Perception of direction of motion reflects the early integration of first and second-order stimulus spatial properties

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Second-order Type I and Type II plaids were constructed by combining two orientation-filtered random-dot gratings. Each component consisted of a dynamic filtered random-dot field, the contrast of which was modulated by a drifting sinusoidal grating. Orienting the two components suitably and interleaving at 120 Hz allowed us to produce a two-dimensional plaid pattern made from one-dimensional second-order components. The perceived direction of motion of both Type I and Type II plaids was measured as a function of the orientation content of the carrier, the contrast, and the duration of the stimulus. Type I plaids had a perceived direction close to the intersection of constraints/vector sum solution (which coincide for Type I patterns) for all conditions when the motion was visible. Type II plaids had a perceived direction that moved away from the vector sum and toward the intersection of constraints solution as the orientation bandwidth of the carrier increased. The data explain discrepancies in previous work using comparable stimuli and are consistent with recent evidence that the previously considered parallel pathways of form and motion have a strong influence upon one another from early stages of cortical visual processing.

Keywords: motion, first-order, second-order, orientation, filtering

Introduction

The ability to accurately identify the motion in an image is a critical property of the visual system and one that has attracted a great deal of research interest over the past 30 years or so. However, despite the wealth of data collected and the extent of the confluence of that data, there is still uncertainty regarding how we detect the motion of the simplest luminance edge, let alone the more complex patterns employed in much of the recent motion psychophysics (Cropper & Wuerger, 2005; Derrington, Allen, & Delicato, 2004). What the evidence does suggest is that the motion detection system is a strongly hierarchical process, and the initial signal specific to the motion subsystem is related to the direction of the motion of an edge (Lennie & Movshon, 2005). The edge is usually coded by a first-order modulation of the image statistics, and the directional signal relating to any one-dimensional edge is only accurate to within ±90 degrees; a property known as the "aperture problem" (Marr & Ullman, 1981). This relatively simple "seed" is progressively built into a signal that ends up as a remarkably complex and powerful contributor to the overall percept of the visual scene, revealing not only the motion in the input but also the depth and, in some cases, the form (Warren,

2004). This hierarchy of signal development is seen both in the behavioral (Wilson, Ferrera, & Yo, 1992) and in the neurophysiological (Duffy, 2004) data and in turn dictates the way in which we define and describe the stimuli that we use.

An example of this is the description of a visual stimulus in terms of its first-order and second-order spatial statistics and of the consideration of each spatial dimension (*x* and *y*) independently. Thus, there has been an argument presented within the motion literature for independent pathways in the system that deal with the first-order and second-order components of the pattern independently (e.g., Badcock & Derrington, 1985; Badcock & Khuu, 2001; Edwards & Badcock, 1995; Ledgeway & Smith, 1994; Lu & Sperling, 1995, 2001; Wilson et al., 1992). Furthermore, it is thought that the early cortical pathways are principally one-dimensional in their sensitivity; a two-dimensional percept being recovered from those one-dimensional components, as is the overall spatial structure.

Counter to this approach, there is, however, some evidence to suggest that these nominal pathways may not be so separate, and that both a two-dimensional representation and a composite spatiotemporal representation may be generated in a more coherent and integrated manner (Geisler, 1999; Johnston, McOwan, & Buxton,

1992). In particular, it has recently been shown that there are strong interactions between form and motion cues in the image; two components previously considered to be quite separate early on in the visual process. Specifically, the orientation properties of elements within a stimulus have a profound impact on the perceived direction of the first-order spatial profile (Badcock, McKendrick, & Ma-Wyatt, 2003; Nishida & Johnston, 1999; Ross, 2004; Ross, Badcock, & Hayes, 2000), and the motion of a pattern also impacts upon its perceived spatial position (Nishida & Johnston, 1999; Whitney & Cavanagh, 2000, 2003).

Both these results suggest that spatial properties such as form and position interact with motion, and Geisler's (1999) model proposes that this is at an early stage when both are coded by luminance modulation. In the context of the hierarchical and parallel approach to motion processing, we were interested to determine whether first-order and second-order spatial signals also interacted within the motion system.

We have addressed this issue by examining the interaction between first-order spatial form and the motion of a second-order profile using two-dimensional plaid stimuli that have independently defined first-order orientation content and second-order motion directional signals. This allows us to examine the effect of the former on the perceived direction of the latter.

