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Speed and direction of locally-paired dot patterns

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Abstract

Phenomenal transparency in random-dot kinematograms is abolished when two motion directions are 'locally-balanced' by pairing limited-lifetime dots at each location [Qian, Andersen and Adelson (1994). *Journal of Neuroscience*, *14*, 7357–7366]. Qian et al. also report that locally-paired stimuli appear as directionless flicker when the paired dots differ in their directions by 90° or more. They attribute this to local inhibition between motion detectors more than 45° apart. We investigated perceived motion in such displays, by requiring subjects to make direction and speed judgements with locally-paired stimuli containing two directions 60, 90 or 120° apart. Subjects perceived coherent motion in these displays and made reliable direction judgements, indicating that the two motions are combined rather than interfering destructively. Our results show that the judged motion of locally-paired stimuli is in the vector-average direction of the two components. This vector-averaging rule also applies when the two sets of component dots differ in their velocity. Similarly, speed judgements comply with a vector-averaging rule for a range of speeds as well as for mixed-speed stimuli. These results suggest that the abolition of transparency does not necessarily imply abolition of a global motion percept. The local interaction abolishing transparency is not exclusively inhibitory, at least for directions up to 120° apart, but generates a vector combination of the superimposed motions.

Keywords: Motion perception; Transparency; Random dot kinematogram; Locally-balanced stimuli

1. Introduction

In recent years there has been increasing attention to the perception of motion transparency, the phenomenon by which two or more distinct motions are perceived simultaneously in the same spatial location. Much of this research has used random dot stimuli, in which two or more populations of dots, with different velocity distributions, are superimposed (e.g. Clarke, 1977; van Doorn & Koenderink, 1982a; Snowden, Treue, Erickson & Andersen, 1991; Mulligan, 1992; de Bruyn & Orban, 1993; Qian, Andersen & Adelson, 1994; Verstraten, Fredericksen & van de Grind, 1994; Braddick, 1997; Wishart & Braddick, 1997a; Smith & Curran, 1998; Smith, Curran & Braddick, 1999).

The visual system's ability to represent simultaneously two transparent motions raises the question: at what scale does this multi-valued representation of velocity occur? Is the visual system capable of representing two motion surfaces at the finest grain for which it analyses motion or, alternatively, is transparency represented only at a coarser, large scale level of processing? This question was addressed by Qian et al. (1994), who found that phenomenal transparency was abolished when two motion directions are 'locally-balanced' by pairing limited-lifetime dots moving in opposite directions at each location. Qian et al. reported that transparency was absent in stimuli where the dots moved over superimposed opposite trajectories of up to 0.4°. Within this range they proposed that transparency is abolished by the opponent interactions of local motion detectors tuned to opposed directions. They reported that phenomenal transparency could be re-established for dot trajectories within this range, provided that the dots were offset by as little as 0.2° in a direction orthogonal to their motion. They also found that transparency was also abolished for locally-paired motions in directions 90° apart. These results, based on subjective reports of transparency, were qualitatively confirmed by Wishart and Braddick (1997b; Braddick, 1997) using their performance-based measure of transparency with locally paired motions. This more rigorous criterion, however, defined a rather smaller region

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of interaction. Wishart and Braddick found that judgements using two directions jointly could be performed with locally-paired stimuli, provided that dot trajectories were 0.25° or longer. For shorter trajectories a minimal orthogonal offset of 0.4° was required to re-establish a measurable transparency effect. Together, the results of Qian et al. and Wishart and Braddick imply that the co-representation of different motions by the visual system occurs only at scales where the resolution is coarser than that of the interaction of local motion detectors.

To understand the nature of this interaction, it is necessary to ask what is perceived, and what information can the visual processing of motion yield, when transparency is abolished in locally-paired motions. Qian et al. (1994) describe the appearance of locally-paired opposed motions as 'directionless flicker'. This result could correspond either to the complete destructive interference of motion signals, or to the cancellation of two equal and opposite motion vectors. Qian et al. also briefly described the case of locally-paired motions at angles less than 180°. They reported that for a range of directions between 90 and 180°, no coherent motion was seen. However, when the directions of paired dots differed by 45°, Qian et al. reported a single coherent motion that was the average of the two motion vectors (a result confirmed in more formal measurements by Qian & Geesaman, 1995). They argue from these observations that inhibitory effects between motion detectors do not occur only for opposite directions of motion, but for any two directions that are 90° or more apart. In the present paper, we use direction and speed judgements to test more fully whether motion signals are abolished for locally-paired motions in the range of direction differences from 60 to 120°, or whether the interaction in this range may lead to a vector combination of the type reported by Qian et al. for 45° differences.

