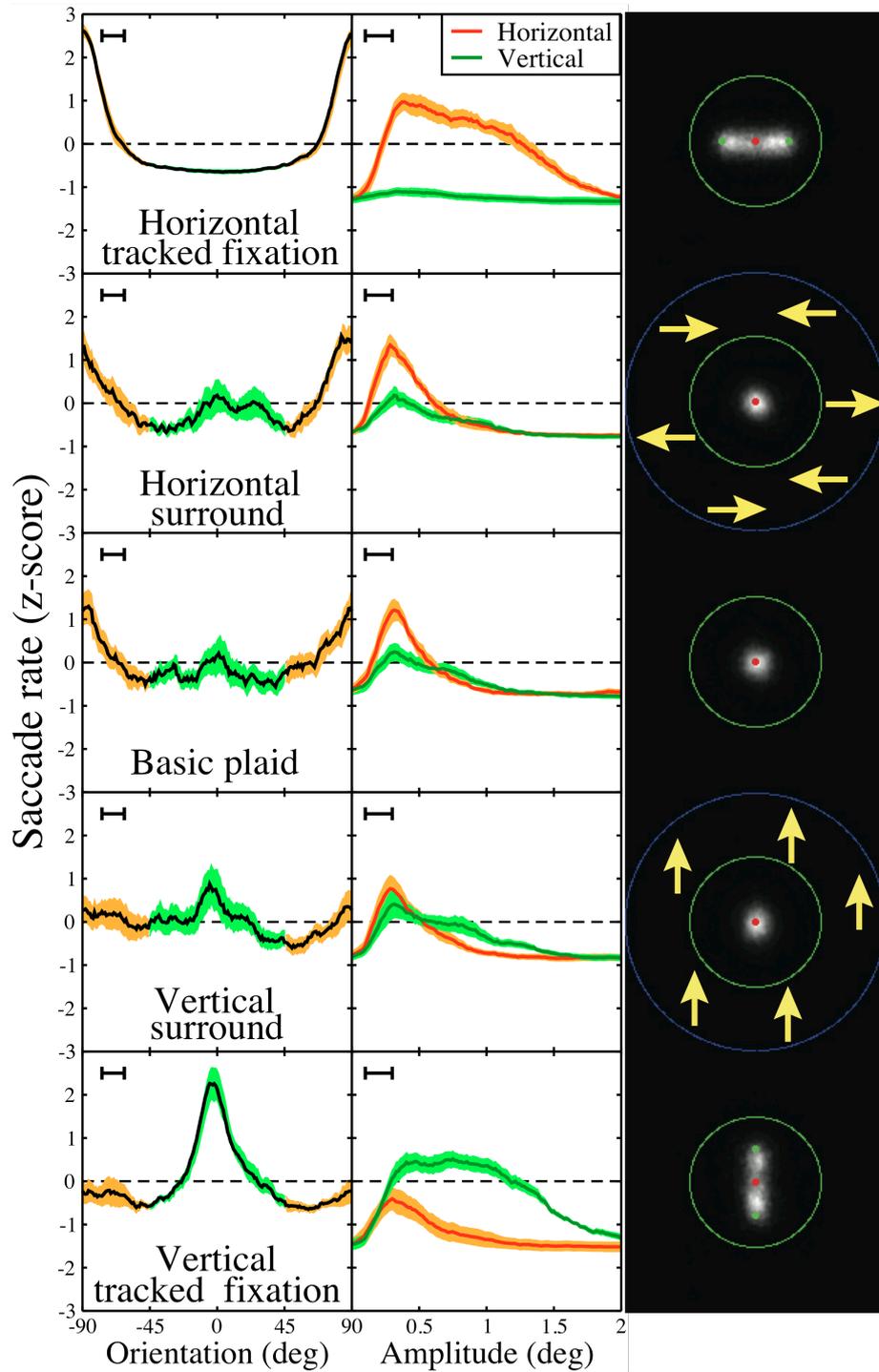


Figure 5: Detailed eye movement statistics. Left column shows normalized saccade rate as a function of orientation, averaged across observers. Middle column gives amplitudes of eye movements apportioned by direction (red/orange is horizontal, green is vertical). Bars in the upper left hand corners indicate the histogram bin widths. Right column shows density distributions for eye position relative to the central fixation (red dot). The inner green circle indicates the stimulus diameter, and the outer blue circle (where shown) the surround diameter. Arrows denote surround direction, and the green dots in the top and bottom panels show the locations of the tracked fixation dot in the induced eye movement conditions. Shaded regions in the graphs denote ± 1 SE across observers ($n=12$). Note that references to colour apply to the electronic version of the article.

4.3 Time course of blinks, saccades and reversals

We analysed the time course of observer responses in relation to both blinks and saccades, pooling across conditions, observers and repetitions. This was achieved by calculating the rate of blinks or eye movements relative to a change in response (i.e. a reported perceptual transition) and also calculating the reversal rate relative to a blink or involuntary saccade. In this analysis the induced eye movement conditions were omitted, and the results for the other three conditions were sufficiently similar to justify pooling across them.

Figure 6A shows this analysis for blink rate relative to a reversal. Blink rate increased around 500-1000ms before observers reported a transition. This is consistent with the latency observed between a physical stimulus transition and an observer's response in similar experimental paradigms (e.g. van Dam & van Ee, 2005; 2006; Laubrock et al., 2008; Baker & Graf, 2009). Given this latency, it seems likely that blinks co-occur with perceptual reversals, although it is not clear whether blinks cause a transition, or transitions initiate a blink. Figure 6B shows that the reversal rate

increases during the 1000ms following a blink by more than one standard deviation (note that although the traces in Figure 6 are approximately mirror-symmetrical across the two panels, they are not identical, and in principle could have been very different, depending on the data). The patterns described above were also evident when the two observers with the highest blink rates (see Fig 4C) were omitted from the analysis.

A similar analysis is shown in Figure 7 for saccades and perceptual transitions. The involuntary saccade rate decreases markedly just before a transition is reported, followed by an increase at around the time of the report (Fig 7A). This is consistent with a similar finding reported by Laubrock et al. (2008) for a different bistable motion stimulus, and by Einhäuser et al. (2008) for a range of bistable stimuli. As expected, the opposite pattern is evident for reversal rate – reversals are more likely to be reported around the time of a saccade, and less likely just afterwards (Fig 7B). Thus, transition reports are not preceded by increased saccades, but instead correspond to a reduction in eye movements. This implies that saccades do not cause perceptual transitions.