Methods

Apparatus and stimuli

The stimuli were plaids with components constructed from contrast-modulated noise. The noise was initially a dense binary, dynamic random-dot array that was filtered to constrain the orientation content and then multiplied by an envelope that was a sinusoidal function of space. Examples of the patterns presented are shown in Figure 1, and all patterns were perceived to move coherently.

The composite plaid pattern was made from the two 1D components, each consisting of filtered, dynamic luminance noise modulated by a sinusoid, by temporally interleaving frames at 120 Hz on a calibrated high resolution monitor (Barco CDCT6551; CIE coordinates of whitepoint 0.333:0.377) controlled by a dedicated graphics card (Cambridge Research Systems VSG 2/3). Each composite pattern had an intersection of constraints (IOC) (Movshon, Adelson, Gizzi, & Newsome, 1986) solution drift rate of 2.5 Hz, and all stimuli were restricted by a Gaussian temporal window (half-width 60, 125, 250, and 500 ms) and radially truncated to fill an 8° circular window. To eliminate systematic motion signals from any first-order-sensitive motion mechanisms, the carrier was refreshed at a rate of 30 Hz (Benton & Johnston, 1997;
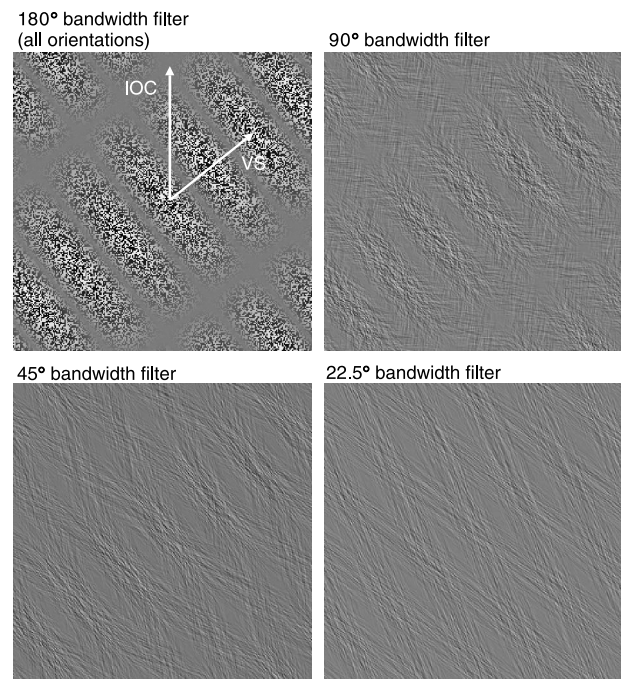

Figure 1. Figure showing representations of the stimuli used in the experiment. The motion vectors indicated by the arrows are for Type II plaids. Four orientation-filter bandwidths are shown. In each case, if the contrast envelope is the same, only the orientation content of the carriers changes. Each image was 256 pixels square and was presented with a luminance resolution of 8 bits.

Cropper, Badcock, & Hayes, 1994; Smith & Ledgeway, 1995). The rerandomization process, along with the spatially broadband nature of the carrier, minimizes the significance that any amplitude modulation component in the *unmodulated* carrier (Kovács & Fehér, 1997) will have upon the consistent motion signals in the composite pattern.

Spectral properties of the stimuli

The unfiltered luminance carrier was a dynamic, random-dot structure; each dot being one square display pixel. The contrast of the noise carrier was modulated by a sinusoid with a spatial frequency of 1 cpd. The orientation of the modulating envelope of each 1D component was parallel to the center orientation of a filter used to restrict the orientation bandwidth of the carrier. Each individual pixel was of uniform brightness,[1] and the local mean luminance was, on average, constant. Therefore, the significant modulation defining the pattern components was restricted to be second-order in its spatial statistics.

To control the first-order orientation content of each component, the random-dot carrier was filtered such that only a limited range of orientations, but the majority of spatial frequencies remained. The filter was defined in the frequency domain in polar coordinates (r, θ): Its edges

were smoothed to zero by a cumulative Gaussian function over a radial angle of $\theta = 2°$ (full range of the function) to minimize edge artefacts (Bracewell, 1965). Thus, apart from the attenuation at the edges, the filter did not alter the amplitude of any orientations within its passband; spatial frequencies below 1.0 cpd were removed by the filter (a cumulative Gaussian profile along r, with a spread of 0.2 cpd centered around 1 cpd) for two reasons. Firstly, the orientation resolution of the FFT is very poor at low spatial frequencies, making it impossible to finely manipulate orientation bandwidth in this range for stimuli of the size used here (256 × 256 pixels). Secondly, it has been argued that any frequency in the carrier below the envelope spatial frequency can potentially contribute a first-order signal to the pattern capable of signaling the same direction as the second-order modulation (Cropper & Johnston, 2001).

