Available online at www.sciencedirect.com
ScienceDirect
Vision Research 47 (2007) 375–383
Vision Research
www.elsevier.com/locate/visres

Perceived direction of plaid motion is not predicted by component speeds ☆

Rebecca A. Champion [a,*], Stephen T. Hammett [a], Peter G. Thompson [b]

[a] *Department of Psychology, Royal Holloway, University of London, Egham TW20 0EX, UK*
[b] *Department of Psychology, University of York, York YO10 5DD, UK*

Received 6 July 2006; received in revised form 11 October 2006

Abstract

It has been shown that the perceived direction of a plaid with components of unequal contrast is biased towards the direction of the higher-contrast component [Stone, L. S., Watson, A. B., & Mulligan, J. B. (1990). Effect of contrast on the perceived direction of a moving plaid. *Vision Research 30*, 1049–1067]. It was proposed that this effect is due to the influence of contrast on the perceived speed of the plaid components. This led to the conclusion that perceived plaid direction is computed by the intersection of constraints (IOC) of the perceived speed of the components rather than their physical speeds. We tested this proposal at a wider range of component speeds (2–16 deg/s) than used previously, across which the effect of contrast on perceived speed is seen to reverse. We find that across this range, perceived plaid direction cannot be predicted either by a model which takes the IOC of physical or perceived component speed. Our results are consistent with an explanation of 2D motion perception proposed by [Bowns, L. (1996). Evidence for a feature tracking explanation of why Type II plaids move in the vector sum direction at short durations. *Vision Research, 36*, 3685–3694.] in which the motion of the zero-crossing edges of the features in the stimulus contribute to the perceived direction of motion.

Keywords: Motion; Plaid; Direction; Contrast; Intersection of constraints (IOC)

1. Introduction

The motion of a two dimensional pattern, such as a moving plaid composed of two superimposed sinusoidal gratings drifting in different directions, may be perceived to have a unique, non-ambiguous direction. Adelson and Movshon (1982) proposed a two stage model for the recovery of such motion direction, known as the intersection of constraints (IOC) model. The first stage involves the extraction of the component velocities which, although ambiguous, may be defined by a line of constraint parallel to the component orientation. The second stage recovers plaid motion by computing the intersection of the component constraint lines, giving a unique direction (Fig. 1).

However, it has been shown that the IOC model does not predict perceived direction when the two components of the plaid differ with regards to parameters such as contrast (Stone, Watson, & Mulligan, 1990) and spatial frequency (Smith & Edgar, 1991). Stone et al. (1990) observed that when plaid components are of unequal contrast, perceived plaid direction is biased toward the direction of the high-contrast component. Similarly Smith and Edgar (1991) found that when plaid components differed in spatial frequency, perceived plaid direction was biased toward the low spatial frequency component. Both papers propose that the source of the distortion is the effect of the unequal component attribute on the relative perceived speed of the component gratings. They conclude that their results are consistent with the IOC model, but only if the input to the second stage is that of the *perceived* component speed rather than the physical com-

☆ A preliminary version of these findings was presented at the Vision Sciences Society Meeting 2006.
* Corresponding author. Present address: School of Psychology, University of Southampton, Southampton SO17 1BJ, UK.
E-mail address: r.a.champion@soton.ac.uk (R.A. Champion).

0042-6989/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2006.10.017

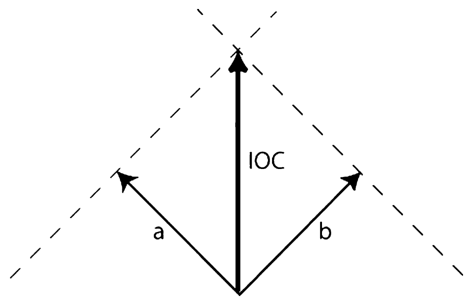

Fig. 1. The intersection of constraint model. **a** and **b** are the velocity vectors of the two plaid components. The dashed lines show the constraint lines for the two components, which meet at the point of the intersection of constraints, IOC.

ponent speed. This modification to the IOC model gained further support from Derrington and Suero (1991) who showed that if the perceived speed of one component of a plaid is reduced by adapting to motion in the direction of that component then the perceived direction of the plaid will be shifted towards the other component.

The dependence of the perceived speed of one-dimensional gratings on contrast has been demonstrated widely (Blakemore & Snowden, 1999; Brooks, 2001; Stone & Thompson, 1992; Thompson, 1982; Thompson, Brooks, & Hammett, 2006). Thompson (1982) and Thompson et al. (2006) have shown that for slow moving gratings, a reduction in contrast induces a perceptual *decrease* in perceived speed, however for faster moving gratings the opposite effect is found, whereby a reduction in contrast induces an *increase* in perceived speed. Thompson (1982) found the cross-over from a decrease to an increase to occur at a temporal frequency of 8 Hz, which was independent of spatial frequency. Thompson et al. (2006) however reported a shift in the cross-over speed from 6 Hz at 2 cycles/deg to 12 Hz at 8 cycles/deg.

