Diverted by dazzle: perceived movement direction is biased by target pattern orientation

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Abstract

'Motion dazzle' is the hypothesis that predators may misjudge the speed or direction of moving prey which have high contrast patterning, such as stripes. However, there is currently little experimental evidence that such patterns cause visual illusions. Here, observers binocularly tracked a Gabor target, moving with a linear trajectory randomly chosen within 18 degrees of the horizontal. This target then became occluded, and observers were asked to judge where they thought it would later cross a vertical line to the side. We found that internal motion of the stripes within the Gabor biased judgements as expected: Gabors with upwards internal stripe motion relative to the overall direction of motion were perceived to be crossing above Gabors with downwards internal stripe movement. However, surprisingly, we found a much stronger effect of the *rigid* pattern orientation. Patches with oblique stripes pointing upwards relative to the direction of motion were perceived to cross above patches with downward pointing stripes. This effect occurred only at high speeds, suggesting that it may reflect an orientation dependent effect in which spatial signals are used in direction judgements. These findings have implications for our understanding of motion dazzle mechanisms and how human motion and form processing interact.

Keywords

Motion dazzle, motion perception, direction perception, psychophysics.

Background

While many animals are patterned in such a way as to make them camouflaged and inconspicuous against their background [1], some animals (including zebras and many fish, insects, snakes, frogs and lizards) instead have striking and high contrast patterning, such as stripes and zigzags [2]. The function of these conspicuous patterns is hotly debated, but one hypothesis is that they may act to prevent capture when in motion, by making it difficult for a predator to accurately track the speed or direction of the moving animal [3–8]. This concept of "motion dazzle" was first proposed over 100 years ago [9] but has only recently been tested scientifically.

When considering the case of striped patterning, a number of studies have found evidence that striped targets are relatively difficult to catch in a touch screen "capture" task with human predators [10–12], suggesting that stripes may be able to disrupt speed or direction perception in human observers. In addition, modelling work predicts that the striped patterns on zebra should cause visual illusions [13]. In the case of speed perception, experimental findings have suggested that static striped patterns do not significantly disrupt speed perception [14] , but that internally moving striped patterns are able to bias speed judgements in a systematic way [15]. However, to date, there has been little work on whether the striped patterns on individual targets can cause trajectory or direction misperceptions.

Human psychophysical studies have rarely considered the interaction between the perceived direction of motion and target form or patterning, at least partly due to the now outdated idea that these two aspects of vision were processed in separate streams [16,17]. However, recent work has shown that these two factors can indeed interact. The perceived overall direction of a target can be strongly biased when the internal striped pattern within a moving stimulus is also moving [18–21], particularly when targets are viewed in the visual periphery, in an effect known as the “motion induced position shift” [22,23]. Interestingly, some animals (such as cuttlefish) can produce similar dynamic patterns when in motion, and it has been proposed that these may have a functional role in trajectory confusion [24–26]. It is therefore of interest to test whether the internal movement of striped patterns in a moving target can also affect trajectory perception in more naturalistic conditions, where observers are able to binocularly track the targets, keeping them foveated.

There is also some psychophysical evidence that rigid orientation cues are able to affect the direction perception of a moving target. For example, the perceived direction of a moving line [27] or a group of moving lines [28,29] can be influenced by line orientation, and the trajectory of a dot moving in the visual periphery can be influenced by the orientation of lines in the background [30]. Similarly, static line cues placed near the stimulus have been shown to influence the perceived direction of random-dot kinematograms [31,32] and the motion of a “barber pole” stimulus [33]. However, the effect of the orientation of a rigid striped pattern within a target, a type of stimulus that is highly relevant for the study of motion dazzle, has not been investigated.

In this study, we consider perception of the trajectory of moving striped targets, both when the stripes move rigidly with the overall target and when the stripes move internally within the target. Observers viewed the target, moving on a linear trajectory, and made a judgement about where they thought it would cross a line on the side of the screen after it had been occluded. As expected from previous research, we found that internal stripe motion does produce biases in observers’ estimates of trajectory; however, these effects are rather small. We also show, more surprisingly, that the rigid orientation of the stripes can create direction misperceptions. We show that this effect is larger than the effect of internal stripe motion but occurs only at relatively high speeds, suggesting that it may reflect an interaction of rigid orientation and motion cues, as would be predicted within a 'motion streak' framework [34].