Once the filtered images were calculated for each frame of the stimulus, the DC component was re-inserted to restore the mean luminance, and then the filtered spectra were returned to a spatial domain representation (rather than frequency domain). As a result of the filtering, the stimuli had reduced peak contrast although the energy at the same orientation as the envelope was unchanged in the upper frequency ranges. This also means that the bandwidth of the filter and the total contrast energy of the stimulus co-varied. However, given the structure of models of the early visual system, in particular those motion models of interest here, this treatment of the contrast of the stimulus ensures that the contrast energy within any single orientation-selective pathway remains the same across all stimuli if that orientation is present in the first-order carrier. The peak carrier contrast for a given component was controlled by the modulating contrast envelope and was 22% for most stimuli. However, to address the relevant question of stimulus visibility, this was increased to 37% and 44% for one condition (data shown in Figure 3).

Psychophysical procedure

The observers' task was to indicate the perceived direction of motion of the pattern at the end of the presentation interval (Cropper et al., 1994; Yo & Wilson, 1992) using a cursor controlled by a mouse presented on the display screen. Thus, the initial task was direction identification (rather than discrimination) with a radial resolution of approximately 1 degree. To control for inter-observer variation, a common problem with these patterns, observers were required to discriminate the direction of the plaid (left or right of vertical) in a two-alternative forced-choice task in the final experiment. Each data point plotted, in all figures, is the result of 80 trials and is plotted with ±1 *SEM*. In all experiments, the absolute (spatial) orientation of the patterns was randomly

interleaved between trials so the actual orientation of the plaids upon the screen was unpredictable. In addition, the orientation-filter bandwidth and the particular conditions expressed in each figure (e.g., contrast, duration, plaid type) were randomly interleaved. The aims of these manipulations were to minimize the impact of any adjacent pixel non-linearity in the display or of specific structural properties of the patterns being remembered and utilized by the observers.

Results

Predictions

Conceptually, the motion of a plaid pattern can be described using linear summation of the component motion vectors (VS) or by using the intersection of constraints (IOC) solution for the motion of a rigid body (Movshon et al., 1986). If the vector sum and IOC predictions lie between the two one-dimensional vectors describing the motion of the envelope components, then the plaid is "Type I"; if the IOC solution is outside this range, then the plaid is "Type II" (Ferrera & Wilson, 1990). We compared both Type I and Type II patterns in this study, and all patterns appeared to move coherently rather than as two transparent components sliding over one another.

For our stimuli, the direction of motion of the two-dimensional contrast-modulated envelope will be the same for all the patterns in Figure 1 (for instance, if an IOC calculation were used), and all two-stage (independent pathway) models of motion perception, which treat first and second-order modulations separately, predict that a common direction would also be extracted by the visual system.

Thus, we can make two clear predictions about the following data if this two-stage approach is appropriate:

1. The orientation content of the carrier will have no effect upon the perceived direction of motion of the pattern.
2. There will be minimal difference between the perceived direction of Type I and Type II plaids across all carrier-orientation content.

Data

The stimuli on each trial were presented with random absolute orientations to prevent response biases but for the purposes of data analysis, the displayed pattern motion was normalized to a particular direction (0° = the IOC solution), and the presented data are expressed as

deviations from this normalized direction. The results of a single-interval direction-identification task for a Type II plaid are presented in Figure 2 for five observers. The normalized perceived direction of motion of the plaid is plotted against the orientation bandwidth of the (first-order) filter. The directions of motion of each plaid component and the vector sum and intersection of constraints solutions for the pattern are plotted as horizontal lines. On Figure 2, we have also plotted the results of two previous studies using either grating (Kim & Wilson, 1993) or unfiltered random-dot carriers (Cropper et al., 1994) in a Type II plaid.

The data plotted in Figure 2 indicate clearly that the perceived direction of motion of the pattern changes significantly as the orientation bandwidth of the carrier increases. The perceived direction of motion of the pattern moves closer to the IOC solution as the range of orientations present in the luminance carrier of the plaid increases. This is more noticeable for some observers than others but present to a significant degree in all cases.

