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Perceived global flow direction reveals local vector weighting by luminance

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ABSTRACT

Global flow occurs when random dots, each selecting their direction of motion randomly each frame from a distribution of directions spanning up to 180°, appear to move as a whole in the mean direction of the components. This percept arises because the visual system integrates the many independent local motion signals over space and time. Through a series of direction discrimination experiments with random-dot cinematograms (RDCs), we show that varying the luminance of dots over a suprathreshold range profoundly affects perceived direction; the brightest dots appear to be weighted more and dimmer dots weighted less when determining perceived global direction. This effect is not observable if all dots in the display have the same luminance but only when the display contains dots with different luminance values. The results are consistent with energy models of motion detectors whose responses are contrast dependent. A Monte Carlo simulation of global direction discrimination employing a 12-mechanism line-element model that weighted the local motion vectors by the normalized squared contrast of the component dots (a proxy for contrast energy) captured well the features of the experimental data.

1. Introduction

The present study focuses on two properties of motion perception: the integration of local vectors into a percept of unidirectional global flow and the creation of the component local motion vectors (the correspondence problem). A display comprising intermingled elements moving in various directions produces a percept of global flow (e.g., Williams & Sekuler, 1984). This global flow, which coexists with the perception of individual elements' own random movements, tends to be in the direction of the mean of the component motions and is the result of the integration of the individual local motion vectors (e.g., Smith, Snowden, & Milne, 1994; Williams & Sekuler, 1984). Watamaniuk, Sekuler, and Williams (1989) proposed a line-element model that described the perceived direction of global as the result of non-linear summation of responses within a set of 12 direction-tuned mechanisms. Although the model did a good job of predicting the precision with which the directions of pairs of global flow stimuli could be discriminated it assumed that the set of motion vectors processed by the visual system mirrored the actual directional statistics of the display, remaining mute on how the visual system might extract those vectors from a noisy and relatively dense display.

A complimentary line of research has studied the process of vector extraction, the correspondence process (e.g., Anstis, 1980; Braddick, 1974; Dawson, 1991; Eagle, Hogervorst, & Blake, 1999; Hibbard, Bradshaw, & Eagle, 2000; Hildreth, 1988; Kolers, 1972; Schuling, Altena, & Mastebroek, 1990; Ullman, 1979). To understand the correspondence process, many researchers have explored how various element characteristics influence the matches from frame-to-frame of an apparent motion stimulus. Features such as color (e.g., Gorea & Papathomas, 1989; Gorea, Papathomas, & Kovacs, 1993; Green, 1989; Papathomas, Gorea, & Julesz, 1991), shape (e.g., Eagle et al., 1999; Mack, Klein, Hill, & Palumbo, 1989; Shechter, Hochstein, & Hillman, 1988), size (e.g., Burt & Sperling, 1981; Eagle et al., 1999; Mack et al., 1989; Shechter & Hochstein, 1989), orientation (e.g., Burt & Sperling, 1981; Gorea & Papathomas, 1989; Green, 1986; Mack et al., 1989), spatial frequency (e.g., Green, 1986; Nishida, Ohtani, & Ejima, 1992), phase (e.g., Sekuler & Bennett, 1996), and luminance (e.g., Burt & Sperling, 1981; Green, 1989; Nishida & Takeuchi, 1990; Shechter & Hochstein, 1989) have been the main variables of investigation. Virtually all of these studies have used ambiguous motion stimuli in which motion in at least two directions could be perceived. These displays were created with the elements arranged such that motions based on correspondence matching of different features were put into competition. After each trial, observers would often be asked to judge which motion they perceived (e.g., Shechter et al., 1988) or to judge the strength of motion along a particular motion path (e.g., Burt & Sperling, 1981). A disadvantage of these methods lies in the subjective nature of the motion-strength estimate and/or forcing observers to choose which single motion they perceived when they might have perceived many (e.g., Burt & Sperling,

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1981). As such, these methods are limited and cannot be used directly to estimate the weights that motion mechanisms put on particular stimulus features.

The present study examined both the correspondence and integration stages of global flow at once by means of common procedures within the same framework. Our empirical approach to the rules for matching and integration are analogous to some tracer methods in neuroanatomy. We labeled certain elements in the display and observed how those labeled elements were treated. By varying the algorithm used to label elements, we have been able to examine matching and integration independently of one another. In our experiments, the label was luminance level. Our stimuli were random-dot cinematograms in which each element's movements, varying from one frame to the next, follow the directions drawn from a uniform distribution. On any trial the observer saw a pair of random-dot cinematograms whose mean component directions differ from one another. The threshold for discriminating the two resulting directions of global flow provided an estimate of the precision with which the visual system computes the mean of each distribution.

2. Method

2.1. Observers

Data for all experiments were collected from two of the authors (SW & RS). Both observers had normal or corrected to normal visual acuity. All observers were treated accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans.