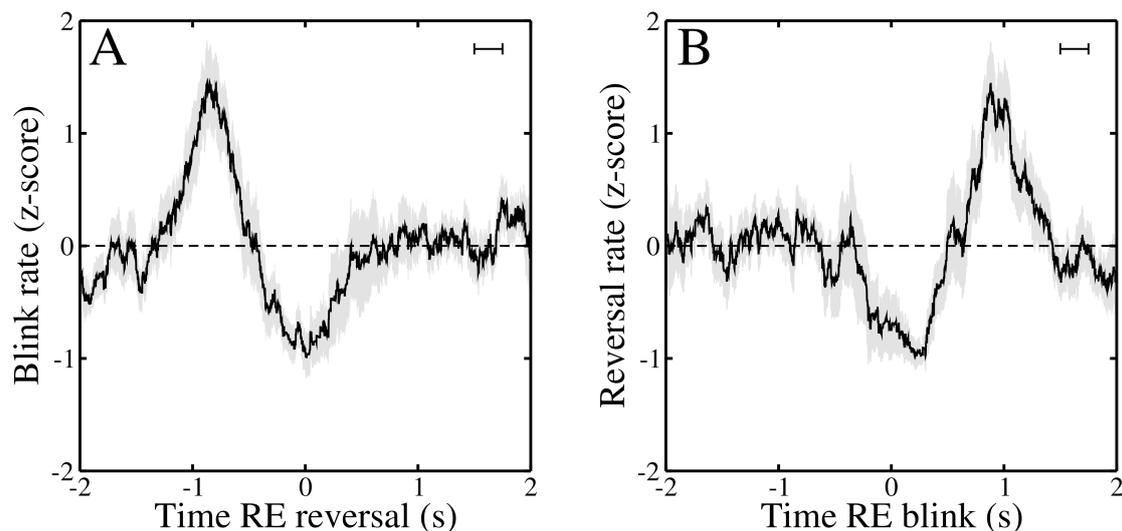


Figure 6: Temporal relationship between blinks and perceptual transitions. Panel A shows the blink rate relative to a reported perceptual transition, and panel B shows the reversal rate relative to a blink offset. Bars in the upper right hand corners indicate the bin width (250ms). Grey shaded regions give ± 1 SE across observers ($n=12$).