Methods

Equipment and stimuli

Stimuli were presented with 800 x 600 pixel resolution on a 19" SONY CRT subtending 38.2 cm x 28.7 degrees from a viewing distance of 57cm. The stimuli were presented at a frame rate of 120Hz by a ViSaGe system (Cambridge Research Systems Ltd., UK) that was programmed using the CRS toolbox for MATLAB (MathWorks, Natick, MA). Stimuli were Gabor patches: a circularly symmetric Gaussian with a standard deviation of 0.5 degrees multiplied by a sinusoidal grating with spatial frequency of 3 cycles/degree and a Michelson contrast of 1.0. The stripes within the patches could be oriented at 90 (vertical), 45 or 315 degrees. For each orientation, three stimuli were produced (see Figure 1, bottom): one with rigid stripes without any internal movement and then two with internally moving stripes. For the oblique stimuli, these stimuli were categorised as net 'upwards' (up and to the left for the 45 degree stimulus, and up and to the right for the 315 degree stimulus (solid arrows in Figure 1); or net 'downwards' (down and to the right for the 45 degree stimulus, and down and to the left for the 315 degree stimulus; dashed arrows in Figure 1). The internal movement directions were arbitrarily to the left and right for the 90 degree vertical stimulus. Internal movement at 6Hz was added to the relevant stimuli using a continuous phase shift of 18° per 8.33ms frame. This meant that the Gaussian envelope moved smoothly in a lateral direction, while the sinusoidal grating moved within the patch.

General trial procedure and analysis

On each trial, a stimulus appeared in one half of the screen and moved across the display, either from right to left or from left to right. If the stimulus moved from left to right, an occluding black bar was displayed at the right hand edge of the screen (Figure 1 top); if it moved from right to left, the bar was at the left hand edge (but was otherwise identical). The occluding bar appeared 200ms before the stimulus movement began to give the observer time to prepare for the trial. The stimulus started its movement on the centre line of the screen on the Y axis, and then moved with a linear trajectory randomly chosen within 18 degrees above and below the horizontal. The exact start position on the X axis was randomised to make the trajectories more difficult to predict. The stimulus disappeared behind the occluding bar during the course of its movement. See Figure 1 (top) for a diagram of the experimental set up.

The observer's task was to estimate where they thought the stimulus would have crossed a white line on the black occluding bar, drawn 7.7 degrees away from the leading edge of the occluding bar, if the target had not disappeared behind the bar. They were instructed to use the centre of the target and front edge of the white line as their reference points. The white line was marked with an arbitrary numerical scale, and subjects recorded the number they thought the target crossed closest to by adjusting a number (initially always set to 15, the middle value on the scale) presented on a response page using a button box after each trial. There was no fixation point, and subjects could track the stimuli freely binocularly. All naïve participants gave written informed consent to take part and experiments were carried out in accordance with the Declaration of Helsinki.

For each trial, the subject's error was calculated by subtracting the veridical crossing point from their response. If the subjects perceived the crossing above the veridical point, the error had a positive value, and if they perceived it below the veridical point, the error had a negative value. Outliers were identified using a method of median-absolute-deviation, S_n, that has been shown to be accurate and robust [35,36]. Visual inspection revealed that there was no systematic bias in the types of trials removed, with roughly equal numbers from each experimental condition and with evenly distributed positive and negative errors.

Analysis was conducted using general linear mixed models in R [37] using the packages *lme4* [38] and *lmerTest* [39]. For all experiments, a full model was initially fit on all trials using all fixed factors of interest and their interactions. This model was then simplified based on the Akaike Information Criterion (AIC) and log likelihood to produce a best fit model [40]. Full details of the models used in each experiment are given below. Where appropriate, post-hoc comparisons were carried out with Tukey tests using the package *multcomp* [41]. Adjusted p values using the single-step method were reported.

Experiment 1

All stimuli travelled at 12 deg/s, and the visible trajectory length varied from approximately 11.4 deg to 25.9 deg. 12 observers took part in the experiment (10 naïve and 2 experimenters) and each completed 288 experimental trials, divided into 4 equal blocks. Within a block, the trials were randomised and balanced to ensure that there were equal numbers for each stimulus type (each combination of stripe orientation and type of internal movement , giving six stimulus types in total), in both directions, and on trajectories above and below the horizontal. Across all subjects, 77 trials in total (2.2%) were treated as outliers and were removed from further analysis. Before beginning the experiment, each subject had completed 10 training trials to familiarise themselves with the procedure.