2.2. Stimuli

Stimuli were random-dot cinematograms (RDCs) composed of 256 dynamic random dots generated by a computer. The dots were plotted on an *X*–*Y* display (Tektronix 604 monitor with P-4 phosphor), at a rate of 50 frames per second. For all experiments, dots took two-dimensional random walks of constant step size (0.24°). With this step size and the geometry of addressable points on the display, the mean direction of the stimulus could be changed in 1° increments. The two-dimensional random walks were created in the following way. For every frame anew, each dot's movement was chosen from a predefined uniform distribution of directions spanning 90° stored as an array of increment values. The increment array held 256 pairs of values, each consisting of an *x*-axis increment and a *y*-axis increment. From this array, the computer chose randomly, without replacement, increment values for the dots' movements.

After 256 *x*- and *y*-samples had been drawn, the chosen increments were added to the dots' current positions and the dots' new *x*- and *y*-positions were transmitted to the cathode ray tube (CRT) display via high-speed digital-to-analog converters. The initial screen location of each dot was randomly determined at the beginning of each sequence of frames. This constantly shifting spatial array made it impossible for an observer to base a direction judgment on information about the spatial pattern of dots.

For all conditions, stimulus duration was held constant at 500 ms (25 frames) and observers viewed the display binocularly from a distance of 57 cm with their head steadied by a chin cup. The height of the CRT placed the center of the display at approximately eye level. A 9° diameter circular mask covered the 10° by 10° screen to remove potential orientation cues provided by the edges of the screen. Dots subtended 4.2 min arc and had a space-averaged luminance between 62.7 and 101.9 cd/m^2 while the veiling luminance of the screen was 44.3 cd/m^2 (space-averaged luminance was measured with a Minolta handheld photometer using a matrix of dots with a center-to-center spacing of 4.8 min arc and a frame rate of 50 Hz).

The parameter varied throughout all experiments was the manner in which luminance values were assigned to the stimulus dots. Prior to conducting any direction discrimination experiments, the three dot luminances to be used in the experiments were determined for each observer. These dot luminances were determined in two steps. First the observers viewed pairs of random-dot displays, with the same characteristics as used in the main experiments. One display had dots of a single luminance while in the other, chosen randomly, one-half of the dots had a luminance of 62.7 cd/m^2 and the other dots had a higher luminance. Using a two-alternative forced-choice staircase procedure, observers decided which interval contained two luminance values. Eight successive correct responses resulted in a reduction in the luminance of the higher luminance dots, while one incorrect response resulted in an increase in the luminance of the higher luminance dots. This staircase continued until five reversals were recorded, the average of the last three reversal values were used to determine the second luminance value. Second, this staircase procedure was repeated but with the luminance value determined from the first run used for one-half of the dots and an even higher luminance value assigned to the other dots. Again, observers decided which interval contained two dot luminance values until 5 reversals were recorded. The average of the last three reversal values from this run were used to determine the third luminance value. Thus, three luminance values, each perceptually discriminable from the next at the 92% ($d' = 2.0$) level (Wetherill & Levitt, 1965), were determined for each observer. The following are the luminance values for each observer: RS: 62.7, 76.7, and 101.92 cd/m^2, SW: 62.7, 74.2, and 87.9 cd/m^2. Since background luminance was constant throughout all experiments, these luminance values correspond to Michelson contrasts of 17.0%, 26.8%, and 39.4% (RS), and 17.0%, 25.2%, and 33.0% (SW). Although the physical luminance values differ between the two observers, in terms of discriminability, they are perceptually equivalent. These luminance values were used for the two observers in all experiments.

Once the luminance values had been determined, various algorithms were used to create different stimulus conditions. In some conditions, all dots were the same luminance as illustrated in Fig. 1A and B (conditions $L1_{hi}$ & $L1_{lo}$). In other conditions, different schemes were used to distribute the three luminance values among the dots. In one condition, the three luminances were distributed randomly among the dots (condition L3-R) as shown in Fig. 1C. Finally, in some conditions the underlying direction distribution was divided into three contiguous ranges, each spanning 30°, and one of the three luminance values was assigned to each range (e.g., condition L3-D) as seen in Fig. 1D. In these conditions, whenever a dot moved in a particular direction in a given frame, it was assigned the luminance value associated with that direction (see Fig. 2).

2.3. Procedure

All experiments used a two-alternative forced-choice staircase procedure. Each trial consisted of two 500 ms stimulus presentations separated by an inter-stimulus interval of approximately 200 ms. The distribution of increments sampled in order to create one stimulus, the standard, had a mean direction of 90° (upwards). On average, this stimulus would be expected to generate global motion in an upward direction. The distribution of increments sampled to create the other stimulus, the comparison, had a mean direction slightly greater than 90°. On average, this stimulus would produce global motion somewhat counterclockwise from upward.

