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Motion induced spatial conflict following binocular integration

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Abstract

When a moving border defined by small changes in luminance (or by differences in colour) is placed in close proximity to moving borders defined by large changes in luminance, the low contrast border can appear to jitter. Previously, the existence and characteristics of this phenomenon were established using subjective reports. Here, we show that spatial judgments become more difficult in the presence of illusory jitter, presumably because of the positional uncertainty that is induced. We also explore the influence of the distance between the different types of moving border. We find that this manipulation influences the salience and amplitude, but not the perceived rate, of illusory jitter. Finally, we show that illusory jitter remains when the different types of moving border are presented to different eyes. These observations suggest that this phenomenon arises at the cortical level and are consistent with our earlier proposal—that illusory jitter can occur because the visual system periodically resolves a spatial conflict that arises when a rigid moving object contains different apparent speeds.
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1. Introduction

Recently, we have shown that a moving border defined by small changes in luminance contrast, or by changes in chromatic contrast, can appear to jitter when placed in close proximity to a high luminance contrast moving border (Arnold & Johnston, 2003). For instance, we found that as a red/green bull's-eye configuration moves over a dark background, the perceived position of the central region of the stimulus can appear to jitter. In this situation, the border between the outer region of the bull's-eye and the dark surround provides a motion signal defined by large changes in luminance whereas the border between the central and outer regions of the bull's-eye provides a motion signal defined by very small changes in luminance—or by chromatic contrast (Arnold & Johnston, 2003).

The illusory jitter that we observed cannot be an artefact caused by artificial lighting or CRT monitor presentation as it could be seen in a printed sun-lit stimulus (Arnold & Johnston, 2003). Nor does the illusory jitter appear to be a general property of motion defined by small changes in brightness, as it could not be seen when a green dot rotated against a static red ring (Arnold & Johnston, 2003). The positional jitter is unlikely to be a simple consequence of small involuntary eye movements (Murakami & Cavanagh, 1998; Murakami, 2003) as illusory jitter could only be seen at a specific point within the stimulus—the moving border defined by little or no difference in luminance (Arnold & Johnston, 2003). This contrasts with involuntary eye movements which typically cause shifts of the entire retinal image or, in rare situations, of all regions of the retinal image other than an area that has been pre-exposed to a period of luminance flicker (Murakami & Cavanagh, 1998; Murakami, 2003).

Surprisingly, the rate of motion induced spatial conflict (MISC) does not appear to be related to object

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speed (Arnold & Johnston, 2003). The rate of apparent jitter was measured by adjusting the rate of physical luminance flicker to achieve a match. Estimates of illusory jitter rate did not vary as a function of object speed, although the probability of seeing illusory jitter (jitter salience) was affected by speed (Arnold & Johnston, 2003).

As MISC rate does not appear to be influenced by stimulus speed and MISC can be seen in a stimulus in which form and motion are invariant, the characteristic rate of MISC ($\sim$22 Hz) is unlikely to be stimulus driven. Instead, MISC rate appears to reflect the time course of a dynamic neural process.

We believe jitter is the result of a number of factors. The perceived speeds of motion defined by large and small changes in luminance (or by changes in colour) can differ (Anstis, 2001; Blakemore & Snowden, 1999; Cavanagh, Tyler, & Favreau, 1984; Thompson, 1982). As perceived position can be influenced by motion (De Valois & De Valois, 1991; Durant & Johnston, 2004; Nishida & Johnston, 1999; Whitney & Cavanagh, 2000; Whitney et al., 2003), unless some form of resolution occurs, adjacent borders defined by large and small changes in luminance might appear to disengage (Nguyen-Tri & Faubert, 2003). The resolution of this conflict could generate the apparent jitter. We have proposed that the characteristic rate of MISC might reflect the temporal dynamics of recurrent neural processes that mediate the integration of motion-based spatial predictions and subsequent spatial processing (Arnold & Johnston, 2003).

The explanation described above places a great emphasis upon the rate of illusory jitter—which falls within the beta range ($\sim$20 Hz). Phase synchronisation in the beta range has been found between separated regions of cortex (Gross et al., 2004; Tallon-Baudry, Bertrand, & Fischer, 2001; von Stein, Rappelsberger, Sarnthein, & Petsche, 1999) and has been implicated in the mediation of interactions between component parts of distributed neural networks (Bibbig, Traub, & Whittington, 2002; Gross et al., 2004; Kopell, Ermentrout, Whittington, & Traub, 2000). Recently, it has been shown that beta frequency synchronisation between different cortical regions correlates positively with target detection, and negatively with non-detection, in the attentional blink paradigm (Gross et al., 2004). This, it was argued, may indicate that network states related to visual sensitivity are dynamically modulated by beta frequency interactions between different regions of cortex (Gross et al., 2004). Given the similar rates, we envisage that MISC might also be driven by intra-cortical region interactions between motion computation and prediction (V5) and spatial processing (V1).