Figure 3 plots data allowing a comparison of performance with Type I and Type II plaids. The results indicate that when the image contains only orientations within a 22.5° band, the perceived direction of motion of both Type I and II patterns is close to that predicted by a vector summation of the envelope components (Wilson & Kim, 1994). As more orientations are included, the perceived direction of motion of the Type II plaid changes to be closer to that which would be predicted using the IOC solution, i.e., an analysis of the motion of the two-dimensional envelope (Cropper et al., 1994; Derrington, Badcock, & Holroyd, 1992). Because the second-order

properties of the stimulus, the contrast envelopes, signal the same direction of motion regardless of their first-order carrier content, and there is no consistent first-order directional signal, this result indicates an interaction between the second-order spatiotemporal signal and the first-order spatial signal. If this were not the case, then all data would fall upon the horizontal (vector sum) line as it does for the Type I plaid.

If this change in direction as orientation content increased was a result of the lower contrast-energy of narrow orientation-band patterns, then it should be influenced by the peak contrast in a given pattern. Figure 3 includes data for plaids of peak time-averaged contrasts of 37% and 44%. These two patterns were clearly different in visibility despite the small numerical difference in contrast, and yet this has no systematic effect upon the perceived direction of motion of the patterns. The data in Figure 3 also show that there is no effect of the increasing filter bandwidth upon perceived direction of Type I plaids. While this is only a moderate increase in contrast, it avoids the potential for the introduction of luminance artifacts in an 8-bit stimulus despite our careful calibration, and the factor of 2 increase represented in the figure would be expected to show any effect of visibility, which it does not. It is also pertinent to note that the stimuli of both Wilson and Kim (1994; 50% contrast carrier components, superimposed) and of Cropper et al. (1994; 50% contrast carrier components, frame-interleaved) were both presented with a higher mean contrast, and the data plotted on Figure 2 show the clear change from a vector sum to an intersection of constraints solution although the peak contrast and possibly the
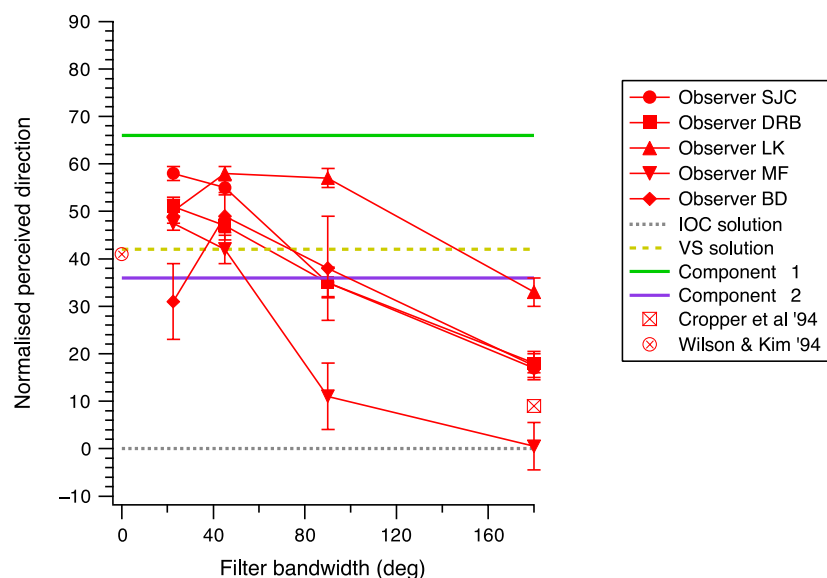