The results of our experiments clearly demonstrate that over the 60–120° range subjects do derive a coherent motion signal from locally-paired combinations over this range, and that the perceived motion is the vector average of the paired components. This implies that the interaction between locally-paired motions cannot be understood solely in terms of suppression.

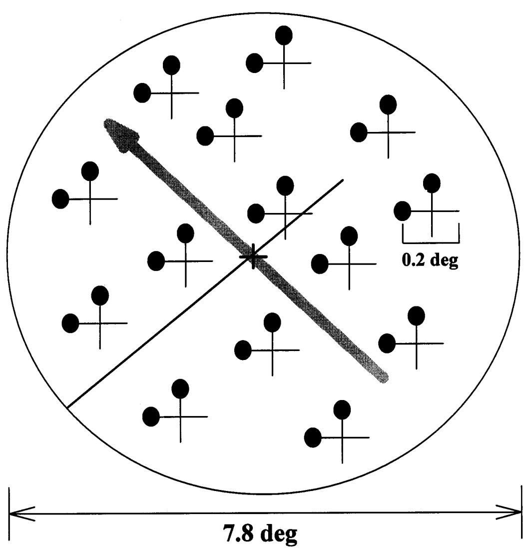

Fig. 1. A schematic representation of the stimuli used in Experiment 1a. The stimulus was viewed through a circular aperture. Dot density was 2 dots/deg^2 and dot speed was 4°/s. Each dot in a pair traversed a distance of 0.2°, their motion paths crossing at the midpoint of their trajectories; when a given dot pair came to the end of its lifetime its replacement was plotted at a randomly chosen location. Stimulus duration was 1 second. A central fixation cross was visible for 500 ms prior to stimulus presentation and remained on the screen for the stimulus duration. On each trial the stimulus was rotated by a random amount chosen from the full 360° range. Subjects' task was to judge whether the angle, α, described by the global motion of the display (indicated by the light grey arrow) and the static line was less or greater than 90°.

2. Experiment 1

2.1. (a) Perceived direction of locally-paired stimuli

As discussed above, Qian et al. (1994) reported apparent coherent motion in locally-paired displays when dot directions differed by 45°, but not for direction differences of 90° and above. In Experiment 1 we aimed to test the limiting direction difference that yields coherent motion, by measuring subjects' ability to judge global direction in displays of locally-paired motions.

2.1.1. Methods

2.1.1.1. Subjects. Three subjects participated in the experiments, including one of the authors. All subjects had extensive experience of psychophysical experiments; two of the subjects were naive as to the purpose of the experiments. All observers had normal or corrected to normal acuity.

2.1.1.2. Stimuli. Each stimulus consisted of a set of approximately 50 dot pairs, plotted to 16-bit precision on an $X-Y$ cathode ray tube (P31 green phosphor) display under the control of a high performance vector point plotter (Cambridge Research Systems D300), in a darkened room. A mask with a circular aperture of 7.8° diameter covered the face of the screen. In addition to the dots, there was a central fixation cross, and a static line (length 3/4 of the display diameter) extending from the border of the display through the centre (Fig. 1). The overall orientation of the stimulus was rotated by a random amount chosen from the full 360° range on each trial. Dot and static line luminance was 8 cd/m^2; background luminance was 0.01 cd/m^2, giving a stimu-