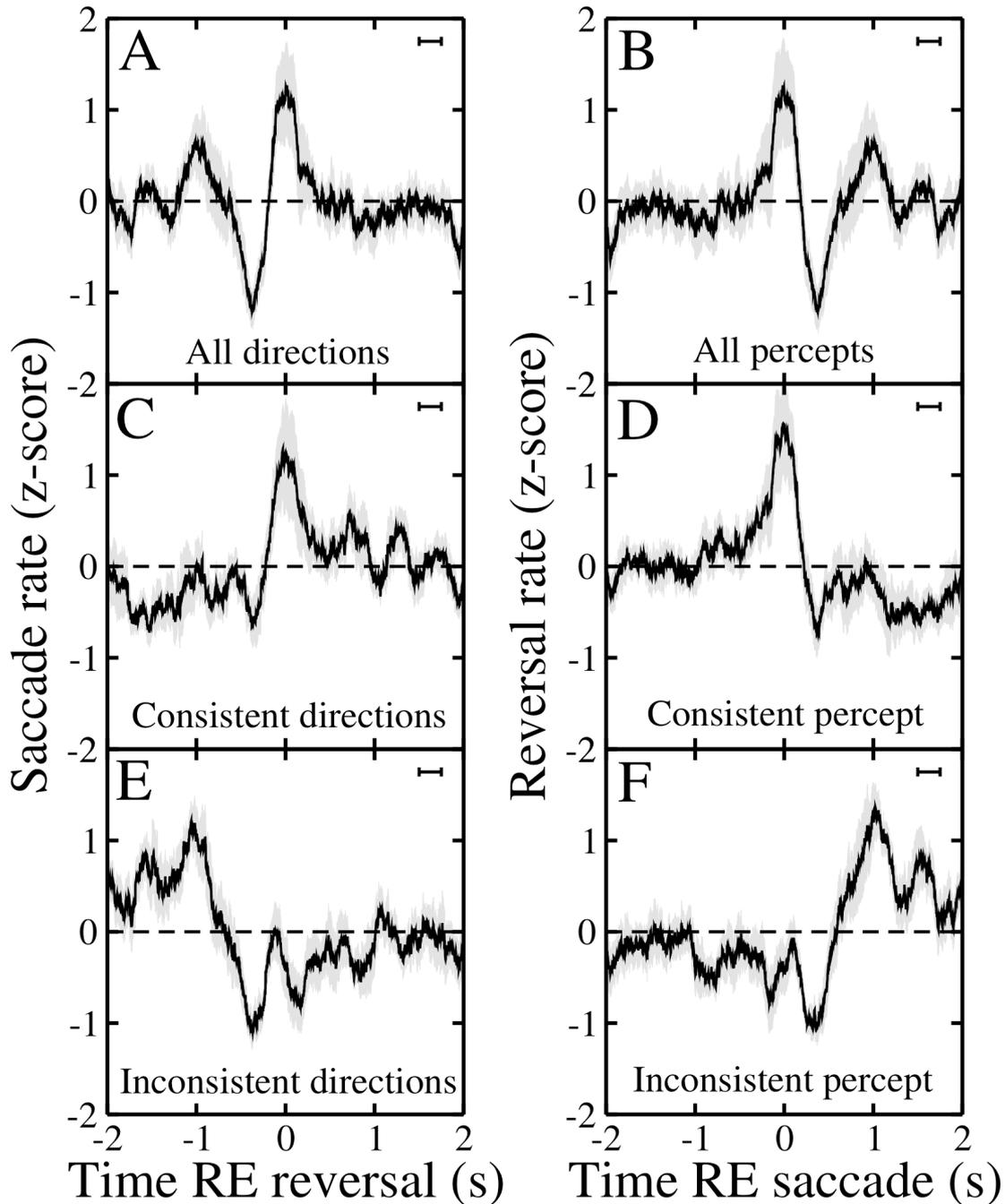


Figure 7: Time-locked eye movement behaviour and reversal rates. Panels A, C & E show involuntary saccade rates relative to a perceptual transition report. Panel A gives the rate of all eye movements, regardless of direction. Panels C & E show rates in either the direction consistent with the switched-to percept (C) or the other direction (E). In panels B, D & F, reversal rates are shown relative to an eye movement, and are again presented for all directions (B), and relative to the direction of the eye movement (D, F). Bars in the upper right hand corners indicate the bin width (250ms). Grey shaded regions give $\pm 1SE$ across observers ($N=12$).

One of our main questions was whether, when observers experience a given percept, involuntary eye movements in a direction *inconsistent* with this percept can instigate a transition. To this end, we also partitioned the data by eye movement direction. The function in Figure 7C shows the rate of eye movements along the axis (horizontal or vertical) consistent with the switched-to percept (i.e. the

percept reported from time=0 onwards). In contrast to the blink data (Fig. 6A), this function peaks at around the time a transition is reported, rather than several hundred milliseconds earlier. This suggests that incongruent eye movements are not responsible for initiating perceptual transitions. Instead, eye movements are likely to occur near the start of a new percept in the direction

consistent with that percept. This observation is supported by the analysis of reversal rates relative to an eye movement in a given direction. At the time a saccade occurs, observers are more likely to already be reporting a transition to the percept consistent with that direction (Fig 7D).