Figure 2. The perceived direction of motion of the stimuli in Figure 2 is plotted against the orientation bandwidth of the filter. Data for Type II plaids are shown for five observers. The directions of motion of each of the components, the vector sum, and IOC solutions are indicated on the graph. The results are plotted for a pattern presented for 0.5 s (half-width of envelope) at a component carrier contrast of 22%. The IOC temporal drift rate is 2.5 Hz. Each symbol is the mean of 80 observations, and error bars are $\hat{A} \pm 1$ SEM throughout. The data are consistent with both the results of Cropper et al. (1994) and Wilson and Kim (1994), as indicated on the figure.
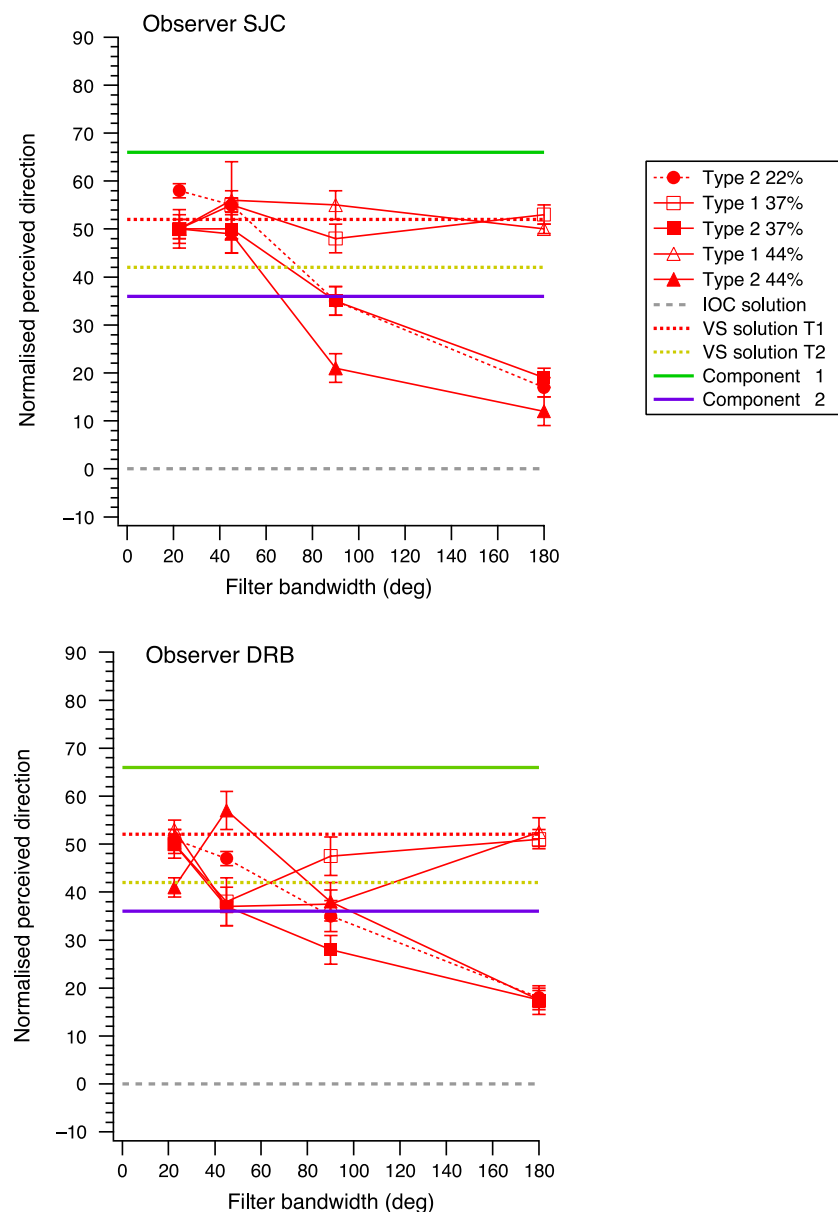
Figure 3. Perceived direction of motion plotted against bandwidth of the filter for Type I and Type II plaids for two observers. Filled symbols are Type II plaids, open symbols represent Type I plaids. The duration is 0.5 s and three peak carrier-contrasts are shown; 22% (from Figure 2), 37%, and 44%.

stimulus visibility were effectively higher in the case of Wilson and Kim's grating carrier compared to the noise carrier of Cropper et al. Wilson and Kim also confirmed their data with a 100% contrast Fourier grating and non-Fourier envelope.

While the data plotted in Figures 2 and 3 constitute the main point of the paper, it is always essential to ensure that the effects attributed to a second-order contrast modulation are not simply the result of luminance artefacts being introduced during image production, prior to any filtering by the visual system, since these would contaminate the contrast profile. To test this, we exploited the duration dependence of the motion detection in a second-order stimulus (Cropper & Derrington, 1994;