Although our earlier data and observations suggest a robust interaction between motion and position coding, to date we have relied upon subjective reports to establish the existence and characteristics of the interaction.

Observers were asked if they could see any jitter—a yes/no task (Arnold & Johnston, 2003). However, if MISC reflects the temporal dynamics of an influence of motion processing on spatial perception, the consequences of this interaction should be seen in a performance-based measure of spatial vision. For instance, if the proximity of moving borders defined by large and small changes in luminance causes periodic shifts in the perceived position of the border defined by small changes in luminance, spatial judgments involving this border should be difficult.

2. General methods

All stimuli were displayed on a 19 in. Sony Trinitron Multiscan 400PS monitor, with a refresh rate of 100 Hz, driven by a VSG 2/5 (Cambridge Research Systems). The stimuli were viewed binocularly in a darkened room from 57 cm with the head placed in a headrest. Stimuli contained two colours, red (Commission Internationale d'Eclairage (CIE) 1931 chromaticity chart: $x = 0.60$, $y = 0.34$) and green (CIE 1931; $x = 0.28$, $y = 0.595$). The luminance of red used in Experiments 1 and 2 was 14.5 cd/m^2. The luminance of red used in Experiment 3 was 11 cd/m^2. Prior to all experiments, the green luminance perceived to match red was measured, for each observer, using the minimum motion technique (Anstis & Cavanagh, 1983). The retinal velocity of all movement in all experiments was 4.67°/s.

2.1. Methods of Experiment 1

Four observers participated in Experiment 1. All observers were naïve as to the purpose of the study and had normal, or corrected-to-normal, visual acuity.

Stimulus configurations used in Experiment 1 are depicted in Figs. 1a–c. In each of three experimental conditions, observers viewed three vertically translating green bars. These bars consisted of a large central bar (width 1.2°, height 0.23°) flanked by two smaller bars (width 0.6°, height 0.23°). There was a 0.2° horizontal separation between the edges of the large and smaller green bars. This configuration was centred either 2.57° to the left or right of a central fixation cross, determined at random on a trial-by-trial basis. On each trial, the trajectory of the large central green bar commenced 2.34° above or below the central fixation cross. Again, this was determined at random on a trial-by-trial basis. The three green bars then drifted upward or downward, depending upon the initial position of the central bar, for 1 s.

As depicted in Figs. 1a–c, there were three modes of stimulus presentation: the three green bars could be presented in isolation against a dark background (Fig. 1a), centred over a static red column (width 1.4°, height 8.4°) so that the central green bar was surrounded by the red
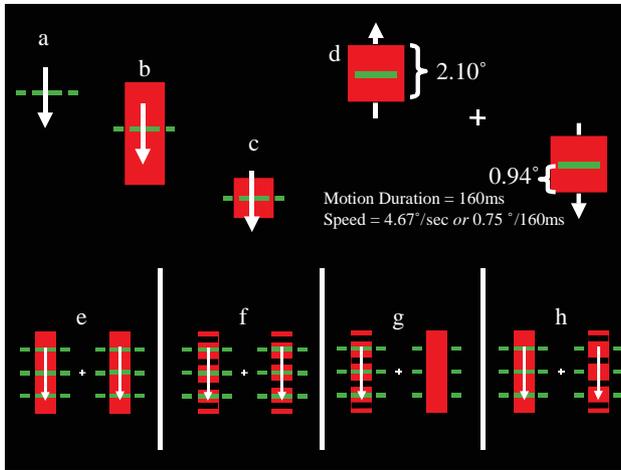
Fig. 1. Schematic diagrams of the stimulus configurations used in Experiments 1 (a–c), 3 (d), and 4 (e–h). (a–c) In Experiment 1, large green and smaller flanking bars were either presented against a dark background, so that the movement of all three was signalled by large differences in luminance contrast (a) with the large green bar superimposed against a static red column so that the motion of the large bar was effectively Isoluminant (b) or with the large green superimposed over a moving red square so that the isoluminant motion signal of the large green bar was effectively *Sandwiched* by the leading and lagging motions signalled by large differences in luminance at the edges of the red square (c). (d) Stimulus and parameters used in Experiment 3. (e–h) Experiment 4, stimulus configurations were viewed with a prism placed in front of the right eye. This prism horizontally reversed the image that reached the right eye. Stimulus configurations e and f were symmetric so identical images were shown to both eyes. We refer to these conditions as the *Isoluminant* (e) and *Binocular* (f). Configurations g and h were asymmetric, so different images were shown to the two eyes. However, because the image presented to the right eye was reversed, all stimulus configurations appeared symmetrical when viewed binocularly. We refer to configuration g as *Ipsilateral*, as the dark and large green bars appeared on the same side of the images shown to either eye, and to h as *Contralateral* as the dark and large green bars were shown on different sides of the images shown to either eye and only appeared to be in close proximity when viewed binocularly.