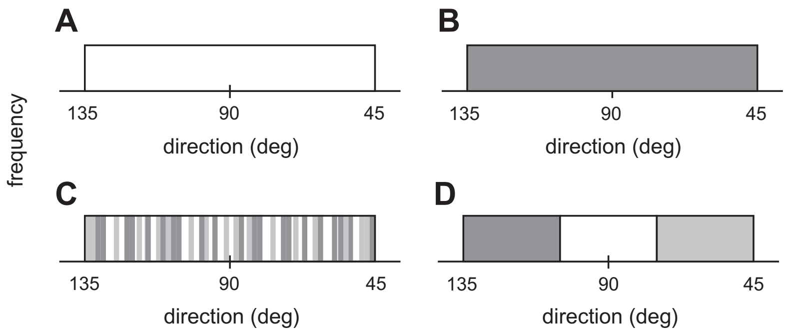

Fig. 1. Schematic representations of various types of stimuli: (A) all directions assigned a single high luminance ($L1_{hi}$), (B) all directions assigned a single low luminance ($L1_{lo}$), (C) three luminance values randomly assigned to directions (L3-R), and (D) three luminance values assigned to contiguous ranges of directions spanning 30° each (L3-D). Shading represents the three levels of dot luminance. All stimuli were random-dot cinematograms with direction distributions spanning 90°.

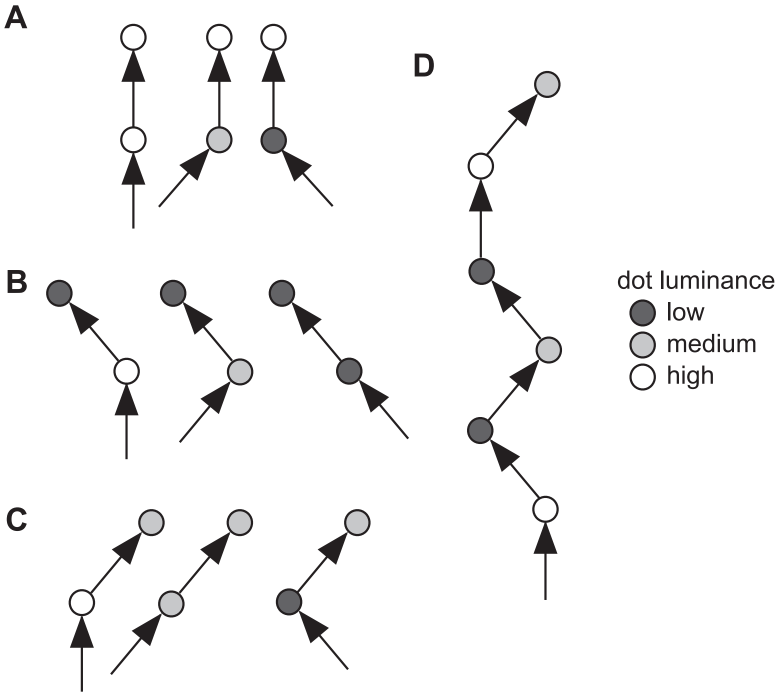

Fig. 2. Schematic representations of the possible ways dot luminance could change when luminance was assigned by direction ranges as in Fig. 1D. Regardless of the dot's previous luminance, when the dot moves in a direction in the central range, dot luminance in that frame is high (panel A); when the dot moves in a direction counterclockwise from the center, dot luminance in that frame is low (panel B); when the dot moves in a direction clockwise from the center, dot luminance in that frame is medium (panel C). Panel D shows an example of a 6-frame dot movement pattern in which dot luminance was assigned according to direction. Unlike the other panels, D shows the luminance state for only a single dot.

On half the trials, randomly chosen, the standard stimulus occupied the first interval. The observer had to determine if the global motion of the second stimulus was to the left (counterclockwise) or right (clockwise) relative to the global motion of the first stimulus.

Each staircase began with a comparison stimulus whose mean was 20° counterclockwise from upward. This large difference between standard and comparison stimuli was generally easy to distinguish under all stimulus conditions. Four successive correct responses were required to decrease the difference between the mean directions while one incorrect response increased the difference. The difference between the mean directions was decreased by 3° for each set of four correct responses until the observer made one error. Thereafter the difference between the mean directions changed by only 1.0°. This procedure continued until 10 reversals were recorded. This decision rule tracked the 84% point on the psychometric function (Wetherill & Levitt, 1965). Only the last six of the ten reversals were used as data for subsequent analysis.

A tone signaled the computer's readiness for the next trial, and the observer initiated the trial by means of a button press. After the trial's two stimuli had been presented, the observer responded by pushing one of two buttons, left or right, corresponding to the perceived direction of the second stimulus relative to the first. An interval of about 4 s separated trials. Observers completed at least two staircases for each experimental condition.