Derrington, Badcock, & Henning, 1993; Yo & Wilson, 1992) and reduced the length of time for which the pattern was visible. This manipulation impairs the ability to detect motion direction in a second-order stimulus but not in first-order stimulus. Thus, any useful luminance artefact would still be available at the reduced duration and be manifest in the results, which are presented in Figure 4. As stimulus duration decreases, the effect of the filter is reduced. This is more obvious between 0.5 and 0.25 s for observer SJC, but at the duration of 0.125 s both observers only show a change at the broadest filter bandwidth. At a stimulus duration of 0.06 s, only ambiguous motion was perceived in all of the stimuli (the data are therefore not shown).
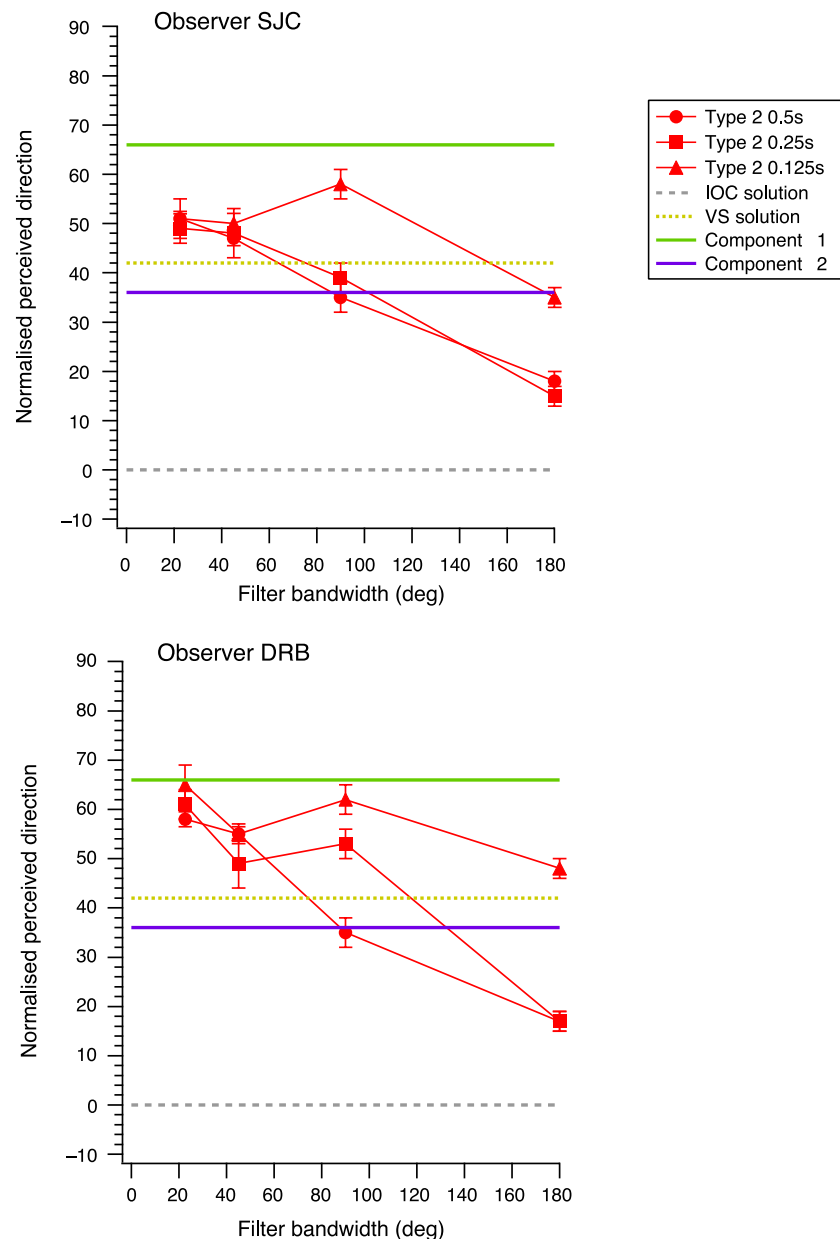
Figure 4. The effect of decreasing stimulus duration is shown for two observers for a Type II plaid. Perceived direction is plotted against filter bandwidth for observers SJC and DRB.

The subjective nature of the perceived direction of motion in Type II plaid patterns has been noted in the literature (Cropper, Mullen, & Badcock, 1996; Ferrera & Wilson, 1990). To address this issue in the context of the current result, Figure 5 presents results from a two-alternative forced-choice direction-discrimination task. Using a 2AFC paradigm will minimize any inter-observer difference by quantizing the measure while retaining its utility. The proportion of patterns judged to be moving to the right (of vertical) is plotted against the bandwidth of the filter. The observer was required to say in which of two intervals the stimulus moved to the right of vertical at the end of the presentation period. The plaids were effectively reflected in the vertical axis of the spatial window between intervals. The plaids were arranged such that the vector sum and component directions always lay on one side of vertical. The IOC solution lay on the same side of vertical as the VS for a Type I plaid (open symbols) and on the other side of vertical for a Type II plaid (filled symbols). If the observer saw the plaid move in the IOC direction, the response is indicated by a low proportion judged to be moving to the right, i.e., they were perceived to be moving left of vertical.