In the statistical model of the results, the dependent variable was the error with respect to the true crossing point. Target orientation (90, 45 or 315 degrees), internal movement type (‘upwards’ or ‘downwards’) and trial direction (left to right or right to left) and all interactions were fixed factors in the initial model. The angle of movement on a given trial and the subject number were random intercepts in the model, and the angle of movement was also used as a random slope for the subject random intercept.

Experiment 2

For this experiment, only the 45 and 315 degree stimuli were used and all stimuli had rigid stripes. Stimuli could travel at one of three speeds (6.66 deg/s, 10 deg/s, 13.33 deg/s) and there were 3 different trajectory lengths, created by varying the starting position on the display: short (4.2 deg of visible trajectory on average), medium (11.4 deg of visible trajectory on average) or long (18.5 deg of visible trajectory on average). As in the previous experiment, the stimuli moved leftwards on half of the trials and rightwards in the other half. The exact start position on the X axis was randomly jittered around these values by up to 25 pixels (1.2 deg) in either direction. 10 naïve participants each completed 10 training trials followed by 360 experimental trials, divided into 5 blocks. As in Experiment 1, the trials were randomised and balanced within a block. Across all subjects, 117 trials in total (3.25%) were treated as outliers.

In the statistical model of the results, the dependent variable was the error from the true crossing point. As Experiment 1 showed a strong interaction between oblique target orientation and the direction of travel, we coded the data to indicate whether the target had rigid stripes pointing upwards or downwards relative to the direction of travel (see Figure 2 for further details). In addition, target speed, trajectory length and all possible interactions were fixed factors in the original model. The random effects structure was the same as in Experiment 1.

Results

Experiment 1

We found, consistent with previous work, that there are effects of internal motion in our occlusion paradigm. Figure 3 shows that, for the 45 degree and 315 degree oriented stimuli, the stimuli with ‘downwards’ internal motion within a triplet (green symbols) are perceived as crossing lower than the stimuli with 'upwards' internal motion within a triplet (blue symbols). The relative position of the no drift condition (red symbols) within a triplet is somewhat variable. The final selected statistical model contained fixed factors for target orientation, internal movement type and trial direction, and the interaction between trial direction and target orientation. A Tukey test showed that if the internal motion was in a 'downwards' direction, subjects' judgements were biased downwards ($Z= -2.421$, $p = 0.041$). If the internal motion was in an 'upwards' direction, their judgements were biased upwards compared to no-drift, but this result was non-significant ($Z = 1.525$, $p = 0.279$). However, the 'upwards' drift was significantly higher than the 'downwards' drift ($Z = 3.940$, $p < 0.001$). These effects (around 0.1 degrees bias on average) were smaller than found in previous literature; this is likely due to the fact that many previous studies have considered effects in peripheral viewing only [19–21,42]. Interestingly, overall biases tended to be slightly positive, with even the no drift stimulus being perceived as crossing above the true subjective crossing point. However, there was individual variation in overall bias: while most observers showed a slightly positive overall bias, others showed little evidence of bias or even slightly negative bias. These biases may therefore reflect idiosyncratic reference repulsion and attraction errors, as have been seen in previous studies [27,43–45].

Perhaps more surprisingly, we found a strong interaction between stripe orientation and direction of travel. In Figure 3, it can be seen that despite some variance between different drift types *within* a 'triplet', there are clear differences *between* the triplets: the average crossing points for each target type (each triplet) depend on the overall direction of movement. The 315 degree oblique target was perceived as crossing significantly lower than the vertical target when travelling from left to right ($t = -4.710$, $p < 0.001$), but was perceived as crossing significantly higher than the vertical target when travelling from right to left ($t = 6.761$, $p < 0.001$). The opposite effects were found for the 45 degree oblique target: when travelling left to right it was perceived as crossing above the vertical target ($t = 7.004$, $p < 0.001$) but was perceived as crossing below the vertical target when travelling right to left

($t = -9.485$, $p < 0.001$). This highly significant effect is independent of any internal motion of the stimulus, and thus suggests that the static orientation of the stripes affects participants' judgements of trajectory. This effect is larger than the internal motion bias in this experiment, with an average bias of approximately 0.5 degrees.