column whereas the flanking bars were adjacent to it (Fig. 1b), or centred over a red square (width/height 1.4°, Fig. 1c) that moved in the same direction and at the same speed as the green bars. In the first condition, the movement of all three bars was signalled by large changes in luminance—the Luminance vs Luminance condition. In the second condition, movement of the flanking green bars was signalled by large changes in luminance whereas the movement of the larger central bar was signalled by very small changes in luminance or by chromatic contrast—the Isoluminant vs Luminance condition. This was also true of the third condition, however, in this condition the isoluminant motion signal was preceded and followed by high luminance motion signals (the edges of the coherently drifting red square). We therefore refer to this motion signal as being sandwiched—the Sandwiched vs Luminance condition.

During a run of trials, the physical vertical separation between the large central, and smaller flanking green bars, was manipulated according to the method of constant stimuli. During a run of trials, seven vertical offsets (ranging ±0.28° from vertical alignment) were each sampled on 10 occasions. After each trial, the observer indicated if they felt that the central bar had been positioned above, below, or in alignment with the flanking green bars by either pressing a response lever up, down, or by pressing a third lever either up or down—a three alternative forced choice task. The third choice—aligned—was provided to minimise any effects of response bias around the point of subjective equality, e.g., a tendency to select the larger central bar as ahead when observers felt that the three bars in the stimulus were aligned. Each trial was scored accordingly—0 if the observer indicated that the central bar was lagging, 0.5 if the observer felt that the central bar was aligned, and 1 if the observer felt that the central bar was leading.

Each run of trials provided a distribution of perceived alignment as a function of the physical offset between the large central and smaller flanking green bars. A psychometric function was fitted to each distribution and the x-coordinate of the point on the fitted function giving a score of 0.5 was taken as an estimate of the spatial offset at which the three bars appeared aligned. The difference between the points on the abscissa that had fitted scores of 0.5 and 0.75 was taken as an estimate of the discrimination threshold—a measure indicating how difficult the observer found the spatial decisions.

Each of the four observers completed a run of trials for each of the three experimental conditions. Performance during the Luminance vs Luminance condition was taken as a baseline, allowing us to compare performance during this condition with the other experimental conditions. We did this by calculating difference scores for each observer. Baseline estimates (Luminance vs Luminance) were subtracted from the estimates of perceived alignment and discrimination threshold for the other experimental conditions (Isoluminant vs Luminance and Sandwiched vs Luminance). Average difference scores and related standard errors are plotted in Figs. 2a (perceived alignment) and b (discrimination thresholds).

2.1.1. Results

As shown in Fig. 2a, the central bar perceptually lagged the flanking bars in the Isoluminant vs Luminance condition relative to the Luminance vs Luminance condition ($t_3 = 4.27$, $p = 0.024$). However, there was no significant difference between the perceived alignments of the bars during the Sandwiched vs Luminance and the Luminance vs Luminance conditions ($t_3 = 1.04$, $p = 0.375$). As shown in Fig. 2b, it was more difficult for observers to complete spatial judgments in
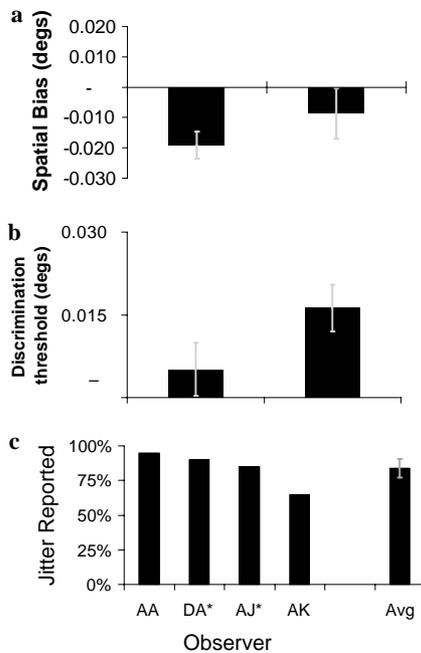
Fig. 2. (a and b) Results from Experiment 1. These bar graphs show average difference scores calculated by subtracting estimates of perceived alignment (d) and discrimination threshold (e) determined with Isoluminant (see Fig. 1b) vs Luminance (Fig. 1a) motions or with Sandwiched (Fig. 1c) vs Luminance motions from estimates determined with Luminance vs Luminance motions. Error bars show ±1 SE between four difference scores. (c) Bar graph showing the percentage of trials during which observers reported seeing illusory jitter in Experiment 3.