The data plotted in Figure 5 show that as the bandwidth of the filter increases, the proportion of Type II plaids judged to be moving in the IOC direction increases. As the stimulus duration decreases, this effect of the orientation filtering is reduced, which means that the
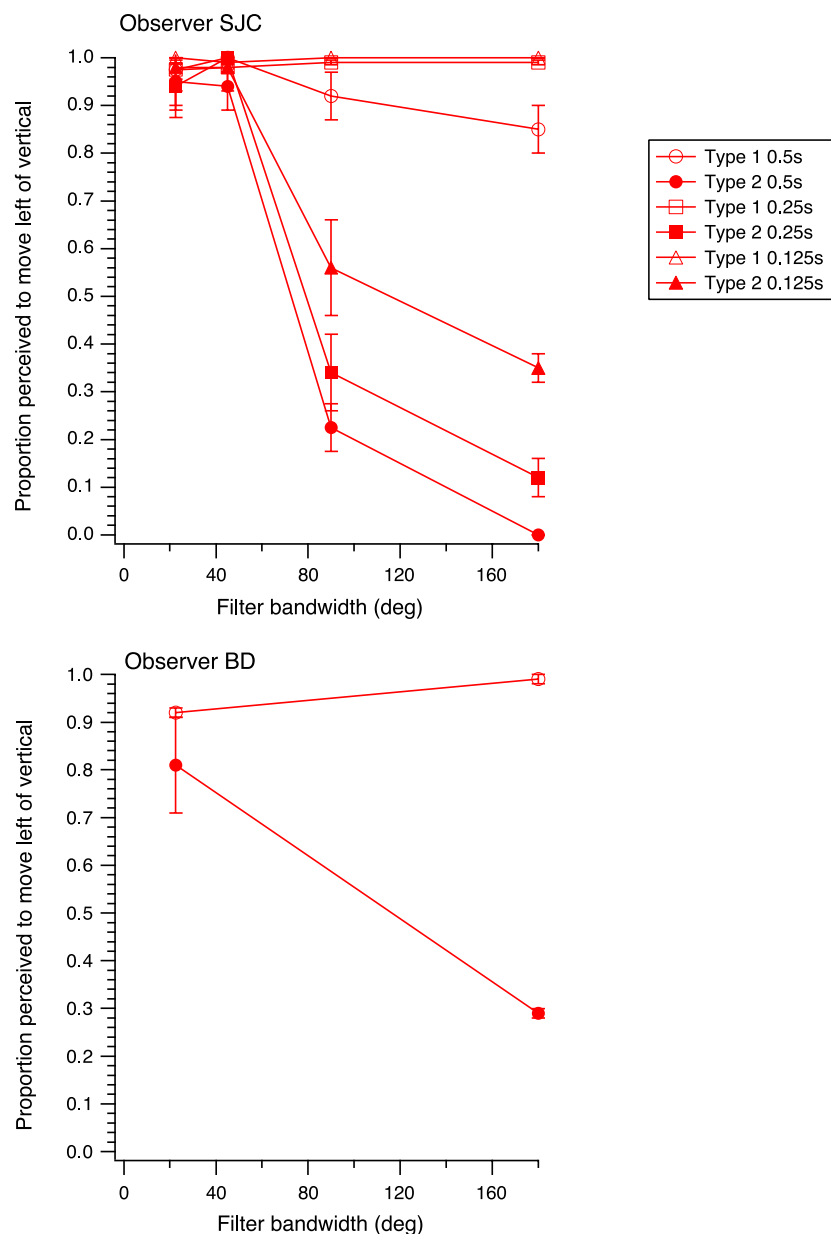
Figure 5. Figures 5a and 5b present data from a two-alternative forced-choice direction-discrimination task for two observers, SJC and BD. Observer BD was naive with regard to the experimental aims. The plaids were presented for durations of 0.5 s, 0.25 s, and 0.125 s.

difference between Type I and II plaids is also reduced (this is consistent with the data presented in Figure 4). This result is inconsistent with there being some external luminance artefact mediating the change in perceived direction caused by the alteration in the carrier-orientation bandwidth.