Experiment 2

The results from Experiment 1 suggested that the orientation of the stripes of a Gabor target relative to the overall direction of motion are critical in determining its perceived trajectory. For example, if the stripes appeared to be pointing 'upwards' relative to the direction of travel, the crossing points were also biased upwards. This is reminiscent of a 'motion streak' effect, where static orientation cues are used by the visual system when calculating motion direction [34]. Critically, this effect is thought to only occur above a certain target speed, because it is dependent upon the slow temporal integration of the motion system. In Experiment 2, we therefore tested the hypothesis that our results were due to a motion streak mechanism by presenting stimuli at a range of speeds.

In the medium and fast speed conditions, the relationship between direction travelled and stripe orientation was as in Experiment 1 (see Figure 4); the subjects' judgements were biased in the same direction as the orientation of the stripes. However, at the slow speed, this relationship was reversed. The final selected statistical model of the results contained fixed factors of stripe orientation, target speed and trajectory length, as well as the interaction between target speed and stripe orientation. The interaction between the target speed and whether the target was oriented up or down relative to its direction of travel was statistically significant ($\chi^2 = 30.907$, $df = 2$, $p < 0.001$), and was driven by the fact that the relationship between 'up' and 'down' oriented targets was different in the slow speed condition compared to the medium and fast speed conditions (t = -

4.487, $p < 0.001$ for the medium speed x down condition and $t = -5.088$, $p < 0.001$ for the fast speed x down condition). The average errors seen in this experiment were smaller than those in Experiment 1; this may be because the internal drift used in Experiment 1 led to observers being generally more uncertain in their judgements.

There was also a significant effect of start position in the model ($\chi^2 = 9.165$, df = 2, $p = 0.010$). A Tukey test suggested this was driven by the long distance group errors overall being slightly higher than the short distance group errors ($Z = 3.000$, $p = 0.008$). As the short group errors were on average closer to veridical, this suggests that observers became less accurate with longer trajectories, consistent with an increased influence of stripe orientation over a longer trajectory.

Discussion

We have shown that internal stripes within a moving Gabor can influence the perceived direction of travel. In agreement with previous studies, we found that internal stripe motion has an effect on direction perception [18–21], but in our study the biases produced were relatively small. However, more strikingly, we have shown that the rigid orientation of stripes within the Gabor can also influence direction judgements. We argue that this effect can be attributed to the interaction of motion processing with form processing via motion streaks [34], since the effect disappears at low speeds. This effect may have important implications for theories of motion dazzle, suggesting that rigid striped patterning may be able to affect the perceived trajectory of targets, perhaps leading to the increased capture difficulty seen in touch screen studies [10–12].

Dynamic internal motion has been shown in a number of paradigms to influence direction perception, with judgements of trajectory being biased in the direction of internal motion, particularly when viewing targets moving in the peripheral visual field [18–21]. Explanations of these trajectory biases have previously used models that assume faulty integration of local and global motion signals, with the local motion biasing the judgement of global motion via a vector sum mechanism [19–21]. Recent approaches have used a Bayesian approach to model this integration process, assuming that the visual system makes a 'best guess' at partitioning the motion signals into local and global signals, which can be biased in the case of high sensory noise, such as in peripheral viewing [46]. Unusually, the biases we see in this study were shown with foveal tracking of an object; however, the biases for drifting stripes were much smaller than those produced by the rigid orientation of the stripes. It therefore seems that subjects are more accurately able to partition the local and global motion signals in this experiment than they are able to ignore the influence of rigid orientation cues.

The effect of rigid stripe orientation on direction perception in our experiment is a surprising new finding. Several previous studies have shown that rigid orientation cues within elongated objects or in the background are able to affect direction perception [27–33]. However, our study is the first to show that orientation cues within the stimulus (as opposed to elongation of the stimulus, or cues placed outside the stimulus) can affect perceived direction. Even more interestingly, our results show that these biases can occur even when observers are tracking a target with an unambiguous 2D global motion trajectory, albeit with the biases being smaller than those shown in previous studies [33,47]. This is particularly unexpected considering that previous research has not found evidence for orientation cues being incorporated into 2D motion processing [47]. Our study suggests that in situations which more closely mimic natural tracking, orientation cues can in fact have an effect on direction judgements.