Stone et al. (1990) proposed that the dependence of perceived component speed on contrast would lead to predictable distortions in the perceived direction of plaids with components of unequal contrast. Specifically, perceived direction would be biased towards the perceptually faster component. Their experiment used plaids that drifted upwards at 2 deg/s or 6 deg/s (the temporal frequencies of the components were around 1.5 or 4.5 Hz) and comprised components of unequal contrast. Their results demonstrated that at a wide range of relative contrasts and over a wide range of absolute contrasts, perceived plaid direction was biased towards the high-contrast component. As the component speeds used were relatively slow, the effect of lowering component contrast would *always* be to reduce the perceived speed of that component. Hence, this result confirmed their prediction that plaid direction would be biased towards the direction of the higher-contrast, and perceptually faster, component and, therefore, supported their revised IOC model.

The main motivation for the present study was to provide a stronger test of Stone et al.'s revised IOC model. Based on Thompson et al.'s finding of a reversal of the relative perceived speeds of low- and high-contrast gratings at speeds higher than a particular cross-over speed (ranging from 6 to 12 Hz), Stone et al.'s model would predict that the perceived *direction* bias would change in sign for unequal contrast plaids with components at faster speeds. Specifically, Stone et al.'s model would predict that at component speeds less than the cross-over speed the perceived direction bias should be towards the higher-contrast (perceptually faster) component and at component speeds of greater than the cross-over speed the direction bias should be towards the lower-contrast (perceptually faster) component. We therefore measured the effect of unequal component contrast on perceived plaid direction over a wider range of speeds than has previously been investigated, ranging from 2 to 16 deg/s (temporal frequency range 2–16 Hz).[1]

2. Experiment 1

Although there is general agreement between previous studies about the effect of contrast on perceived speed, there is a degree of variation between results with regard to the cross-over speed (the speed at which the effect of contrast on relative perceived speed reverses). Therefore in Experiment 1, we measured the baseline effect in our subjects. These results were later used as the basis for our predictions of plaid direction distortions.

2.1. Methods

2.1.1. Apparatus

Stimuli were generated on an Apple Mac G4 using Matlab 7.01 (Mathworks Inc.) in conjunction with Psychtoolbox (Brainard, 1997; Pelli, 1997). They were presented on a Sony GDM-F520 CRT display with 8 bit resolution, against a uniform grey background of 31.3 cd m^{-2} mean luminance. The frame rate was 75 Hz. The display was gamma-corrected using internal look-up tables. The active display subtended 38.5 deg × 29 deg at a viewing distance of 57 cm. Experiments were conducted binocularly in a darkened room with head position fixed using a chin rest.

2.1.2. Stimuli

Stimuli consisted of sinusoidal gratings with a spatial frequency of 1 c/deg, presented in circular windows of diameter 6 deg. A small fixation point in the centre of the window appeared throughout the presentation of the stimulus. The gratings were oriented at −45 deg (anti-clockwise) or +45 deg (clockwise) relative to vertical and drifted upwards and to the right or left, respectively. Two contrasts were used: high contrast (60%) and low contrast (30%). High-contrast stimuli travelled at one of five speeds: 2, 4, 8, 12, 16 deg/s. Low-contrast stimuli travelled at a range of speeds close to those of the high-contrast stimuli. Stimuli were presented for 250 ms. Both spatial and temporal windows had hard edges.

[1] As spatial frequency remained constant at 1 c/deg for all our stimuli, the speed and temporal frequency of the stimuli covaried. Henceforth we will refer to the rate of motion of stimuli in terms of speed (deg/s).

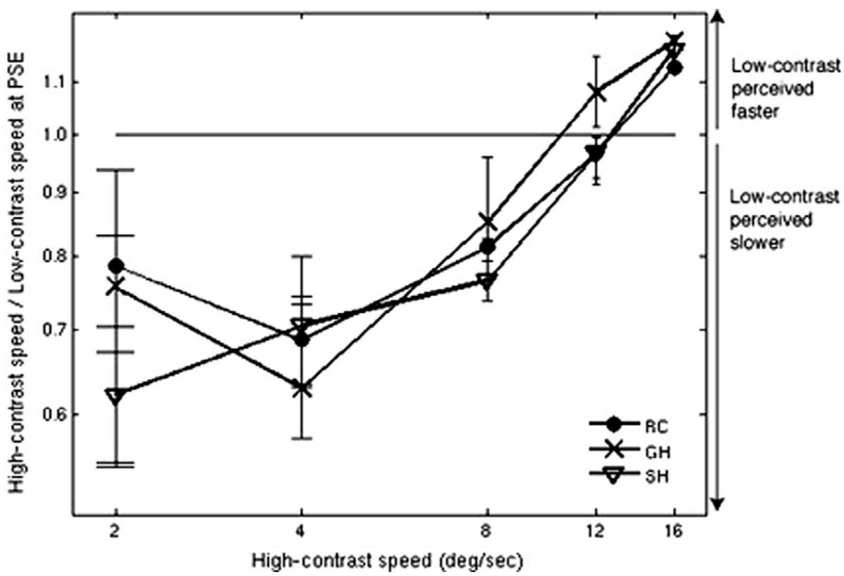

Fig. 2. High-contrast (60%) grating speed relative to low-contrast (30%) grating speed at PSE as a function of high-contrast grating speed for three subjects. Error bars represent 95% confidence intervals.