Discussion

The data presented in this paper sheds light not only upon the hierarchy of motion processing but also reinforces the finding that the form (orientation) and motion signals in the neural image combine to some significant degree at an early stage of processing (Badcock et al., 2003; Nishida & Johnston, 1999; Ross, 2004; Ross et al., 2000; Whitney & Cavanagh, 2000, 2003). Both of these observations place revised constraints upon models of early visual processing.

There are currently two broad classes of human motion models that each combine the first-stage filter responses in different ways. One class of models computes the spatiotemporal gradient (e.g., Johnston et al., 1992; Limb & Murphy, 1975; Marr & Ullman, 1981). The other broad class of model can be mathematically described as spatiotemporal correlation (e.g., Adelson & Bergen,

1985; Hassenstein & Reichardt, 1956; Reichardt, 1961; van Santen & Sperling, 1985; Watson & Ahumada, 1985; Wilson et al., 1992).

While the gradient-based model recovers the motion of both first- and second-order modulation as an emergent property of its self-similar hierarchical structure, the spatiotemporal correlation class of models requires that a specific additional stage or pathway be incorporated in the structure in order to code the motion of any second-order spatial modulation. In these two-stage models of motion detection, the initial linear filtering stage is followed by some non-linear process to reveal the second-order signal to a subsequent linear operation (e.g., Lu & Sperling, 1995, 2001; Wilson et al., 1992). With this type of model, which remains the most popular explanation in the literature (Derrington et al., 2004), if the carrier is visible to the initial (linear) filters, then the non-linear product of each pattern will have the same orientation and movement properties: only the magnitude of the signal may vary. Furthermore, the motion signal extracted by the linear mechanism will always be ambiguous (because their signals are dynamically randomized).

The data presented in the current paper show a clear dependence of the perceived direction of motion of a two-dimensional contrast-coded plaid pattern upon the orientation content of the luminance carrier; this result cannot be easily explained by the two-stage approach to motion detection. These results are commensurate with the idea that the motion of contrast-coded stimuli is detected in a different manner to that of luminance coded stimuli (Badcock & Derrington, 1985; Cropper, 1998; Cropper & Derrington, 1994; Cropper & Hammett, 1997) but contradict the common suggestion that the orientations present at the first-stage of filtering are essentially irrelevant to the computations conducted at the second stage of filtering.

The structure of the second-order filter arrangement, and whether it is necessary to be explicitly represented as such, has been a contentious subject within the field to date (e.g., Johnston et al., 1992; Wilson et al., 1992). The current work addresses this issue to some degree and places serious constraints upon any models proposing to explain our analysis of motion in the visual scene. We suggest that the two-stage type models need significant modifications to account for the strong orientation dependence shown by data presented here; probably too much modification to permit them to remain in the same class. It is possible, though as yet untested, that the alternative class of model, based around the calculation of successive-order spatiotemporal gradients simultaneously across orientation and scale, may provide a more parsimonious way toward explaining the orientation dependence shown in the present paper (Johnston & Clifford, 1995; Johnston, McOwan, & Benton, 1999; Johnston et al., 1992). It is the case that recent theoretical (Rust, Mante, Simoncelli, & Movshon, 2006) and experimental (Schrater, Knill, & Simoncelli, 2000) work,

concerned with the integration of noisy motion signals into an overall directional percept, implies a far less "selective" process than initially thought and modeled that is, in turn, a framework most consistent with the type of model implemented by Johnston and colleagues.

Finally, it is also worth noting that there is no *a priori* reason why both methods of motion extraction, gradient and correlation, are not implemented by the system. If this were the case, then it may explain some of the difficulty in discriminating between the two possibilities experimentally.

Conclusions

The early stages of visual processing are usually represented as parallel independent "streams" of processing contributing to the construction of the neural representation. These streams are thought to relate to the percepts of colour, depth, form, and motion, separately and independently of one another. While there is evidence supporting this modular view of the cortex, there is growing evidence that some of these "streams" of processing interact significantly with one another at all stages. The current work highlights an interaction between form and motion information that has critical implications for the extant models of motion processing in human vision.

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Footnote

[1] This requires a display with no pixel interactions along the raster (Klein, Hu, & Carney, 1996). While we took no specific steps to correct the lookup tables to account for adjacent-pixel interactions, the randomization of the absolute stimulus orientation on each presentation reduces the effect such a non-linearity will have upon the data as it is only significant along the monitor raster lines. In addition, the data for the short duration stimuli indicate there were no first-order artefacts in our stimuli.

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