In some previous studies, motion biases have been attributed to the presence of motion streaks [34], which are thought to occur when an object moves quickly, as its neural image becomes 'smeared' because of the slow temporal integration of the visual system, leaving a spatial streak oriented in the direction of motion which can be used by the visual system to judge motion direction. For example, one study found effects of rigid cues on direction perception even when these cues were placed slightly away from the aperture of the stimulus [33]. This supports the involvement of motion streaks because an orientation based mechanism should integrate over a slightly wider area than just the stimulus itself, given that motion streaks would be found behind the current position of the moving stimulus. In addition, orientation cues have been shown to be incorporated into 1D motion processing [47], but only when the orientation cues were high contrast, in agreement with findings suggesting that form processing units have low contrast sensitivity [48].

In our experiment, the putative 'motion streak' biases disappeared at slower presentation speeds, or even appeared to have reversed, with targets containing 'upwards' pointing stripes now being perceived to cross below those with 'downwards' pointing stripes. This could suggest that at slower speeds, motion streaks are no longer available as a cue and instead the motion is being biased by a problem inherent to local motion measurements: the aperture effect [49–51]. This arises because the neurons that signal local motion have small receptive fields that are sensitive to orientation, meaning that they are only able to signal the 1D motion orthogonal to the orientation of the edge that is passing through their receptive field. In the case of targets with 'upwards' pointing stripes, the motion parallel to the stripes would therefore not be detected, leaving only the orthogonal 'downwards' component of motion and thus perhaps biasing overall trajectory judgements in this direction. This explanation therefore supports the idea that different motion detection mechanisms are recruited at different speeds of movement.

Our findings have important implications for motion dazzle research: our findings provide the first experimental evidence in support of the predicted trajectory biases caused by stripes [13], and suggest that the effects seen may be larger than those caused by dynamic stripes, which have been shown to have robust effects on direction perception in previous psychophysical studies [18–21]. The fact that these biases are seen in relatively natural viewing conditions suggests that these effects may apply in more realistic situations. We have also previously shown a similar effect in a more traditional 2IFC psychophysics experiment without occlusion [52], suggesting that the exact paradigm used may not be critical. However, different animals have different visual systems [53], and therefore one important avenue for future research is to test to see whether the true observers of these patterns in nature show similar visual illusions. For example, many species have different contrast sensitivity functions and visual acuity compared to humans [54], and these factors may therefore have an effect on the perceived contrast of putative dazzle patterns, or their visibility at a given viewing distance. In addition, many striped animals are found in groups, and it would be interesting to test whether the observed effects of oblique stripes on trajectory perception scale with group size. Recent work has shown that human observers show increased tracking errors for targets with parallel stripes compared to targets with perpendicular stripes when moving in groups [55,56], but did not test oblique patterns.

In conclusion, our study adds to an increasing body of evidence that suggests that motion and form processing appear to be tightly linked in humans, even in cases where this causes biases in motion perception. This may have important implications for our understanding of the function of patterning types in the natural world, perhaps providing a mechanistic basis for ‘motion dazzle’ effects.

Data, code and materials

The datasets supporting this article have been uploaded as part of the supplementary material.

Competing interests

We have no competing interests.

Authors' contributions

AEH designed and programmed the experiments, carried out the analyses and wrote the initial draft of the manuscript; DJT conceived of the initial experiments, contributed to designing the experiments and helped draft the manuscript; CJ and KJ collected data. All authors reviewed and edited the manuscript and gave final approval for publication.