2.1.3. Procedure

The experiment used the method of constant stimuli to find the speed at which high- and low-contrast gratings were perceived to drift at equal speeds (the point of subjective equality or PSE). For each high-contrast grating, 7 low-contrast gratings were generated which drifted at a range of speeds varying around the high-contrast speed (the exact range of speeds varied between subjects and was determined on the basis of pilot trials). Each grating was generated at both −45 and +45 deg orientation.

On one trial of the experiment, low- and a high-contrast stimuli were presented in separate temporal intervals, separated by a 300 ms blank field. The temporal order of the high- and low-contrast stimuli was randomized. The subject's task was to indicate, by means of a key press, which grating (1st or 2nd interval) was moving faster. Over one complete run, each high-contrast grating was presented with each of the seven low-contrast gratings travelling in the same direction. Hence, one complete run consisted of the presentation of all 70 conditions (5 high-contrast speeds × 7 low-contrast speeds × 2 orientations) in a pseudo-random order. Twenty runs were completed by each subject.

Three subjects took part in the experiment, two authors (RC & SH) and one naïve subject (GH). All were experienced psychophysical observers and wore their appropriate optical correction.[2]

2.1.4. Analysis

Data from the two orientations were pooled, giving 40 repetitions of each condition. For each high-contrast speed condition the proportion of 'high-contrast faster' responses was plotted as a function of low-contrast speed. A cumulative Gaussian was fit to the data using psignifit (Wichmann & Hill, 2001a). Pilot data for each subject were also included in the fit, hence each fit was based on a minimum of 280 trials. From each fit the 50% point was estimated and taken as the PSE. Confidence intervals on the PSEs were obtained using a bootstrap resampling technique (Wichmann & Hill, 2001b).

2.2. Results and discussion

Fig. 2 shows the speed of the high-contrast stimulus relative to the low-contrast stimulus at the PSE as a function of speed for three subjects. A value for this ratio of less than one indicates a reduction in perceived speed of the low-contrast stimulus relative to the high-contrast stimulus, and a value of greater than one indicates an increase in perceived speed of the low-contrast stimulus relative to the high-contrast stimulus. This figure demonstrates that for all subjects perceived speed is reduced at lower contrasts for slower speeds and is increased at lower contrasts for the fastest speeds. This finding is consistent with previous findings (Blakemore & Snowden, 1999; Thompson, 1982; Thompson et al., 2006). For all subjects the cross-over from a decrease to an increase occurs at a speed of around 12 deg/s (or temporal frequency 12 Hz). Previous reports have found the cross-over to occur at a range of temporal frequencies from 6 to 12 Hz (Thompson, 1982; Thompson et al., 2006) and it seems reasonable to assume that the exact point of the cross-over will be sensitive to stimulus parameters.

[2] A fourth subject was initially tested, however this subject showed no effect of contrast on perceived speed. As proposed by Blakemore and Snowden (1999) the use of a foveal stimulus and successive presentation may have facilitated a tracking strategy or alternatively the presence of a fixation spot could have been used as a cue to relative motion. As this study was explicitly looking at the influence of a contrast-induced misperception of speed on plaid direction, this subject was not included in further experiments.

3. Experiment 2

Experiment 1 confirmed previous reports of the effect of contrast on perceived speed. In Experiments 2 and 3, we investigated the influence of unequal component contrast on the perceived direction of plaids. Based on Stone et al.'s revised IOC model, we predict that at slower component speeds, when low-contrast components are perceived to be slower than high-contrast components, perceived plaid direction should be biased towards the high-contrast component. However at faster component speeds, when lower-contrast components are perceived to be faster than higher-contrast components, we predict that the perceived direction of the plaid should be biased towards the low-contrast component.

In order to measure the perceived direction bias, Stone et al. manipulated plaid direction by varying the speed ratio of the two components. This meant that the components of a plaid differed in both speed and contrast, making precise predictions of the direction biases difficult. In Experiments 2 and 3, we manipulated plaid direction by varying the orientation of the plaid but keeping the speeds of the components constant. In Experiment 2, components had equal physical speed. In Experiment 3, components had equal *perceived* speed, as measured in Experiment 1, which enabled us to generate precise predictions of the revised IOC model.

3.1. Methods

3.1.1. Apparatus and stimuli

The apparatus was the same as that used in Experiment 1. Stimuli consisted of plaids composed of two sinusoidal grating components with spatial frequency of 1 c/deg. The plaids were presented in circular windows of diameter 6 deg. A small fixation point in the centre of the window appeared throughout the presentation of the stimulus. Each plaid was composed of one high-contrast component (60%) and one low-contrast component (30%). Components drifted at speeds of 2, 4, 8, 12, or 16 deg/s and both components within one stimulus always drifted at the same speed. The two components were always orthogonal, however their orientation relative to vertical was varied. When the components were at −45 deg and 45 deg relative to vertical this was referred to as a plaid direction of 0 (the true direction of plaid drift was vertical). A plaid direction anticlockwise of vertical was defined as a negative plaid direction and a plaid direction clockwise of vertical was defined as a positive plaid direction. Stimuli were presented for 250 ms.