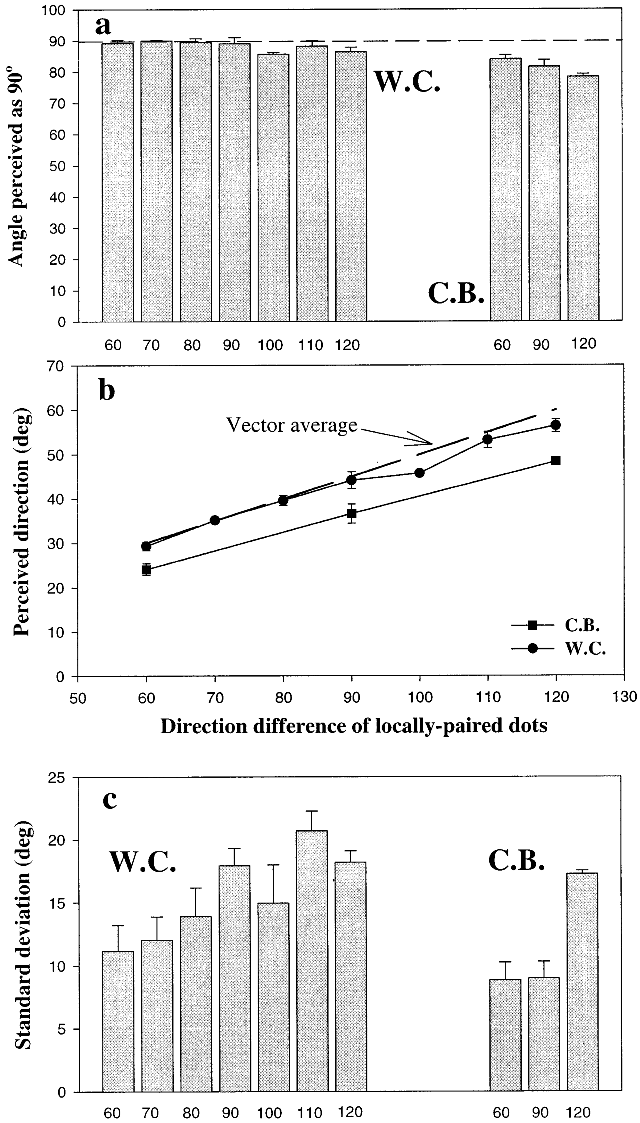

Fig. 2. The results of the two subjects tested in Experiment 1a. (a) The angle between the static line and the mean direction of the locally-paired dots when subjects perceived the dots moving orthogonal to the static line. (b) The perceived direction of locally-paired dots relative to the direction of one of the component dots, as a function of direction difference. (c) Standard deviations from the direction-difference conditions indicate subjects were able to make reliable quantitative judgements of the direction of coherent motion from all stimuli conditions. Error bars in these and subsequent figures represent ± 1 S.E.

lus contrast of 0.99. Observers viewed the display binocularly from a distance of 57 cm, resulting in a dot density of 2 dots/deg^2 (i.e. 1 dot pair/deg^2). The effective frame rate[1] was 100 Hz, with displays presented as a 100-frame sequence lasting 1 s. The dots were displaced on each frame to give a speed of 4°/s. Dot lifetime was set to 50 ms to correspond to a dot trajectory of 0.2°, well within the range for which transparency is abolished. The lifetimes of different dots began and ended asynchronously. The 100 frames that constituted the stimulus were treated as if they were a sample from a longer sequence, therefore some dot pairs could end their lifetime in the first frames of the sequence. The two dots in each pair travelled in directions differing by either 60, 90, or 120°, their motion paths crossing at the midpoint of their trajectories. When a dot pair came to the end of its lifetime its replacement was plotted at a randomly chosen location.

2.1.1.3. Procedure. After several practice trials the experiment proper began. The task of the observer was to judge whether the angle between the apparent motion direction of the locally-paired dots and the static line was greater or less than 90°, using a two alternative forced choice procedure (2AFC) (Braddick, 1997). The central fixation cross was presented 500 ms prior to stimulus presentation and was displayed for the stimulus duration (1 s). Subjects were instructed to fixate the central cross and not to make head movements during stimulus presentations. Stimuli were presented in blocks of 100 trials, with the direction difference remaining constant within a block. The angle between the static line and the mean direction of the locally-paired dots was chosen by Adaptive Probit Estimation (APE), a method that dynamically updates the set of stimuli being presented to an observer depending on their previous responses (Watt & Andrews, 1981), so that stimulus values lie around the observer's 'point of subjective equality' (PSE). In this case the PSE is the angle at which the line and the global motion were perceived to be 90° apart. APE yields an estimate both of the PSE and of the standard deviation of a probit function fitted to the psychometric function. The angle between the dots and static line was determined by APE, but the orientation of the whole stimulus was randomised between each trial, so that no anisotropies of the motion system would have a systematic effect on the results. Subjects were tested with four blocks of trials for each value of the direction difference within the dot pairs. One of the subjects was tested with four additional direction differences — 70, 80, 100 and 110°.