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Figure legends

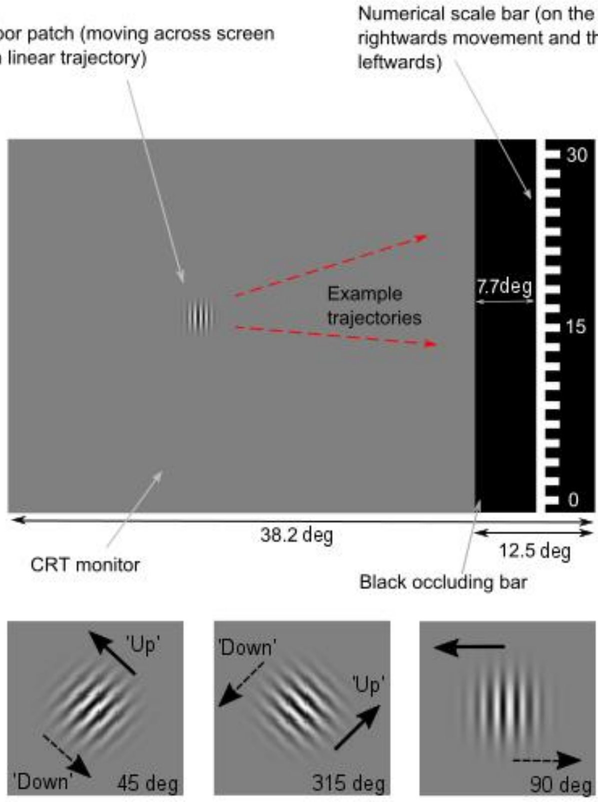

Figure 1: Top – diagram of the experimental set up as programmed for left to right movement (not to scale). The scale bar shows only the range of numbers used; all numbers from 0 to 30 were visible in the experiment. The red arrows represent possible target trajectories and were not present during the real experiment. Bottom – target types used. The Gabor patches used are formed from the multiplication of a sinusoidal wave with a Gaussian function. From left to right: 45 degree oblique Gabor, 315 degree oblique Gabor and vertical (90 degree) Gabor. Solid arrows indicate the direction of net 'upwards' movement (upwards and to the left for the 45 degree stimulus, upwards and to the right for the 315 degree stimulus) and dashed arrows indicate the direction of net 'downwards' movement (down and to the right for the 45 degree stimulus, down and to the left for the 315 degree stimulus. For the vertical stimulus, 'upwards' and 'downwards' were set arbitrarily to allow completion of statistical tests (see text): 'upwards' to the left for the vertical stimulus and 'downwards' to the right for the vertical stimulus).