3.1.2. Procedure

The method of constant stimuli was used to find the plaid direction that was perceived to drift vertically (a perceived plaid direction of 0). For each component speed condition, 7 plaids were generated which travelled in a range of directions varying around 0 (the exact range of directions varied between subjects and was determined on the basis of pilot trials). For each plaid a mirror image was also generated (e.g. in the case where one plaid had a high-contrast component at an orientation of −50 deg and a low-contrast component at an orientation of 40 deg, another plaid was generated with a high-contrast component orientation of 50 deg and a low-contrast component orientation of −40 deg).

On one trial of the experiment one plaid was presented in a single interval. The subject's task was to indicate, by means of a key press, whether the plaid was moving to the left or right of vertical. One complete run consisted of the presentation of all 70 conditions (5 component speeds × 7 plaid directions × 2 mirror images) in a pseudo-random order. Twenty runs were completed by each subject. The same three subjects were used as in Experiment 1. It should be noted that participants reported that the motion perceived was coherent for all plaids in Experiments 2 and 3.

3.1.3. Analysis

Data from the two mirror images were pooled, giving 40 repetitions of each condition. For each component speed condition the proportion of responses in which 'perceived direction was biased towards the direction of the high-contrast component' was plotted as a function of plaid direction. A cumulative Gaussian was fit to the data as in Experiment 1 and the 50% point was estimated and taken as the perceived direction error.

3.2. Results and discussion

Fig. 3 shows the perceived direction error as a function of component speed, for three subjects. The IOC prediction (i.e. based on *physical* component speeds) of veridical performance is indicated by the horizontal line at zero. A negative direction error indicates that perceived direction was biased towards the direction of the high-contrast component and a positive direction error indicates that perceived direction was biased towards the direction of the low-contrast component. This figure clearly demonstrates non-veridical performance for all subjects, suggesting that perceived plaid direction is not computed from the IOC combination of physical component speeds. Furthermore, the results show that for all subjects the bias in perceived direction towards the direction of the high-contrast component increases as the component speed increases. At the slowest component speed of 2 deg/s, two subjects show a bias towards the direction of the low-contrast component, whilst the third subject (RC) shows no bias. This result is in stark contrast to that obtained by Stone et al., who found that for slow component speeds of around 1 deg/s perceived direction is always biased towards the high-contrast component. The pattern of results across speeds is also highly inconsistent with the prediction based on Stone et al.'s model that at slow speeds the high-contrast component should dominate and at fast speeds the low-contrast component should dominate perceived direction. In Experiment

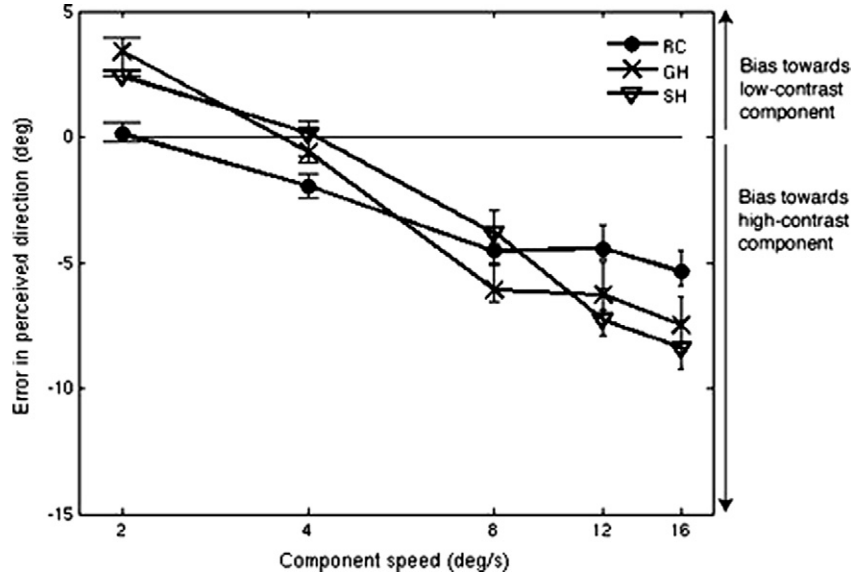

Fig. 3. Errors in perceived plaid direction as a function of component speed for plaids of equal physical component speed, for three subjects. The solid horizontal line at zero represents physically veridical perception and the prediction of the IOC model. Error bars represent 95% confidence intervals.

3 we modify the design of Experiment 2 to allow us to make more precise predictions of the perceived direction errors predicted by Stone et al.'s model.

4. Experiment 3

This experiment was a replication of Experiment 2, however in this experiment the speeds of the two components were no longer equal. The PSE values obtained in Experiment 1, were used to produce plaids with physically different but *perceptually* equal component speeds. Hence for each plaid the high-contrast component speed was 2, 4, 8, 12, or 16 deg/s and the low-contrast component speed was the appropriate PSE value obtained for each subject. Using these values precise predictions of Stone et al.'s model could be obtained. All other aspects of the stimuli and procedure were identical to that of Experiment 2.