the Sandwiched vs Luminance condition relative to the Luminance vs Luminance condition ($t_3 = 3.813$, $p = 0.032$). However, there was no significant difference in task difficulty during the Isoluminant vs Sandwiched and Luminant vs Luminant conditions ($t_3 = 1.059$, $p = 0.367$).

2.1.2. Discussion

The results of Experiment 1 can be summarised as follows: moving isoluminant borders perceptually lag moving borders defined by large luminance differences, but this does not make alignment judgments more difficult. In contrast, alignment judgments are more difficult when moving isoluminant borders are sandwiched between adjacent high contrast moving borders, but the isoluminant border does not appear to lag.

The results of Experiment 1 are consistent with our earlier observations, that when moving borders defined by small differences in luminance (or by chromatic contrast) are placed in close proximity to moving borders defined by large differences in luminance, the position of the border defined by small changes can appear to jitter. Presumably, in Experiment 1, the positional uncertainty caused by illusory positional jitter made spatial decisions more difficult.

Previously, we have shown that proximity is a necessary condition for MISC to occur by showing that MISC is not seen in the absence of motion defined by large differences in luminance (Arnold & Johnston, 2003). However, we have not yet systematically explored the issue of spatial proximity. We could reasonably expect the rate of recurrent lateral interactions within a cortical region to be proportional to the distance over which information must propagate. The rates of recurrent interactions between cortical regions, however, may be less dependent upon intra-cortical distance.

We have not yet systematically explored the amplitude of illusory jitter. Previously we have shown that MISC rate did not vary as a function of stimulus speed although the frequency of reporting jitter, and presumably jitter salience, did vary with speed. Since jitter amplitude and salience may be related, we will explore MISC amplitude in addition to MISC rate in Experiment 2—in this instance as a function of inter-moving-border distance.

2.2. Methods of Experiment 2

Four observers participated in this experiment, the first author and three observers who were naïve as to the purpose of the study. All observers had normal, or corrected-to-normal, visual acuity.

In different runs of trials, observers completed either frequency or amplitude matching tasks. The sequence of events that occurred during each trial is depicted in Figs. 3a (frequency matching) and b (amplitude matching). In both cases, during each trial observers viewed a vertically translating green bar (width 1.2°, height 0.23°) superimposed on, and therefore surrounded by, a coherently drifting red bar. Red bar width was 1.4° and the height could be 1.4°, 1.9°, 2.8° or 3.8°. As the green bar was centred within the larger red bar, these heights corresponded to inter-moving-border distances of 0.58°, 0.83°, 1.28°, and 1.78°.

The moving red and superimposed green bars were centred 3.75° either left or right of a central fixation cross, determined at random on a trial-by-trial basis. On each trial, the trajectory of the green bar commenced 1.17° above or below the central fixation cross, again determined at random on a trial-by-trial basis. The green and surrounding red bars then drifted upward or downward, depending upon their initial position, for a period of 500 ms and were followed by a blank inter-stimulus interval of 500 ms. Following the inter-stimulus interval, observers were either shown a static green disc (diameter subtending 0.93°; frequency matching task) or a pair of static green bars (width 1.2°, height 0.23°; amplitude matching task) centred 3.75° on the other side of fixation relative to the previous moving stimulus (see Fig. 3).