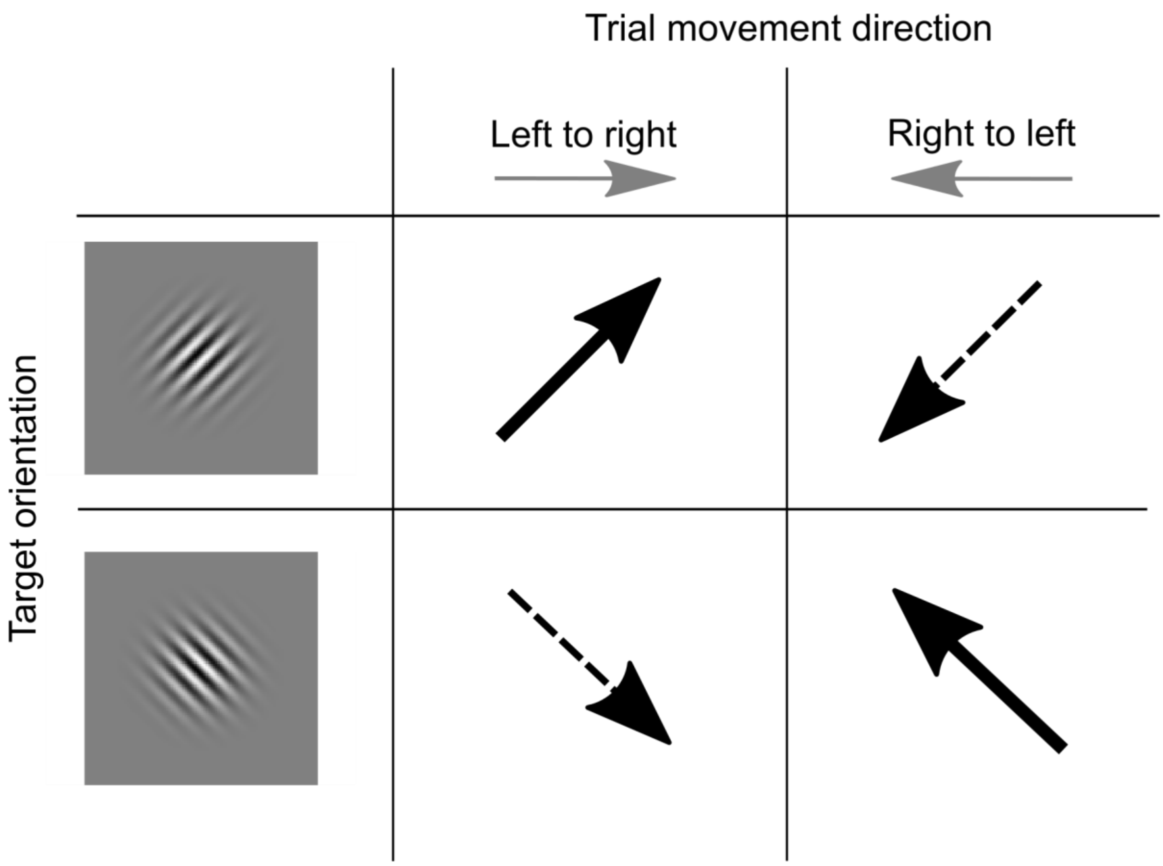

Figure 2: Schematic diagram to indicate how target types were coded in the statistical model used in Experiment 2. Solid arrows indicate combinations of rigid stripe orientation and direction of movement that were classified as pointing ‘upwards’; dashed arrows indicate the combinations that were classified as pointing ‘downwards’.

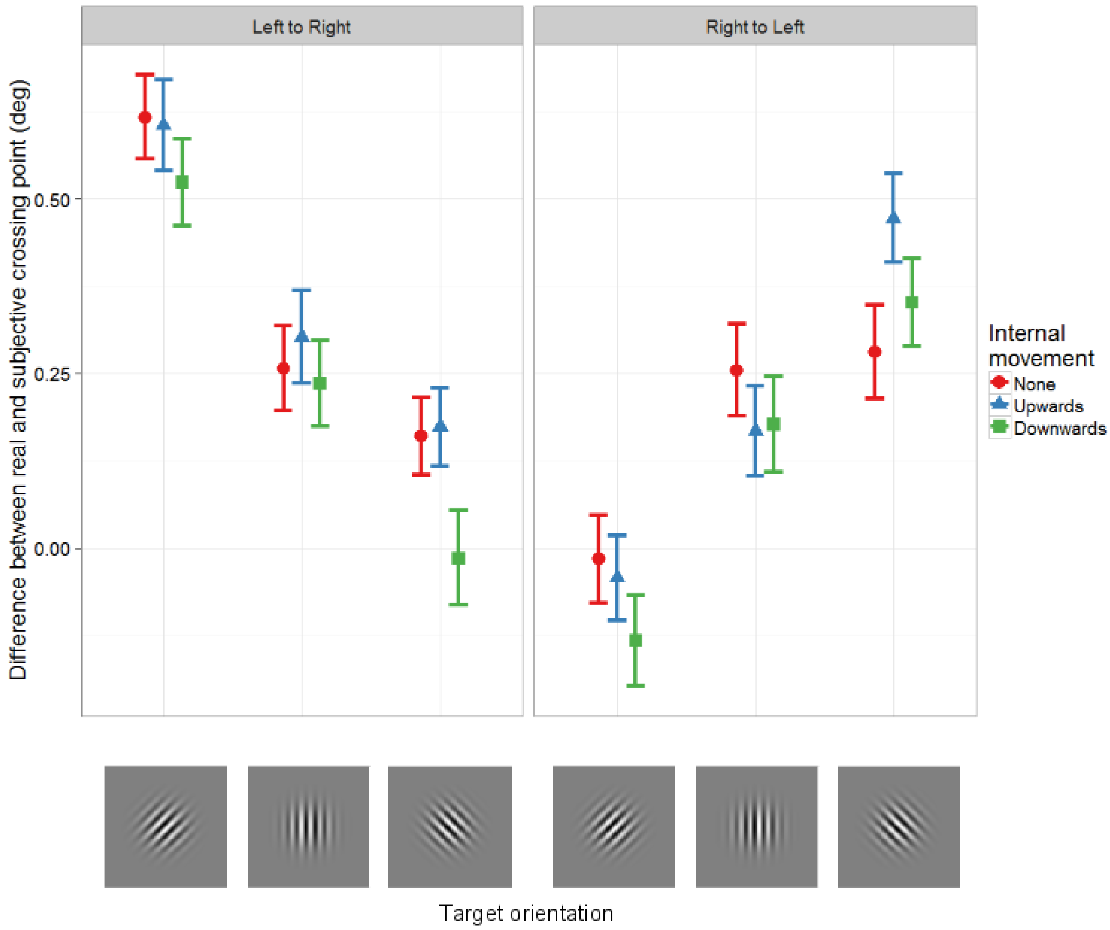

Figure 3: Graph showing results of Experiment 1. Each data point represents the mean difference between the real and subjective crossing points of the target in degrees for one experimental condition (target orientation, drift type and target direction). Each mean reflects the average of all trials for that condition, across all subjects. The error bars are +/- 1 bootstrapped standard error.