4.1. Results and discussion

Fig. 4 shows the perceived direction error (relative to the physically veridical direction), as a function of component speed for three subjects. As in Fig. 3, the IOC model prediction of veridical performance is indicated by the horizontal line at zero. A negative error indicates that perceived direction was biased towards the direction of the high-contrast

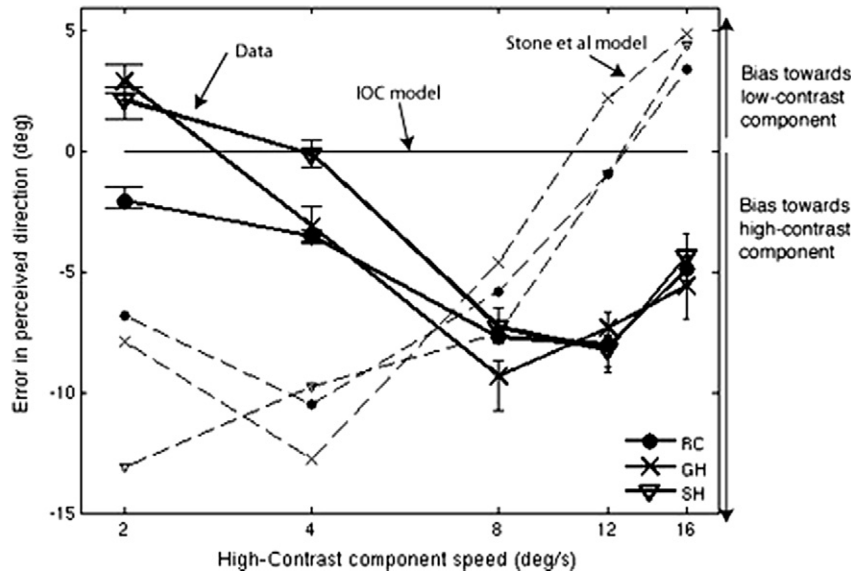

Fig. 4. Errors in perceived plaid direction as a function of high-contrast component speed for plaids of equal perceived component speed, for three subjects. Dashed lines show predicted errors based on the revised IOC model of Stone et al. The solid horizontal line at zero represents physically veridical perception and the prediction of the IOC model. Error bars represent 95% confidence intervals.

component and a positive error indicates that perceived direction was biased towards the direction of the low-contrast component. In addition, the predicted errors derived using Stone et al.'s revised IOC model (i.e. based on the IOC of the *perceived* speeds of the components) are shown for each subject (dashed lines). These lines demonstrate the prediction of a bias towards the high-contrast component at slower speeds and towards the low-contrast component at the fastest speed.

Fig. 4 demonstrates clearly that the subjects' results do not conform to the predictions either of the IOC model or those of Stone et al.'s model. This suggests that perceived plaid direction is not computed by IOC combination of either the physical component speeds or the perceived component speeds. The results for all three subjects are very similar to those of Experiment 2, demonstrating a general increase in perceived direction bias towards the high-contrast component with increasing speed. However, there is one interesting difference to the results of Experiment 2, which is the 'U' shape of the curve at the higher speeds. This effect is consistent across all three subjects and demonstrates that at the highest speed there is a reduction in the bias towards the high-contrast component.

5. General discussion

The results of Experiment 1 reinforce the increasing corpus of data suggesting that at low speeds, reducing contrast reduces perceived speed and that at higher speeds these effects are reduced and even reverse. Consequently, reducing contrast for fast moving patterns increases their perceived speed.

The results of Experiments 2 and 3, indicate that the perceived direction of moving plaids with unequal component contrast is biased towards the direction of the higher-contrast component at all speeds except the slowest. We also found that the magnitude of the bias generally increases as speed increases. This pattern of results is inconsistent with Adelson and Movshon's (1982) IOC model which predicts that perceived direction is computed from the physical speeds of the components. It is also inconsistent with Stone et al.'s (1990) revised IOC model which predicts that perceived plaid direction is computed from the *perceived* speeds of the components.

Our results further contribute to a number of psychophysical findings that are inconsistent with the IOC model (Derrington, Badcock, & Holroyd, 1992; Heeley & Buchanan-Smith, 1994; Wilson & Kim, 1994). In particular, Ferrera and Wilson (1990) showed that the IOC model failed to predict the perceived direction of motion of Type II plaids. Type II plaids are those whose components share very similar orientations but different speeds which leads to a discrepancy between the IOC direction and the direction predicted by the vector sum of the components. (Note: for Type I plaids, as used in our study, the IOC and vector sum directions are the same). Ferrera and Wilson found that the perceived direction of Type II plaids was consistently biased[3] towards the vector sum direction.

A variety of models for 2D motion have been proposed to account for Ferrera and Wilson's Type II plaid finding. We shall discuss five such models and in each case the extent to which they may account for our findings.