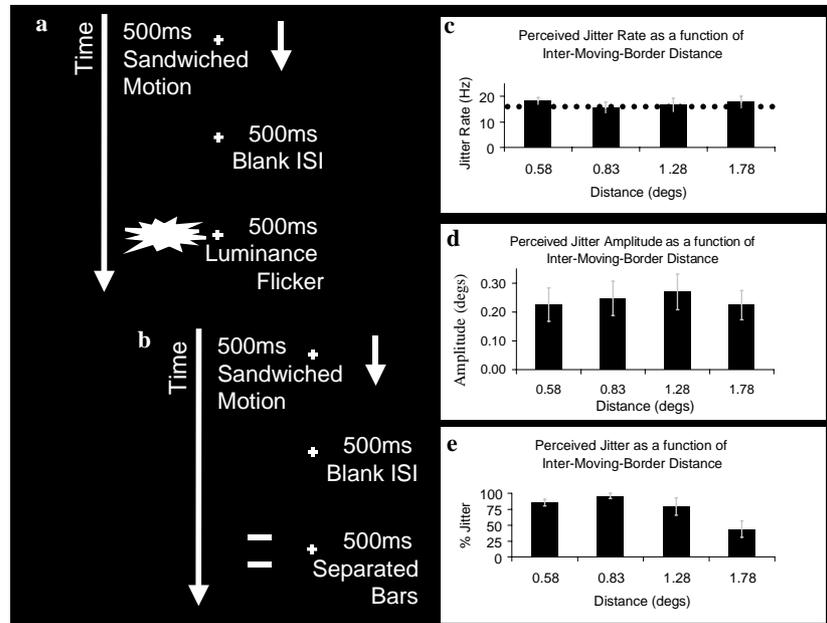In trial runs where the observer completed the frequency matching task, the static green disc contained a

Fig. 3. Schematic diagram depicting trial sequences from Experiment 2 during rate (a) and amplitude (b) matching tasks and bar graphs showing estimates of the perceived rate (c), amplitude (d), and percentage of times that illusory jitter was seen (e) as a function of inter-motion-border distance.

sine-wave luminance flicker (modulating between ±50% of the luminance level of the moving green bar) sampled at the monitor refresh rate of 100 Hz. The initial frequency of the luminance flicker was 5 or 25 Hz, determined at random. After each trial, the observer reported if they felt that the illusory jitter or physical luminance flicker rate had been faster by pressing one of two response levers. The rate of luminance flicker was then adjusted by 2 Hz in order to make it more similar to the rate of illusory jitter—a method of adjustment. This sequence was repeated until the observer indicated that the rates of illusory jitter and physical luminance flicker matched (by pressing a third response lever upward) or that no illusory jitter had been seen during the trial (by pressing the third response lever downward). During different runs of trials, each observer completed this task 15 times for each of the four inter-moving-border distances sampled. We were therefore able to determine an average estimate of the rate of illusory jitter (on occasions when it was seen) and to record the percentage of times that the observer perceived illusory jitter as a function of the inter-moving-border distance.

The procedure for estimating MISC amplitude was similar. The initial vertical separation between the pair of green bars was 0.09° or 1.1°, determined at random. After each trial, the observer reported if they felt that the amplitude of illusory jitter or the separation between the pair of static green bars was larger by pressing one of two response levers. Separation was then adjusted by 0.09°. This sequence repeated until the observer

indicated that the jitter amplitude matched the separation between the pair of static green bars.

2.2.1. Results

As shown in Fig. 3c, there was no significant variation between estimates of MISC rate as a function of the inter-moving-border distance ($F_{3,12} = 0.301$, $p = 0.824$). As shown in Fig. 3e, there was, however, a significant effect on the saliency of MISC as indicated by the percentage of trial sequences in which MISC was reported ($F_{3,12} = 5.044$, $p = 0.017$). Illusory jitter was seen most often at an inter-moving-border distance of 0.83°. If the distance between the different types of moving border was increased or decreased, illusory jitter was reported on progressively fewer occasions. Fig. 3d shows the estimated amplitude of illusory jitter. Analysis of variance (one-way repeated-measures AN-OVA) revealed that there was also a significant influence of inter-moving-border distance upon jitter amplitude ($F_{3,9} = 4.973$, $p = 0.026$). Amplitude was greatest at an inter-moving-border distance of 1.28° and decreased if the distance was increased or decreased.

2.2.2. Discussion

The findings of Experiment 2 suggest that the distance between the different types of moving border influences the salience and amplitude of MISC, but not the perceived rate. Previously, we found a similar pattern of results for the effects of stimulus speed on MISC rate (Arnold & Johnston, 2003).