In addition, the directional analysis reveals the source of the reduction in total eye movements just before a switch (see above). This effect is driven by less frequent eye movements along the axis consistent with the pre-transition percept (Fig 7E). It is also clear that this reduction in incongruent saccades continues during the first second or so of a new percept. One previous study (Einhäuser et al., 2008) that used similar stimuli did not partition eye movements by direction, so this pattern of behaviour was presumably obscured by the concomitant increase in congruent eye movements. Using a dot motion stimulus, Laubrock et al. (2008) found a percept-dependent pattern of eye-movements for unambiguous motion, which they attribute to

5 Discussion

In two experiments, we explored the role surround motion plays in the perception of bistable plaids, as well as the influence of eye movements. In Experiment I we confirmed that surrounding motion can influence perception when it is matched in speed and direction to one of the bistable percepts, mostly by increasing percept durations in the surround direction. In Experiment II, we found that whilst blinks are associated with perceptual transitions, saccades were unlikely to be responsible for changes in perceptual state. Taken together, these findings suggest that involuntary eye movements and surrounds influence perception by prolonging percept durations in one direction, rather than reducing durations in the other direction (by initiating a reversal).

We have replicated a key finding of previous studies, that saccade rate reduces at around the time of a perceptual transition (just before the transition is reported). Our data indicate that this is driven by a reduction in eye movements in the orthogonal direction to the new percept, and is shortly followed by an increase in eye movements in the direction consistent with the new percept. We find no evidence that eye movements incongruent with a percept can initiate a switch away from that percept. Since both eye movements and surround motion extend percept durations, it is possible that at

an OKN-like response in the opposite direction to the perceived motion. However, this effect was not clearly present for ambiguous motion in their study.