2.1.2. Results

As expected from previous work, subjects did not perceive motion transparency in these displays. Fig. 2(a–c) depicts the data on direction judgements obtained from two subjects. Fig. 2a plots, as a function of direction difference, the angle between the line and the mean direction of the locally-paired dots for which subjects perceived the global motion as orthogonal to

[1] Unlike raster displays, vector point plotters do not have frames in the conventional sense. Rather the display rapidly plots one point after another in a continuous sequence. A corresponding value for the frame duration can be determined by the time lapse between a dot being plotted in one position and subsequently being updated to its next position.

Table 1
Speed values used in Experiment 1b

Speed 1 (°/s)	Speed 2 (°/s)	Ratio
2	3	1:1.5
4	6	
1	2	1:2
2	4	

the static line. From this measure one can calculate the direction in which the locally-paired stimuli appear to move[2]. Fig. 2b shows this direction, expressed relative to one of the component directions, as a function of the direction difference between the component dots. Fig. 2c plots the standard deviations of the estimated psychometric functions.

The standard deviations of 20° or less indicate that subjects were able to make reliable quantitative judgements of the direction of coherent motion from all these stimuli. The precision of the judgements increased when the angle between the paired motions was smaller. It should be noted that all the standard deviations are larger than those typically found when direction of a single dot stream is judged in this task (Braddick, 1997).

Thus coherent motion was visible in locally-paired stimuli in which the directions of the component dots differed by as much as 120°. This perceived motion was in a direction close to the direction of the vector average of the locally paired components.

In this experiment the paired dots travelled at identical speeds. In the next experiment we investigated whether the vector averaging rule demonstrated in Experiment 1a generalises to locally-paired stimuli in which the two components have different speeds.

2.2. (b) Perceived direction of locally-paired dots with different speeds

Displays were similar to the 90° direction-difference condition of Experiment 1a, except that the two dots in each pair differed in speed by either 50 or 100%, with two speed combinations for each ratio (Table 1). In each of the speed-combination conditions dot lifetime was identical for all dots and was constrained such that the slower moving dot in a pair travelled for 0.2° during its lifetime. This entailed that the faster moving dots in each condition had a longer trajectory (0.3° for speed ratio 1:1.5, and 0.4° for ratio 1:2). In all other respects, the stimulus parameters, and methods were the same as for Experiment 1a. As in that experiment, the subject's task was to decide whether the direction of perceived motion was less or greater than 90° relative to the static line. Three subjects were tested.

2.2.1. Results

None of the displays was reported to appear transparent, and subjects could make reliable judgements of the coherent direction in each case. The perceived directions of the locally-paired stimuli are plotted in Fig. 3a and b for the speed ratios 1:1.5 and 1:2, respectively. The data shown are the means for the three subjects. For both speed combinations shown in Fig. 3a, the perceived motion direction lies in the direction of the vector average. For the 1:2 speed ratio (Fig. 3b), the perceived motion lies in a direction intermediate to the vector average and the direction of the faster moving dots.

The offset of perceived direction from the vector average in the 1:2 speed ratio conditions may be a consequence of the trajectory of the faster moving dots, which in these conditions had a length of 0.4°. We know that transparency can be seen in locally-paired displays when both dots have trajectories greater than 0.25° (Wishart & Braddick, 1997b). Although subjects did not report seeing two motion components, it is possible that the faster dots made some additional contribution to the perceived direction because they exceeded this threshold trajectory below which the individual motions are lost. Experiment 1c explores this possibility.