The results of Experiment 2 and our previous results (Arnold & Johnston, 2003) are not compatible with the view that MISC rate is stimulus driven. In our previous study, characteristic MISC rates were observed when the temporal and spatial properties of the stimulus were invariant. Similar MISC rates were observed in this experiment. These estimated MISC rates do not vary when we change the spatial dimensions of the stimulus (Experiment 2), or the speed of object motion (Arnold & Johnston, 2003), nor do the apparent rates correspond with any physical properties of the display.

The invariance of MISC rate as a function of stimulus speed and spatial configuration appears to discredit some form of masking (see Brietmeyer, 1984) as a causal mechanism for MISC. Hypothetically, perhaps the leading border defined by large changes in luminance might intermittently mask the following border defined by very small changes in luminance (or by chromatic contrast). Of course, any masking account of MISC would necessarily assume that the underlying mechanism is both spatially and temporally dependent as MISC does not occur in the absence of retinal motion no matter what the stimulus duration (Arnold & Johnston, 2003), an observation that rules against purely temporal dependence. Given these observations, we would expect the rate of any intermittent masking to be related both to speed and the spatial dimensions of the stimulus as these factors would determine the relative timings at which the two types of moving border are in the same location on the retina. Motion adaptation (see Mather, Verstraten, & Anstis, 1998) does not appear to contribute as we have also observed MISC, admittedly during informal observations, during very brief stimulus presentations (∼100 ms, Arnold & Johnston, 2003). We can, however, address both these possibilities empirically by systematically manipulating the duration of stimulus motion.

2.3. Methods of Experiment 3

Four observers participated in this experiment, the two authors and two observers who were naïve as to the purpose of the study. All observers had normal, or corrected-to-normal, visual acuity and colour vision.

During each trial, observers viewed a pair of stimuli consisting of green bars (width 1.4°, height 0.23°) superimposed onto larger red squares (2.1°) that were displayed against a dark background (see Fig. 1d). The stimuli were centred 4.67° to the left and right of a central fixation cross. At the start of each trial, the two stimuli would appear and one would move upwards while the other moved downwards for a period of 160 ms. When the stimuli appeared, the green bars were physically aligned with the fixation point. After the period of motion, the two stimuli would remain in their final positions until the observer terminated the trial, at which point the stimuli disappeared, by pressing one

of two response levers. The observers' response on each trial indicated if the green bars appeared to jitter while moving. Each observer completed 20 such trials and the percentage of trials, following which observers reported MISC, was recorded.

2.3.1. Results and discussion

As shown in Fig. 2c, robust illusory jitter was observed when the duration of stimulus motion was restricted to just 160 ms ($t_3 = 12.74$, $p = 0.001$). Given the very brief duration of the stimulus motion, this seems to dictate that motion adaptation does not play a causal role in MISC generation. In addition, given that the green bars never occupied the same positions as the edges of the red squares, it seems highly improbable that MISC could result from some form masking that is both spatially and temporally dependent.

Of course, the possibility that some form of spatially and temporally dependent masking might play a causal role in MISC generation is further undermined by the invariance of MISC rate as a function of stimulus speed (Arnold & Johnston, 2003) and spatial configuration (Experiment 2). As MISC rate does not vary as a function of these stimulus characteristics, we have proposed that MISC rate might be generated *within* the visual system by a neural process that has a characteristic beta range frequency. We hope that MISC rate will provide a means of identifying the neural mechanisms underlying MISC using brain-imaging techniques, such as time-frequency analyses of MEG. At this point, however, we have no strong evidence to suggest at what point within the visual hierarchy MISC might be generated.

Often it is possible to ascertain at what point in the visual pathway a percept is generated using psychophysical techniques. For instance, if a phenomenon displays inter-ocular transfer, a cortical locus is implicated. Inter-ocular transfer is evident if a stimulus shown selectively to one eye has an influence upon a stimulus shown to the other eye. Inter-ocular transfer demonstrates cortical involvement because information arising independently from the two eyes only becomes integrated within the cortex. One can also use dichoptic displays in which different stimuli are presented to each of the two eyes. Integration of these stimuli requires the combination of information in the monocular views. Consequently, one way to show that MISC is caused by cortical activity would be to show that it could occur when one type of moving border (say high luminance contrast) is presented to one eye and the other type of moving border (low luminance contrast) is presented to the other. We explore this possibility in Experiment 4.

2.4. Methods of Experiment 4

Five observers participated in this experiment, the two authors and three observers who were naïve as to

the purpose of the study. All observers had normal stereovision and normal, or corrected-to-normal, visual acuity.