3. Results

3.1. Single- and multi-luminance stimuli

The first experiment measured direction discrimination for three types of RDCs. One type presented all dots at the same luminance. This is typically the way previous RDC stimuli have been constructed (e.g., Bennett, Sekuler, & Sekuler, 2007; Smith et al., 1994; Snowden & Braddick, 1991; van Doorn & Koenderink, 1982a, 1982b; Watamaniuk & Sekuler, 1992; Watamaniuk et al., 1989; Williams & Sekuler, 1984). Discrimination thresholds were measured for two different luminance values for each observer, the high (L1$_{\mathrm{hi}}$) and low (L1$_{\mathrm{lo}}$) levels, and served as baseline data. The other two types of RDCs each contained all three luminance values and were designed to determine if luminance was a characteristic that determined how the visual system 'matched' dots from one frame to another. The initial hypothesis was that the visual system would ignore dot luminance when evaluating local motion vectors and that these vectors would then be integrated to yield a percept of global flow. This hypothesis implies that so long as the programmed motion statistics of the display that are input to the matching process are constant, then the outcome should be independent of how luminance is distributed. We tested this hypothesis by comparing direction discrimination thresholds for two types of displays, one in which the three luminance values were randomly assigned to directions (L3-R) and one in which luminance was assigned according to directions (L3-D—see Fig. 2). For both types of stimuli, the assignment of luminance was different for each interval within a trial. Recall that the luminance values used for each observer were those determined earlier and that the two extreme luminance values were discriminable from one another at the $d' = 4$ level.

Fig. 3 shows the direction discrimination thresholds and standard errors for the two observers for the four stimulus conditions. It is clear that while the thresholds for the single-luminance conditions, L1$_{\mathrm{hi}}$ and L1$_{\mathrm{lo}}$, and one in which the luminance values were randomly assigned to directions (L3-R) were similar, performance was much poorer when luminance values were assigned to a particular range of the direction distribution (L3-D) which changed between stimuli within a trial.

3.2. Is matching luminance-dependent?

The previous experiment shows that although dot luminance per se does not affect the precision of global flow direction judgments, the way that luminances are assigned to directions does. The essential difference between the random assignment of luminance used for condition L3-R and the direction-dependent assignment used for L3-D is the overall range of directions associated with a given luminance. Perhaps in L3-D the observer attended to only one luminance, e.g., the bright dots, and ignored the other two luminance values.

If true, the direction-dependent assignment (L3-D) would force the observer to make a judgment about global flow based on one of the small ranges of directions, e.g. that identified by the brightest dots, which randomly varied from one test interval to the other. It is obvious that this random fluctuation between intervals would degrade the precision of the judgment. However, if the observer used the same strategy – attend only to the brightest dots – for the random assignment stimulus (L3-R), why are their L3-R judgments as precise as judgments based on a single luminance (L1$_{\mathrm{hi}}$)? Attending to only the bright dots would reduce the sample size to about 1/3 of the sample for a single luminance. Moreover, the mismatches of bright dots to bright dots should increase the range of directions relative to the programmed range. Both effects (smaller sample size and larger directional range) have been shown to degrade the precision of direction judgments (Watamaniuk et al., 1989).

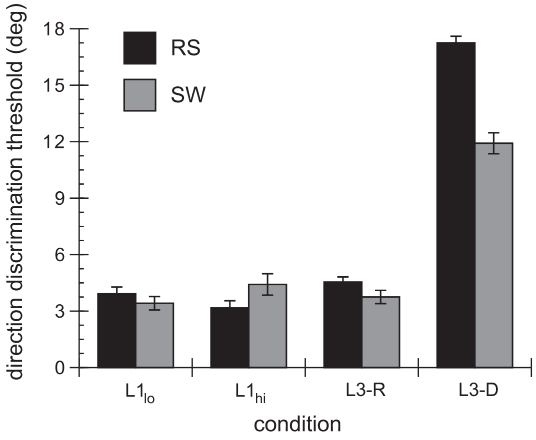

Fig. 3. Direction discrimination thresholds for two observers for four stimulus conditions. Error bars represent one standard error of the mean computed for each condition across the reversal values from all staircases.

To test the idea that observers might selectively attend to dots of one luminance, we measured direction discrimination for stimuli constructed in the same manner as those in condition L3-R, but we only illuminated the dots when they were assigned the highest luminance (condition L3-R$_{\mathrm{hi}}$); when the dots were to be assigned one of the other two luminance values, the dots were not illuminated and were therefore invisible.

The leftmost two bars in Fig. 4 show data for two observers for the new condition, L3-R$_{\mathrm{hi}}$, along with that for L3-R replotted from Fig. 3. Notice that thresholds for L3-R$_{\mathrm{hi}}$ are much higher than for L3-R. This suggests that each set of within-luminance matches does not provide a representative sample of the underlying directional distribution and that performance in condition L3-R must be due to the motion system making matches between elements that differ in luminance. This is consistent with Adelson and Bergen's (1985) motion energy detector model in which motion detectors do not make correspondence matches per se but simply compute motion signals based upon whatever luminous elements fall within their receptive fields. However, this still leaves the question as to why performance in conditions L3-R and L3-D were not equivalent (see Fig. 3).