2.3. (c) Effects of trajectory length

In this experiment subjects were again tested with mixed-speed, locally-paired stimuli with a speed ratio of 1:2. The speed combinations used were the same as for this ratio in Experiment 1b, and the procedures and parameters were identical in all but one respect — the extent of dot trajectories. The lifetime of the slower and faster dots was set such that their motion trajectories were 0.1 and 0.2° long. Thus both trajectories fell well within the range for which transparency is abolished, according to the data of Wishart and Braddick (1997b).

2.3.1. Results

Fig. 4 plots the mean results for the three subjects, comparing the trajectory combinations used in this experiment with those for the 1:2 speed ratio in Experiment 1b. The data show that, when both dot trajectories are less than 0.25°, perceived motion direction does not differ significantly from the vector average of the

[2] The perceived direction, P_d, of the locally-paired stimuli is calculated as follows:

$$P_d = \frac{\alpha}{2} - (90 - \beta)$$

where α is the angle between the two motion directions and β is the angle between the static line and the bisector of the two motion directions.

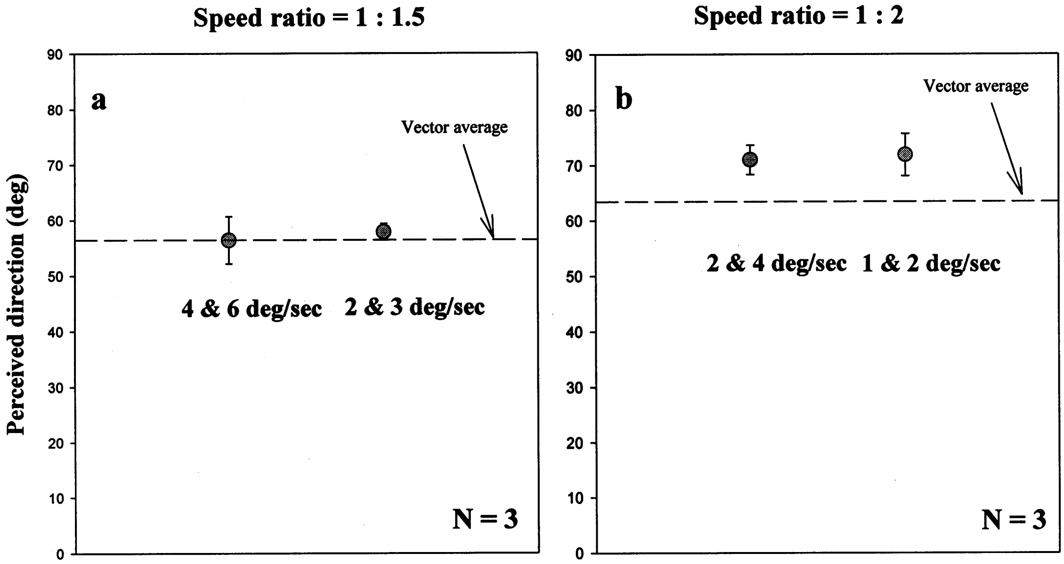

Fig. 3. Perceived direction of locally-paired dots with speeds ratio of 1:1.5 and 1:2. Subjects were tested with two speed combinations for each speed ratio condition. (a) For a speed ratio of 1:1.5 perceived motion direction of both speed combinations lies in the direction of the vector average. (b) For the 1:2 speed ratio, the perceived motion lies in a direction between the vector average and the direction of the faster moving dots.

locally-paired dots, although the bias is still towards the direction of the faster dots.

2.3.2. Sensitivity as a function of speed

One possible explanation of the bias in perceived direction towards the faster moving dots in Experiment 1b is that it reflects differences in sensitivity to motions of different speeds. If so, the results of Experiment 1c would suggest that such sensitivity differences are much reduced for shorter dot trajectories.