The stimulus was viewed binocularly from 57 cm in a darkened room with the observers' head restrained by a headrest. A prism was positioned in front of the observers' right eye. The prism mirror reversed the image reaching the right eye, so that points lying physically to the left of fixation were seen to the right. No prism was placed in front of the left eye.

The stimulus configurations used in Experiment 4 are depicted in Figs. 1e–h. In all configurations, static red columns (width 1.4°, height 8.4°) were positioned 2.57° to the left and right of a central fixation cross. Pairs of small green bars (width 0.6°, height 0.23°) were placed to the left and right of both red columns, with a 0.2° gap between the edges of the small green bars and the edge of the red column. There was a 2.1° vertical separation between the pairs of small green bars. As the small green bars and red columns were always shown on both sides of fixation, they served as an effective fusion lock.

In all configurations, large green bars (width 1.4°, height 0.23°) were superimposed on one or both red columns. In the configurations depicted in Figs. 1e and f, large green bars were superimposed on both red columns. In the configurations depicted in Figs. 1g and h, the large green bars were superimposed only on the left red column. In the configurations depicted in Figs. 1f–h, the large green bars could be interspersed with black bars superimposed on either both (1f), the left (1g) or the right (1h) red column. The width of the black bars was 0.7°, so the vertical gap between the edges of the large green and black bars was 0.7°.

At the start of each trial, the stimulus was static and only contained the static red columns and the smaller flanking green bars. Depending upon the configuration, dark bars and the appropriate large green bars then appeared and, after 250 ms, all the bars drifted downwards for a period of 500 ms. Movement then ceased and the dark and large green bars disappeared.

In configurations depicted in Figs. 1e and f, the stimuli were symmetrical. As a consequence, although the image reaching the right eye was mirror reversed, both eyes were actually shown the same image. However, in the configurations depicted in Figs. 1g and h, the stimulus configuration was asymmetric so the images reaching the two eyes differed. This creates the possibility of classical binocular rivalry between the different eye views (for a review of this issue, refer to Blake & Logothetis, 2002). However, the sudden appearance of the dark and large green bars and the brief presentation of the stimulus were designed to counter rivalry and ensure that both the dark and large green bars were perceived.

In the configuration depicted in Fig. 1e, the large green bars translated across subjectively isoluminant red surfaces, so we refer to this as the Isoluminant condition. In the configuration depicted in Fig. 1f, large green bars were interspersed with dark bars on both sides of fixation. We refer to this as the Binocular condition. In the configuration depicted in Fig. 1g, the large green and interspersed dark bars were shown on the same side of the image. However, as the right eye image was mirror reversed, the large green and dark bars were seen on both sides of fixation. We refer to this as the Ipsilateral condition. In the configuration depicted in Fig. 1h, the large green and dark bars were shown on opposite sides of the images. However, as the right eye image was mirror reversed, large green and dark bars were also seen on both sides of fixation in this configuration. We refer to this as the Contralateral condition.

After each trial, the observer indicated if they felt that they had seen any illusory jitter of the large green bars by pressing a response lever either up or down. During a run of trials, the four stimulus configurations were each presented 15 times in a pseudorandom order.

2.4.1. Results

As shown in Fig. 4, there was significant variation between the percentages of times that MISC was reported following presentations of the four different stimulus configurations ($F_{3,14} = 4.006$, $p = 0.03$). There was no significant evidence of MISC during the Isoluminant condition ($t_4 = 1.767$, $p = 0.152$), however, there was significant evidence of MISC during the Binocular ($t_4 = 34.462$, $p < 0.001$), Ipsilateral ($t_4 = 8.020$, $p = 0.001$) and Contralateral conditions ($t_4 = 4.014$, $p = 0.016$).

2.4.2. Discussion

The results of Experiment 4 show that MISC can be induced by an interaction between different types of moving border that are shown selectively to different eyes. It should be noted that MISC observed in these circumstances is less robust than that observed when the different types of moving border are shown to the same eye. This, perhaps, is because MISC is disrupted by
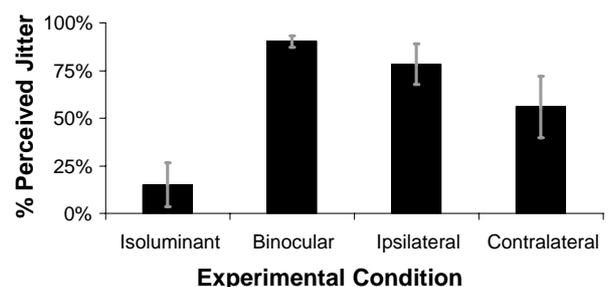

Fig. 4. Bar graphs showing the average percentage of times that illusory jitter was seen by four observers in each of the four stimulus configurations tested in Experiment 4. Error bars show ±1 SE between four individuals estimates of jitter percentage.

classical binocular rivalry or because the neural mechanism that causes MISC is at least partially monocular. In either case, the fact that MISC can be induced in these circumstances suggests that the process is at least partially binocular and therefore strongly implicates the cortex in MISC generation.