Weiss, Simoncelli, and Adelson (2002) proposed a variation on the IOC model whereby the motion of the underlying components are computed by a Bayesian estimator. The estimated velocities of the components are influenced by a 'prior' for slow motion under conditions of uncertainty (i.e. greater noise), for example low contrast. This model has been shown to account for the finding that perceived Type II plaid direction is biased towards the vector sum direction. This model also expects that for Type I plaids with unequal contrast components, the plaid's motion will always be biased towards the higher-contrast component. This description is consistent with our finding, however, this model is essentially equivalent to the model proposed by Stone et al and critically depends on the perceived speeds of the components being slower at low contrast. Our results from experiment 1, in addition to the results of Thompson et al. (2006), demonstrate that this is not the case, hence this model does not explain our results.

Wilson, Ferrera, and Yo (1992) proposed a model for the computation of 2D motion which introduces a non-linearity in order to detect 2nd-order, or non-Fourier, motion. This model incorporates two parallel pathways, the first of which extracts the motion energy of the 1st-order components. The second pathway, rectifies and filters the stimulus to obtain the 2nd-order components before extracting the motion energy of these components. The plaid motion is then computed as the vector sum of the combined 1st-order and 2nd-order components. They demonstrate that this model can account for the finding that the perceived direction of Type II plaids is biased in the vector sum direction.

Wilson et al.'s model would not, however, predict any bias in the perceived direction of an unequal contrast Type I plaid. Although this model does incorporate a contrast gain control operation at the stage of 1st-order motion energy extraction, this operation makes the model virtually independent of contrast above 10%. The use of this contrast gain function is shown to account for the results of Stone et al which used low absolute contrast stimuli (5–40%), however no influence of contrast would be predicted in the higher contrast stimuli we used (absolute contrast 90%). Although a modification of the gain control function could be proposed (such as that proposed by Thompson et al., 2006), again this would lead to predictions based on the contrast effects on the independent components, which cannot predict our results.

The 2nd-order stage of the model also predicts no difference between equal and unequal contrast plaids. At this

[3] As the IOC direction is equal to the physical direction of the plaid, any reference to a 'bias' in perceived direction refers to a bias away from the IOC direction.

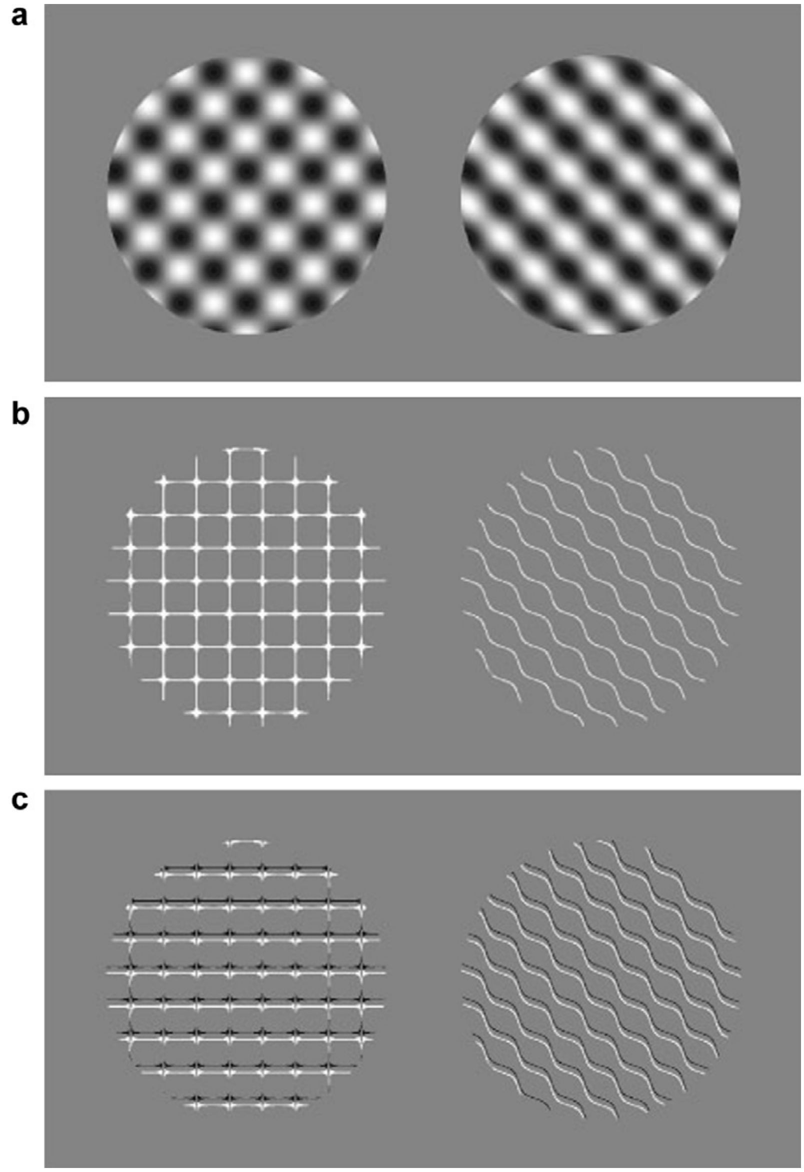

Fig. 5. The effect of unequal component contrast on the orientation of 2nd-order components. Left, equal-contrast plaid; right, unequal-contrast plaid. (a) Plaids with orthogonal components. (b) Zero-crossing edges computed by convolving images with a Laplacian of Gaussian operator. (c) Displacement of zero-crossing edges over time when 1st-order components travel at equal physical speeds. Time 1, white; Time 2, black.

stage, four 2nd-order components are generated by the rectification process. Two components will have orientations aligned with the 1st-order components, and the other two components will have orientations half-way between the orientations of the 1st-order components and perpendicular to each other. The model then filters at a lower spatial frequency which will remove the components aligned with the 1st-order components and leave only one pair of 2nd-order components. Any differences in the 2nd-order components generated from equal and unequal contrast plaids will be removed by this filtering stage. In conclusion, Wilson et al.'s model would predict motion in the IOC direction for both equal and unequal contrast Type I plaids.