If saccades are not associated with stimulus transitions, might they be responsible for prolonging percepts in a given direction? We investigated this by calculating the percentage of saccades in the direction congruent to the percept being reported at the time of each saccade (note that this is a conservative test because of the observer response latency discussed above). If saccade direction were unaffected by the current percept, this should average out at 50% when pooled across all conditions and trials. Instead, 55.7% of eye movements were in the direction congruent with the reported percept; significantly more than 50% (one sample t-test across observers; $t_{1,11}=3.04$, $p<0.05$, $d = 0.88$). This small effect is consistent with the finding that induced eye movements prolonged percept durations in the congruent direction (Figure 3).

least part of the surround effect is due to the surround slightly increasing the number of congruent eye movements during a congruent percept. However, the speed tuning reported in Experiment I makes it unlikely that eye movements are solely responsible for the surround effects.

5.1. Integration, not segmentation

In the processing of visual motion, surrounding information can be treated in two ways – through integration or segmentation (Braddick, 1993). Integration over area is key to producing a smooth coherent percept of motion, particularly for optic flow perception and global direction judgments (Webb, Ledgeway & McGraw, 2007; Amano, Edwards, Badcock & Nishida, 2009). Segmentation, on the other hand, is important for delineating objects from their backgrounds ('pop-out' effects). There is evidence that anatomically distinct populations of neurones in area MT (a cortical region devoted to motion processing) are specialised for one or other operation (Born & Tootell, 1992). More recently, it has been demonstrated that MT neurones can adaptively switch between integration and segmentation depending on the stimulus (Huang, Albright & Stoner, 2007).

The results of both of our experiments favour an integration process, consistent with recent related work (Kozák & Castelo-Branco, 2009). This is of interest because in the related

phenomenon of binocular rivalry, both integration and segmentation can occur. Segmentation is characterised by a reduction in dominance of a bistable percept which closely matches the surround (or increased dominance of the other percept). This has been reported for orientation (Ichihara & Goryo, 1978; Carter, Campbell, Liu & Wallis, 2004; Paffen, Tadin, te Pas & Blake, 2006), colour (Carter et al, 2004; Paffen, et al. 2006), phase (Ooi & He, 2006) and motion direction (Paffen, te Pas, Kanai, van der Smagt & Verstraten, 2004; Baker & Graf, 2008). However, this pattern can reverse at low contrasts, producing a facilitatory integration effect (Paffen et al., 2006). Further integration effects of context have been reported when one rivalling stimulus is consistent with a global scene interpretation, both for motion (Alais & Blake, 1998) and depth-defined (Graf & Adams, 2008) stimuli. These findings suggest the possibility that under specific circumstances, bistable plaids may also show segmentation effects, though this is not evident in the present study.

5.2. Figure-ground assignments

The present behavioural results differ slightly from those reported by Kozák & Castelo-Branco (2009) for the most comparable conditions. Specifically, whereas we report predominance changes for surrounds in both percept directions, their effect for surrounds moving in the pattern direction (see their Figure 5a) is minimal. One possibility is that could be a range effect, as their centre regions were generally biased towards the coherent pattern state, whereas ours were more equally balanced. We also find that surrounds mostly increase congruent percept durations, but Kozák & Castelo-Branco (2009) observed some reduction of the incongruent percept durations also (see their Fig 5e).

An intriguing explanation for these discrepancies (raised by one of our reviewers) is that figure-ground assignments may be different between the two studies. In our stimuli, the luminance profile of the surround was very different (dots) from that of the centre (plaid), which might encourage them to be interpreted as two different surfaces or objects, or as a moving object (plaid) against a translating background (dots). In the Kozák and Castelo-Branco study, the surrounds comprised a plaid (identical to that in the centre) with unambiguously moving dots superimposed on it. This arrangement promotes the interpretation of centre and

surround as being part of the same moving object, with the dots appearing on only part of the object. Given this, one might expect stronger grouping, and therefore larger effects, with such an arrangement. This is certainly the case for the transparent (component) percept, yet the coherent (pattern) percept is modulated less strongly. Of course, it is also likely that such discrepancies are due to some of the other differences between studies, such as luminance, plaid speed, angle and size, observers etc.