3. General discussion

We have recently observed that different types of moving border, defined by large and small differences in luminance, interact to create an illusory spatial jitter (Arnold & Johnston, 2003). Previously, we relied upon subjective reports to identify the character of the illusion. In Experiment 1, we used a performance measure that showed that subjective MISC is associated with impaired spatial acuity—consistent with the characterisation of MISC as spatial jitter.

One of the most surprising aspects of MISC is that the rate of illusory jitter appears to be driven by the rate of a dynamic neural circuit—not by any physical property of the display. Previously, we showed that MISC rate does not change when we adjust the speed of the stimulus (Arnold & Johnston, 2003). Experiment 2 shows that MISC rate is not influenced by the proximity of the different types of moving border either. However, both speed and inter-moving-border distances appear to influence MISC saliency. Less MISC was reported at relatively rapid (~9°) and slow (~4.5°) speeds (Arnold & Johnston, 2003) and at larger inter-moving border distances (Experiment 2).

Here, and previously (Arnold & Johnston, 2003), we have used a method of adjustment to match rates of illusory jitter and physical luminance flicker. We decided against a forced choice paradigm where observers are shown two stimuli and are required to choose one of them. During beta testing, we used a forced choice task to explore MISC rate and found that observers were more likely to choose the illusory jitter that appeared most salient (as revealed by the results of Experiment 2). Consequently, we chose to adopt the method of adjustment as it focuses observers upon the relevant dimension—in this case jitter rate rather than jitter salience.

The fact that we did not observe any variation in the estimated rate of MISC as a function of inter-moving-border distance may indicate that the rate of MISC does not depend upon lateral propagation velocities. However, MISC rate may depend upon interactions between, rather than within, cortical regions. Alternatively, the lack of systematic variation may arise because the increase in the time required for neural activity to propagate over increased cortical distances is too subtle to be detected psychophysically.

We have suggested that the functional purpose of MISC might be to maintain object integrity (Arnold & Johnston, 2003). Because the perceived speeds signalled by high and low luminance contrasts differ, when these types of contour are placed in close proximity the motion cues are consistently at variance with the unchanging spatial configuration. Unless some form of resolution occurs, the two boundaries might appear to disengage (Nguyen-Tri & Faubert, 2003). We have proposed that MISC may be a visible consequence of this resolution.

According to this proposal, we would expect MISC to be mediated within cortex—where reciprocal activity from motion sensitive mechanisms could influence spatial coding. This suggestion is consistent with the results of Experiment 4, which show that different types of moving border can interact and cause MISC when shown selectively to different eyes. The observation that MISC is probably caused by cortical activity suggests that, in future, we may be able to identify the neural correlate of this perceptual experience by identifying cortical activity that displays the same characteristic frequency.

Of course, at this point, our interpretation of MISC remains speculative. However, it does not appear that MISC can be directly related to more extensively studied visual phenomena like visual masking (see Brietmeyer, 1984) or motion adaptation (see Mather et al., 1998). We believe that the characteristic rate of MISC suggests some association between this phenomenon and the beta-band phase synchronisations that have been recorded in cortex (Tallon-Baudry et al., 2001; von Stein et al., 1999) and implicated in mediating interactions between distributed regions (Bibbig et al., 2002; Gross et al., 2004; Kopell et al., 2000). However, further work will be needed to link this perceptual phenomenon with its underlying neurophysiological substrate.

4. Conclusions

When motion signals associated with large and small differences in luminance-contrast (or by chromatic-contrast) occur in close spatial proximity, the low contrast border can appear to jitter—a phenomenon we refer to as MISC. Here, we show that this subjective phenomenon is concomitant with a reduction in performance in a spatial judgment task—supporting the view that there are shifts in the apparent location of the low contrast boundary. We believe that MISC rate is related to the dynamic characteristics a cortical feedback circuit rather than to any physical properties of the stimulus. We propose that the functional purpose of this process is to maintain object integrity when spatial conflict is suggested by motion cues that are consistently at variance with the configuration of the stimulus.

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