Bowns (2001a, 2002) proposed a model which involves decomposition of the image into its 1st-order components, followed by the extraction of the zero-crossings of these components. The zero-crossings for the two components are then combined, the intersections are extracted, and the movement of these intersections is then computed. This model has been shown to account for a number of discrepancies from IOC predictions, however in the case of unequal contrast Type I plaids it would predict motion in the IOC direction. Decomposing stimuli into 1st-order components and then extracting the zero-crossings would discard all contrast information and hence no difference between equal and unequal contrast components would be predicted. Therefore this model cannot explain our findings.

Alais, Wenderoth, and Burke (1994) propose a model which extracts and tracks features from the 2D image. The model incorporates the motion of the local luminance peaks and troughs or 'blobs' in the stimulus which always move in the IOC direction. Hence if the motion of these blobs is combined with the vector sum of the 1st-order components, this could explain the Ferrera and Wilson Type II plaid finding. However, this model cannot explain our finding, as for all Type I plaids both the combined motion of the 1st-order components and the motion of the blobs would indicate an IOC direction of motion.

An alternative to the Alais et al 2D feature tracking model was proposed by Bowns (1996, 2001b). This model demonstrates that, although the minimum and maximum luminance features move in the IOC direction, the zero-crossing edges of these features do not. For Type II plaids these edges move in the vector sum direction. Hence if the motion of these edges was combined with motion vectors in the IOC direction this model is able to explain the Ferrera and Wilson findings. In addition, this model may offer an explanation for our finding of a bias toward the higher-contrast component. Fig. 5a shows two plaids, each constructed from identical parameters except for the relative contrast of the components: equal contrasts on the left and unequal contrasts on the right. Fig. 5b illustrates the zero-crossing edges in each image obtained by convolving the image with a Laplacian of Gaussian operator. These images demonstrate the impact of unequal component contrast on the orientation of the zero-crossings, for the equal contrast plaid the zero-crossing edges create bounded regions, for the unequal contrast plaid the zero-crossing edges become aligned with the high-contrast component. Fig. 5c shows how the zero-crossing edges move over time when the two 1st-order components travel at the same physical speed. Note that the IOC prediction (based on physical speeds) for both plaids will be motion in the vertical direction (as shown in Fig. 1). If it is assumed that motion perpendicular to the zero-crossing edge is extracted, as assumed by Bowns (1996), it is clear that in the case of the equal-contrast plaid, the motion extracted will be in the vertical direction, consistent with the IOC prediction. In the case of the unequal-contrast plaid, as the edge is not straight no consistent direction will be extracted at all points along the edge, however, on average the motion extracted will be in the direction consistent with the motion of the high-contrast component. Consequently a combination of the motion of the 1st-order components, the luminance features and the zero-crossing edges could offer an explanation for our finding of a bias in perceived direction towards the direction of the high-contrast component in unequal contrast Type I plaids (see Fig. 6).

Although Bowns (1996, 2001a, 2001b) model of zero-crossing extraction may offer an explanation for the bias we obtained, it does not explain the speed dependence of this bias. Evidence for the effect of speed on luminance blob tracking mechanisms has shown that these respond optimally at low temporal frequencies (Alais et al., 1994), hence this would predict a stronger contribution from these mechanisms at slower speeds. If it were the case that

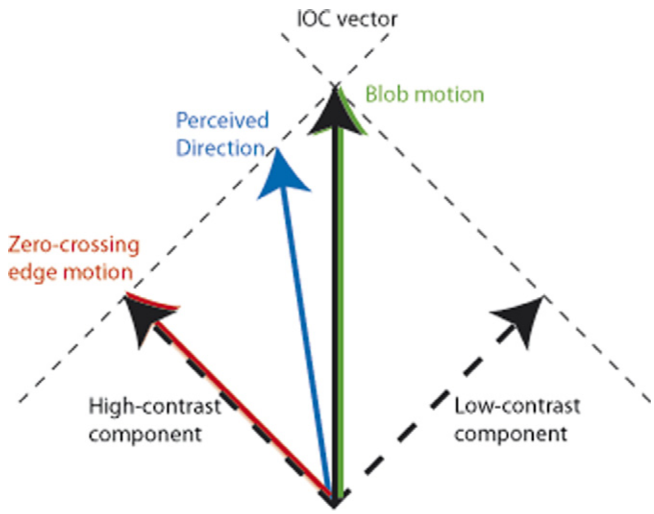

Fig. 6. Motion vectors present in unequal contrast Type I plaids: (1) The 1st-order component vectors (black dashed lines) have directions of ±45 deg and the IOC vector (black solid line) for the 1st-order components has a direction of 0 deg. (2) The zero-crossing edge vector (red line) is consistent with the high-contrast 1st-order component. (3) The Blob motion (green line) is consistent with the IOC vector. A combination of the motion of 1st-order components, zero-crossing edges and blobs will lead to a bias in perceived direction in the direction of the high-contrast component.