3.3. Assigning luminance by direction

To gain insight into why performance in the L3-D condition was so poor, we considered how motion detector cells in the brain

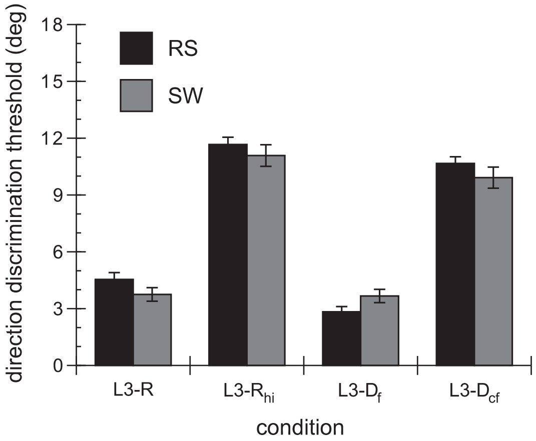

Fig. 4. Direction discrimination thresholds for two observers for stimuli in which luminance was assigned (a) randomly to dots each frame but only those assigned the highest luminance value were plotted (L3-R$_{\mathrm{hi}}$), (b) to consecutive direction ranges of the underlying distribution of directions (L3-D$_{\mathrm{f}}$) that remained fixed within a trial, (c) to consecutive direction ranges of the underlying distribution of directions but the assignment of the flanking direction ranges was different for the two stimuli within a trial while the central range was always assigned the highest luminance (L3-D$_{\mathrm{cf}}$). For comparison, data from condition L3-R has also been plotted. Error bars represent one standard error of the mean computed for each condition across the reversal values from all staircases.

would be affected by the stimuli. Recall that for condition L3-D, we randomized the assignment of luminance to each of the three direction ranges within a trial. Because the responses of motion energy detectors are contrast dependent (Adelson & Bergen, 1985) and since the background of our display was constant, increasing dot luminance was equivalent to increasing contrast. It is likely that matches are made across contrast but that the directional information from each match is weighted by the contrast of the participating (i.e., matched) elements. If this were the case, then one would expect that a motion vector produced by two bright dots would result in a stronger motion energy signal than a motion vector produced by two dim dots. It is then reasonable to propose that these weighted vectors would be used to compute the direction of global flow. As such, division of the stimulus' directional range into luminances as Medium, Low and High (from counterclockwise to clockwise) would yield a different weighted direction of global flow than would the assignment of the same luminances but in a different order (e.g., High, Low and Medium). Thus, in the first experiment, variation in the assignment of luminances to direction ranges within a trial could have caused the perceived direction to vary independently of the shift of the underlying directional distribution as seen in Fig. 5.

If this reasoning holds, then one would expect that if luminance was assigned according to direction but the assignment remained fixed across both intervals within a trial (L3-D$_f$), direction discrimination performance should be similar to that for condition L3-R (random assignment of luminance). Fig. 4 shows thresholds for the two observers for this new condition and the data compare well to that of the L3-R condition.

The results for condition L3-D$_f$ are consistent with a model in which directional information, formed by dots displaced from frame-to-frame, is weighted by the luminance of the participating (i.e., matched) elements. However, there is another possible scenario that could have produced these results. Suppose that local motion vectors are segregated or labeled according to luminance, and then computations (like mean direction and speed) are done on each set separately and NOT combined with the information from other vector groups. This type of grouping rule could have predicted the observation that discrimination in condition L3-D$_f$ would be the same as that from condition L3-R. Specifically, if an observer were 'tracking' the highest-luminance vector group, then when luminance was distributed randomly among the dots (L3-R), the average direction should have been similar to the actual mean direction, resulting in good performance. However, if an observer used the same strategy when luminance was distributed according to direction and the assignment changed within a trial, the mean direction of the highest-luminance vector group would have changed independent of the shift in the direction distribution of the stimulus, leading to poor discrimination performance and high thresholds.

We designed a new stimulus to discriminate between the segregation-by-luminance and the weighting-by-luminance hypotheses; luminance was assigned according to direction as in the L3-D condition but only the outer direction wedges changed within a trial and the central direction wedge was always assigned the highest luminance value (condition L3-D$_{cf}$, see Fig. 5B). For this experiment, observers were instructed to judge the direction of just the brightest dots. For this stimulus, one can make the following predictions. If the motion signal is weighted by luminance then one would expect that direction discrimination performance for condition L3-D$_{cf}$ should be poorer that of condition L3-D$_f$ because the changing of the luminance of the flanking directions would influence the global mean direction independent of the actual stimulus direction shift. Alternatively, if vectors are segregated by luminance and observers make judgments based on only the highest-luminance set then performance in conditions L3-D$_{cf}$ and L3-D$_f$ should be similar because the mean direction of the central wedge of directions (highest luminance) shifts an identical amount as the global mean direction.

As can be seen in the data in Fig. 4, performance in condition L3-D$_{cf}$ was much poorer that in condition L3-D$_f$. Thus, it is unlikely that motion signals are segregated by luminance and that observers make judgments based on one set of dots defined by a particular luminance value. Thus the data support the hypothesis that motion signals are combined and weighted by their luminance.