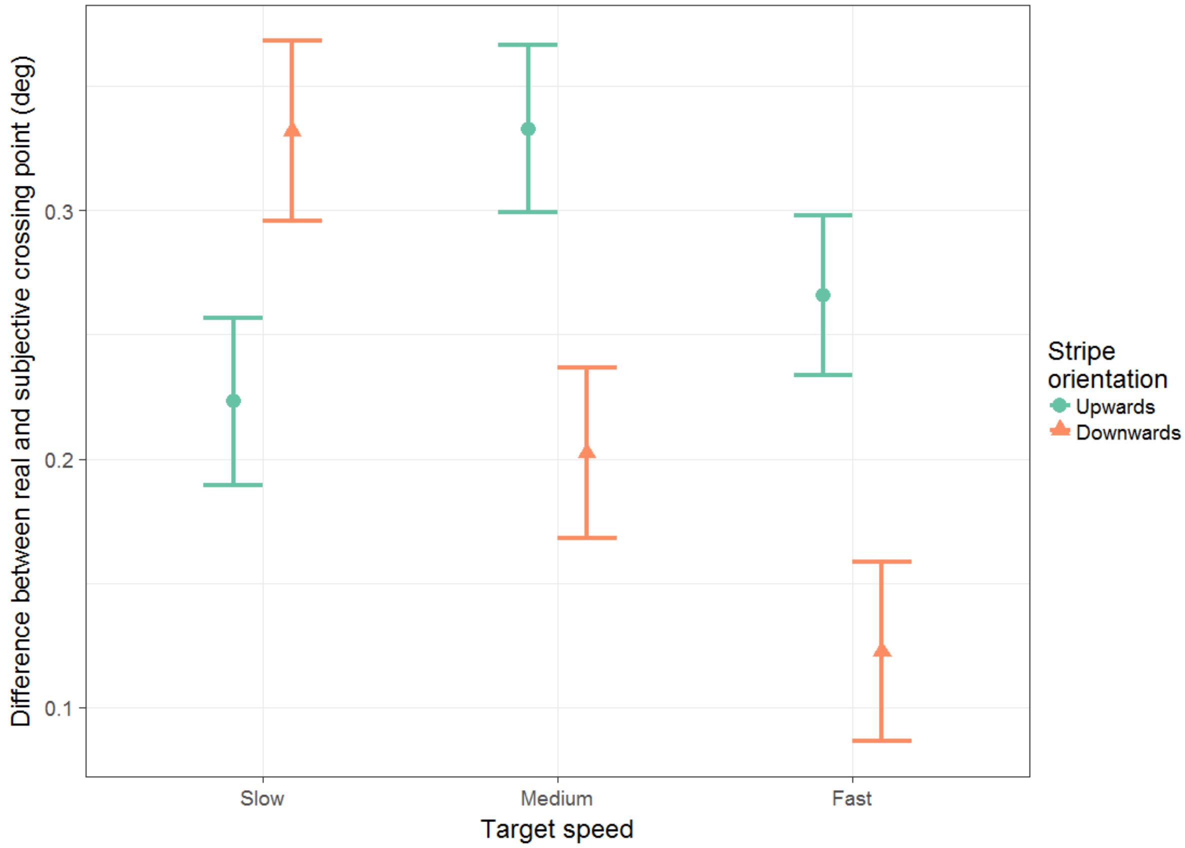

Figure 4: Graph showing results of Experiment 2. Each data point represents the mean difference between the real and subjective crossing points of the target in degrees for one experimental condition (stripe orientation and target speed). Each mean reflects the average of all trials for that condition, across all subjects. The error bars are +/- 1 bootstrapped standard error. Stripe orientation group “upwards” includes all trials where the orientation of the stripes appears to be pointing upwards relative to the direction of travel irrespective of direction of travel; group “downwards” includes the trials where the stripes appear to be pointing downwards relative to the direction of travel (see Figure 2 for further explanation).