the mechanism tracking the luminance blobs was different to that tracking the zero-crossing edges this may account for our result as follows: an increase in speed would cause a reduction in the influence of the blob tracker, this in turn may lead to a relative increase in the influence of the zero-crossing tracker, causing an increase in bias towards the high-contrast direction.

In addition to the speed dependence of the blob tracking mechanism, Alais et al. also found that this mechanism responded optimally at high contrasts. This result may offer an explanation for the discrepancy between our findings and those of Stone et al. (1990). Stone et al. found a bias toward the high-contrast component at slow components speeds of around 1 deg/s (temporal frequency 1.5 Hz). We found no such bias at a similar speed (2 deg/s or 2 Hz). One significant difference between our stimuli and those of Stone et al. was the absolute contrast used; Stone et al used absolute contrasts ranging from 5 to 40%, we used an absolute contrast of 90%. It may be the case that at the lower absolute contrast used by Stone, the blob tracking mechanism was not responding optimally and therefore the zero-crossing tracker had a greater relative influence, leading to a greater bias than in our stimuli. We do not currently have any evidence for this proposal, hence further investigation is necessary in order to test it.

In summary, our results demonstrate that the perceived direction of drifting plaids with unequal component contrast cannot be explained by either the IOC solution of the physical component speeds, or the IOC solution of the perceived component speeds. We have further demonstrated that this result is inconsistent with a number of models of

2D motion perception, but may be consistent with a model which extracts the zero-crossing edges of the features in the stimulus. In conclusion, we provide further evidence that the perceived direction of plaids is not predicted solely by either physical or perceived component speeds.

Acknowledgments

This work was supported by a Wellcome Trust Project Grant (GR065624) to S.T.H. and P.G.T. Many thanks to Paul Warren for helpful comments and suggestions and also to two anonymous reviewers.

References

Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature, 300*, 523–525.

Alais, D., Wenderoth, P., & Burke, D. (1994). The contribution of one-dimensional motion mechanisms to the perceived direction of drifting plaids and their aftereffects. *Vision Research, 34*, 1823–1834.

Blakemore, M. R., & Snowden, R. J. (1999). The effect of contrast upon perceived speed: a general phenomenon? *Perception, 28*, 33–48.

Bowns, L. (1996). Evidence for a feature tracking explanation of why Type II plaids move in the vector sum direction at short durations. *Vision Research, 36*, 3685–3694.

Bowns, L. (2001a). Features derived from first-order motion mechanisms predict anomalies in motion perception. *Perception, 30*, 9–19.

Bowns, L. (2001b). IOC, vector sum and squaring: three different motion effects or one? *Vision Research, 41*, 965–972.

Bowns, L. (2002). Can spatio-temporal energy models of motion predict feature motion? *Vision Research, 42*, 1671–1681.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436.

Brooks, K. (2001). Stereomotion speed perception is contrast dependent. *Perception, 30*, 725–731.

Derrington, A., & Suero, M. (1991). Motion of complex patterns is computed from the perceived motions of their components. *Vision Research, 31*, 139–149.

Derrington, A. M., Badcock, D. R., & Holroyd, S. A. (1992). Analysis of the motion of 2-dimensional patterns: Evidence for a 2nd-order process. *Vision Research, 32*, 699–707.

Ferrera, V. P., & Wilson, H. R. (1990). Perceived direction of moving 2-dimensional patterns. *Vision Research, 30*, 273–287.

Heeley, D. W., & Buchanan-Smith, H. M. (1994). Changes in the perceived direction of drifting plaids, induced by asymmetrical changes in the spatio-temporal structure of the underlying components. *Vision Research, 34*, 775–797.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision, 10*, 437–442.

Smith, A. T., & Edgar, G. K. (1991). Perceived speed and direction of complex gratings and plaids, J. *Journal of the Optical Society of America, 8*, 1161–1171.

Stone, L. S., & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research, 32*, 1535–1549.

Stone, L. S., Watson, A. B., & Mulligan, J. B. (1990). Effect of contrast on the perceived direction of a moving plaid. *Vision Research, 30*, 1049–1067.

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research, 22*, 377–380.

Thompson, P., Brooks, K., & Hammett, S. T. (2006). Speed can go up as well as down at low contrast: implications for models of motion perception. *Vision Research, 46*, 782–786.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*, 598–604.

Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling and goodness-of-fit. *Perception and Psychophysics, 63*, 1293–1313.

Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception and Psychophysics, 63*, 1293–1313.

Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9*, 79–97.

Wilson, H. R., & Kim, J. (1994). Perceived motion in the vector sum direction. *Vision Research, 34*, 1835–1842.