4. Simulations

To determine whether weighting direction signals by luminance could account for the data, we performed a Monte Carlo simulation of the direction discrimination task. The discriminability of the direction of two global flow stimuli was computed using a line-element model. The model was similar to one that has been used to successfully account for other global discrimination tasks (Bennett et al., 2007; Watamaniuk et al., 1989; Williams, Tweten, & Sekuler, 1991). The basic model comprises 12 equally spaced direction-selective mechanisms that span the entire range of 2D directions. Each mechanism has the same Gaussian profile with a half-amplitude half-bandwidth of 30° (see Watamaniuk et al., 1989, Eq. (2)). In Watamaniuk et al. (1989), a mechanism's response to a random-dot stimulus was given first by multiplying the mechanism's

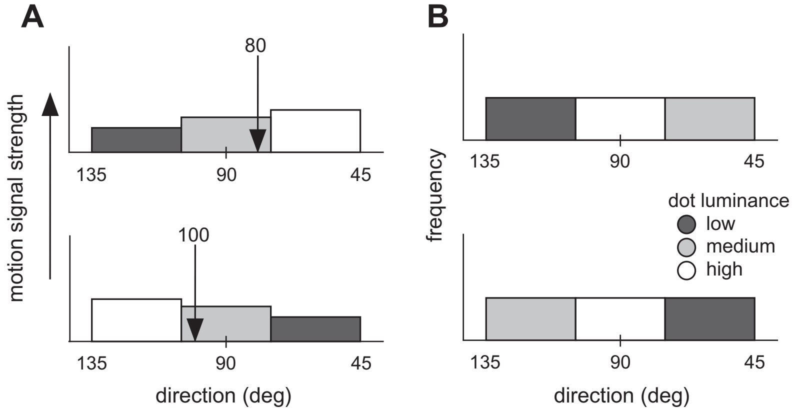

Fig. 5. Schematic representations of stimuli in which the luminance assignment (contiguous 30° spans) is varied. (A) If one assumes that the strength of the motion signal varies with luminance (contrast), then alternating luminance assignment may result in a large shift in the perceived direction of the global flow (indicated by the arrows). (B) Representation of stimuli used within a trial of condition L3-D$_{cf}$.

sensitivity to a component local direction by the proportion of dots that moved in that direction, and then summing over all directions present in a stimulus (see Watamaniuk et al., 1989, Eq. (3)). This computation explicitly assumes that within a mechanism, local direction vectors are weighted only by a mechanism's sensitivity, which is reasonable when all dots are presented at the same luminance. However, in the present study, component dots were assigned any one of three luminance values within any one frame. To capture the effect of dot luminance, each local direction vector (defined by a dot's movement over two contiguous frames) was weighted by the sum of the two dots' Michelson contrasts (ω_l), which were squared as a proxy for motion energy

$$wt_{ij} = \left(\omega^2_{l_{i-1,j}} + \omega^2_{l_{i,j}}\right) \qquad (1)$$

The contrast values used in the model were different for the two observers since dot luminance values for the two observers were different (see Section 2.2). The summed response of every mechanism was normalized to the average of all vector weights appearing within the stimulus (response normalization is common in models of motion processing and, for example, appears in several stages in the MT model of Simoncelli and Heeger (1998)). This computation was performed for all 256 dots of every frame, starting at frame 2 for a stimulus lasting 25 frames, the same duration as our experimental trials. The response of the *m*th mechanism to a stimulus with a distribution of directions (D) comprising multiple luminance values is given by

$$R_m(D) = \sum_{i=2}^{25} \frac{\sum_{j=1}^{n} S_m(\theta_j)\, wt_{ij}(n^{-1})}{\overline{wt}}, \qquad (2)$$

where $S_m(\theta)$ is the *m*th mechanism's sensitivity to direction θ, n is the number of dots, and $\overline{wt}$ is the average vector contrast weight in the stimulus. Since the step size of dot displacements was constant across all dots and directions, there was no need to include a speed parameter. As in Watamaniuk et al. (1989) and Williams et al. (1991), the discriminability of two stimuli was computed by taking the difference between a mechanism's response to the two stimuli and pooling those differences across all 12 mechanisms using a Qth norm rule (Quick, 1974; see Watamaniuk et al., 1989, Eqs. (4) and (5)) with $Q = 2$. As tested, the model has no free parameters; weights corresponded to the contrasts used in the experiments and all other parameters were set equal to those used by Watamaniuk et al. (1989) as they provided good fits to direction discrimination data for distributions of directions of similar widths and duration.