5.3. Observer biases

Can our results be explained by observer biases? It was clear to observers in both experiments whether a surround was present or not, and in which direction it was moving. In principle, observers might guess that this was intended to influence their percepts, and respond in a biased manner. We think this unlikely, however, as our hypothesis was not direction specific (either integration or segmentation was a plausible outcome, see section 5.1), yet all observers exhibit effects in the same direction (favouring integration). Furthermore, one might expect that in Experiment I any bias would be independent of speed, or might be some increasing function of speed. The finding of the same speed-tuned effects in all three observers (two of whom were naïve) is highly unlikely to be due to bias.

5.4. Other surround effects

Surround motion can have a number of effects; most notably it can cause changes in the perceived speed of central stimuli (Loomis & Nakayama, 1973; Tynan & Sekuler, 1975; Norman, Norman, Todd & Lindsey, 1996; Baker & Graf, 2008, 2010; Wertheim & Paffen, 2009). In general, when centre and surround move in the same direction, perceived centre speed is reduced, and when they move in opposite directions, perceived centre speed increases (see Baker & Graf, 2008, 2010). We have recently demonstrated (Baker & Graf, 2008) that these changes in perceived speed can account for changes in dominance during binocular rivalry produced by a moving surround (e.g. Paffen, te Pas, Kanai, van der Smagt & Verstraten, 2004).

Could the surrounds in the present study also affect the perceived speed of the plaid (or its components) and alter dominance in that way? When the surround moves in the pattern direction, it should reduce the perceived

pattern speed, and perhaps increase the (orthogonal) perceived component speeds (see Baker & Graf, 2010). Hupé & Rubin (2003) report that increasing component speeds favours the transparent percept, yet our pattern-direction surrounds have the opposite effect, promoting the coherent percept. For surrounds moving in the component directions, the net effect of both populations of dots (moving in opposite directions) should cancel and not substantially affect perceived component speed. There may be an increase in the perceived pattern speed, which might be expected to increase its predominance, but again this effect is in the opposite direction to that observed. Finally, the speed tuning reported here (Experiment I) is very different from the increase in effect size with speed and subsequent plateau reported for perceived speed changes (Wertheim & Paffen, 2009; Baker & Graf, 2010). In summary then, perceived speed effects shown to influence dominance during binocular rivalry are unlikely to be responsible for the results reported here.

6 Conclusions

Two experiments have demonstrated that bistable plaid motion can be influenced by motion in the surround. This occurs through a facilitatory process of integration, and can be viewed as an attempt by the visual system to select the most plausible of two ambiguous solutions. We also find that blinks, but not eye movements, are associated with perceptual transitions. Instead, eye movements appear to influence perception by prolonging percepts in a given direction.

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Supplementary materials – ANOVA tables for Experiment II

Table S1 – ANOVA summary for proportion of coherent responses (Experiment II).

Source	SS	df	MS	F	<i>p</i>	h_p^2
Observer	2.53	11	0.23	14.34	<0.001	0.397
Condition	1.24	4	0.31	19.39	<0.001	0.244
Interaction	2.32	44	0.05	3.29	<0.001	0.377
Error	3.85	240	0.02			
Total	9.94	299				

Table S2 – ANOVA summary for mean coherent durations (Experiment II).

Source	SS	df	MS	F	<i>p</i>	h_p^2
Observer	15.93	11	1.45	1.23	0.265	0.054
Condition	12.63	4	3.16	2.69	0.032	0.043
Interaction	45.33	44	1.03	0.88	0.691	0.139
Error	281.67	240	1.17			
Total	355.56	299				

Table S3 – ANOVA summary for mean transparent durations (Experiment II).

Source	SS	df	MS	F	<i>p</i>	h_p^2
Observer	5.16	11	0.47	1.01	0.438	0.044
Condition	5.30	4	1.32	2.85	0.025	0.045
Interaction	29.16	44	0.66	1.43	0.050	0.207
Error	111.58	240	0.46			
Total	151.21	299				