For each trial of the direction discrimination Monte Carlo simulation, the model's response was computed for both a standard stimulus with a mean direction of 90° and a comparison stimulus with a mean direction greater than 90°. The Monte Carlo experiment used a staircase procedure, similar to that in the experiment, with the initial value of the comparison being 20° counterclockwise of the standard. Since we did not have psychometric functions for the observers, but rather just their discrimination thresholds for the various conditions, we developed a discrimination decision criterion for the model. To this end, we ran the model for the L3-R condition (3 luminance values randomly assigned to dots each frame) for direction differences ranging from 1° to 20°. Ten trials for each direction difference were run and then the average model output for each direction difference was computed. We used interpolation to determine the model output that corresponded to each observer's direction discrimination threshold for the L3-R condition. This then was used as the criterion value against which the model's output was compared for its response decision during the staircase runs. Thus in each trial, if the model's response was greater than the criterion, a correct discrimination was registered; if the model's response was less than the criterion, a random response was rendered which produced an incorrect discrimination half of the time and a correct discrimination half of the time. While this decision heuristic, in the strictest sense, does not accurately represent human performance, it was the best approximation attainable without psychometric functions to constrain model responses. The model runs followed the 4-down 1-up staircase rule as used in the experimental trials, including decreasing the direction difference between the standard and comparison stimuli by 3° for every four correct trials until one error was made after which the difference changed in 1° steps. Ten Monte Carlo staircases were run for each observer for each of the stimulus conditions.

Fig. 6 shows the results of the Monte Carlo study for the two observers along with their experimental data replotted from Figs. 3 and 4 for comparison. There are several points to notice about the simulated data. First, notice that assigning luminances to directions randomly (L3-R) or assigning them to three contiguous direction ranges but keeping the assignments fixed for both intervals within a trial (L3-D$_\text{f}$) had no effect on discrimination thresholds as also evidenced in the experimental data. Second, conditions that were difficult for the human observers also garnered the highest thresholds for the Monte Carlo simulation. Condition L3-D$_\text{cf}$ produced thresholds about 2.5 times larger than the single luminance thresholds (L1$_\text{hi}$ & L1$_\text{lo}$) and condition L3-D produced even higher thresholds along with greater variability, similar to the experimental data. Third, the pattern of simulated thresholds is similar across all conditions to that observed experimentally suggesting that the 12-mechanism line-element model, with mechanism responses

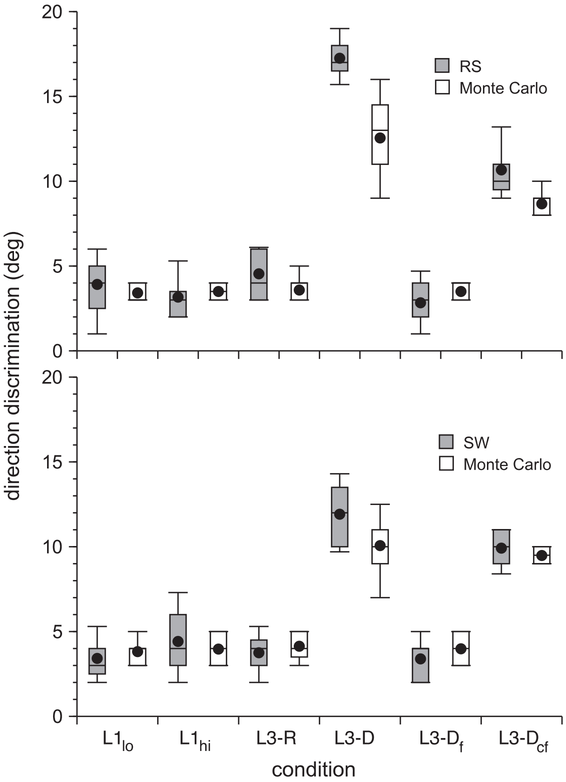

Fig. 6. Direction discrimination thresholds for a Monte Carlo simulation of direction discrimination using a 12-mechanisms line-element model in which responses to motion directions were weighted by their contrast energy normalized to the sum of dot contrasts within the stimulus. Observer data are shown for comparison. The data (all reversal points used to calculate thresholds) are presented as box and whisker plots. The boxes are defined by the 1st and 3rd quartile, with the median indicated by a horizontal line and the mean by the filled circle. The whiskers extend from the 10th to the 90th percentile.

weighted by normalized contrast, captures the important features of the human global motion processing system.

5. Discussion

Our main findings show that luminance plays a very different role in both the correspondence and integration stages that give rise to global flow. At the correspondence stage, when dots move with random walks, varying their direction and luminance each frame, matches are made across luminance, maintaining the directional integrity of the underlying direction distribution. At the integration stage, the directional signal or vector, produced by the matching of elements from one frame to another, are weighted by the luminance of the elements participating in the match. These weighted values are used in computing the direction of global flow.

Previous research measuring coherence thresholds (e.g., Newsome & Paré, 1988; Williams & Sekuler, 1984) have shown that motion matches can be made between elements of different luminance. Edwards and Badcock (1994) reported that motion coherence thresholds were not sensitive to changes in signal dot luminance during the trial – thresholds were the same for constant-luminance signal dots and for signal dots that changed mid-trial from bright to dim (see their Experiment 5). Subsequently, Edwards, Badcock, and Nishida (1996) demonstrated that motion coherence thresholds improved as the contrast of the dots uniformly increased, saturating at a contrast of about 15%. However, when displays contained dots of differing contrasts, the strength of motion signals increased for dot contrasts up to 80% – noise dots with higher contrast than the signal dots were more effective at masking the coherent motion and coherence thresholds increased. The present results mirror these in the context of a direction discrimination paradigm.

Similar observations of the effects of luminance/contrast on the perceived direction of movement in ambiguous motion displays have also been previously reported. Anstis and Mather (1985) created a stimulus composed of two bars, one black and one white, that were located one slightly above the other. They found that when they simultaneously switched the color of the bars, the perceived motion depended upon the color of the background; on a light-gray background the black bar appeared to move while on a dark-gray background the white bar appeared to move. Hence, the high-contrast bar determined the perceived direction of movement. Similarly, using a split-motion stimulus in which a single central bar in frame 1 was replaced by two flanking bars in frame 2, Nishida and Takeuchi (1990) found that motion to one flanking bar was stronger if it had a higher luminance than the other flanking bar. Anstis and Ito (2002) found that the motion of high-contrast dots was weighted more heavily than low-contrast dots in determining the perceived direction of a stimulus in which two small dots, of different contrasts, jumped back and forth along orthogonal crossing paths. Similarly, for unambiguous motion, Morgan and Chubb (1999) showed that the threshold contrast for identifying the direction of a 90° phase shift (2 cpd grating) in a 2-frame display depended upon the contrast of the grating in each frame. The baseline contrast was that needed to produce 62% correct direction identification when both frames were presented at the same contrast. When the two frames were presented at different contrasts, the same level of performance could be obtained for a below-baseline contrast first frame followed by an above-baseline contrast second frame. These and the present data are consistent with contrast-dependent motion detectors processing local motion signals (e.g., Adelson & Bergen, 1985; Pantle & Hicks, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). Similar to these effects found with motion, Petrov (2004) found that stereo-matches are affected by contrast. Specifically, the human visual system preferred to match the image in one eye to a higher-contrast image in the other eye even when an equal-contrast match was available. This behavior goes against the commonly assumed strategy of stereo-matches being based on similarity (e.g., Marr & Poggio, 1979) and suggests that the visual system may be maximizing the contrast signal that results from a stereo-match.

As noted in the Introduction, past studies on the effects of stimulus characteristics on correspondence matching used more subjective research methods and did not provide data to directly estimate the weights that motion mechanisms put on particular stimulus features (e.g., Burt & Sperling, 1981; Nishida & Takeuchi, 1990; Papathomas et al., 1991; Shechter & Hochstein, 1989). The present study is unique because it did not constrain the local correspondences available in the stimulus or observer responses. Since global flow is the result of the integration of local motion vectors over time and space (e.g., Smith et al., 1994), the perceived direction reflects all of the directions in the stimulus and the strength associated with each signal. Thus one can assume that when dot luminance is uniform, the strength associated with each motion signal is equal, and the direction of global flow corresponds to the mean direction of the underlying direction distribution (e.g., Watamaniuk et al., 1989; Williams & Sekuler, 1984). However, when dots with different luminance values are presented within the same stimulus, the strength of each motion signal will be modulated by the luminance of the component dots. The present data show that in such multi-luminance stimuli, motion signals are not equal but weighted according to the luminance values of the dots creating each vector, with the vectors comprising the highest luminance given the largest weight (see also Edwards et al., 1996). This stimulus can therefore be used to directly measure the relative strength associated with given luminance levels. One way that this could be done is to measure perceived direction of global flow for a stimulus that contains dots of all one luminance being assigned directions from a given direction distribution. One could then assign a proportion of dots moving at an extreme direction a brighter luminance or higher contrast and measure how the perceived direction of global flow changes. Alternatively, one could use a nulling technique in which the shift in perceived direction produced by adding a given number of dots moving in one direction is compensated by increasing the luminance of dots moving in a complimentary direction. In this way one can equate luminance with number of motion vectors of a standard luminance.

6. Conclusion

Energy models of motion detectors are contrast dependent and thus they produce a larger response when high-contrast rather than low-contrast objects move through their receptive field. A previous study showed that direction discrimination of sine wave gratings asymptotes at a relatively low contrast (Nakayama & Silverman, 1985) and the present results confirmed that increasing dot luminance from 62.7 to 101.92 cd/m^2 (contrast: 17–39.4%) did not improve global flow direction discrimination. However, the present data also show that motion signals do reflect differential weighting as a function of luminance when a single stimulus contains motion created by elements at different luminance levels. These results confirm that motion detector responses do not saturate at low contrasts and that energy models capture important features of the human motion processing system. A Monte Carlo simulation utilizing a 12-mechanisms line-element model that weighted local motion direction by the normalized square of dot contrast captured the critical features of our experimental data. The multi-luminance random-dot stimulus introduced here shows high promise for allowing the assessment of the relative contribution of luminance to motion perception.

Commercial relationships

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