An appropriate way to measure sensitivity to the motion of dot patterns is the motion coherence threshold. This is the minimum percentage of signal dots with a common motion, in a field of noise dots that are randomly repositioned on each frame, that is necessary to detect the direction of signal motion. We measured such thresholds for stimuli with the same range of dot speeds and trajectories used in Experiments 1b and c, and with a dot density of 1 dot/deg^2. Random dot kinematograms were presented with the signal dots moving in an upward direction, either 10° to the left or right of vertical. The subject's task was to decide whether perceived motion was left or right of vertical. Viewing distance, stimulus luminance and contrast were identical to the earlier experiments. A three-up two-down staircase method was used to determine the threshold percentage coherence; a run was ended after ten staircase reversals, and the threshold was taken as the average of the last eight reversals. One of the authors, WC, was tested.

Table 2 shows the results for the dot speed and trajectory combinations tested; the results for each speed/trajectory combination are the average of three experimental runs. The first two rows correspond to the 2 and 4°/s conditions in Experiment 1b. The thresholds are very similar and give no indication of the greater sensitivity to the higher speed that would be necessary to account for the bias seen in Figs. 3 and 4. When dot trajectories are reduced for these two speeds (rows 3 and 4) motion coherence thresholds are raised much more for 2°/s than for 4°/s. This change is in the direction opposite to that needed to account for the

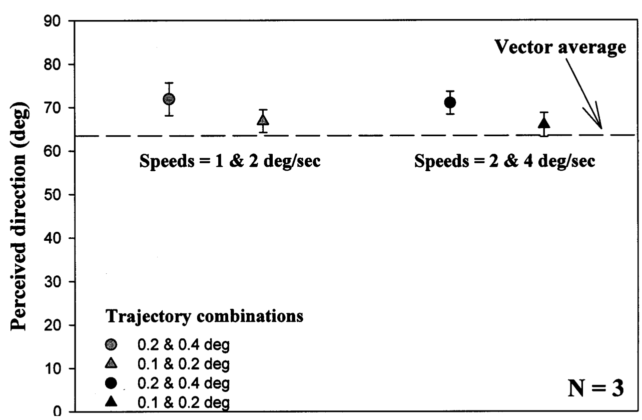

Fig. 4. Perceived direction of locally-paired stimuli as a function of speed combination — 1 and 2°/s (light grey symbols), and 2 and 4°/s (dark symbols). The filled circles are data from Experiment 1b, in which the slower and faster dots had trajectories of 0.2 and 0.4°, respectively. The filled triangles are the data from Experiment 1c, in which the slower and faster dots had trajectories of 0.1 and 0.2°, respectively. When both trajectories are less than 0.25°, perceived motion is close to the vector average, although the bias is still towards the direction of the faster moving dots.

results of Experiment 1b and c as a consequence of differential sensitivity. We see a similar pattern of results for the 1 and 2°/s speed conditions, with the difference between the thresholds increasing substantially as dot trajectory is reduced. The small amount of variation of coherence threshold with speed for the longer lifetimes is consistent with the results of van de Grind, van Doorn and Koenderink (1983) who, under the conditions of central viewing closest to the present measurements, found a broad plateau of optimum performance between about 1 and 10°/s.

In Experiments 1b and c, the angle between the direction of the faster moving dots and the static reference line was always less than the angle between the slower moving dots and the line. It might be argued that this could introduce a systematic bias into subjects' responses. A control condition was run with one subject (WC) to test this possibility. The experiment comprised three experimental runs of 200 trials each. The component dots forming the smallest angle with the static line was randomised from trial to trial; on 50% of trials the faster dots formed the smaller angle, otherwise the slower dots formed the smaller angle. The paired dot speeds were 2 and 3°/s. As in previous experiments, the task was to judge whether the angle between the global motion of moving dots and the static line was greater or less than 90°. Two psychometric functions were derived from each experimental run. The mean perceived direction of motion was 58° when the faster dots formed the smaller angle (vector average = 56.3°), and 31° when the slower dots formed the smaller angle (vector average = 33.69°). That is, the perceived direction was close to the vector average and biased towards the direction of the faster moving dots in each case.

Together, the results of Experiments 1a–c provide compelling evidence that locally-paired stimuli, with direction differences of up to 120°, yield coherent motion in the direction of the vector average for a range of speed and trajectory combinations. The next series of experiments was designed to test whether this vector averaging rule applies also to the perceived speed of locally-paired stimuli.

Table 2
Motion coherence thresholds as a function of dot speed and trajectory

Speed (°/s)	Dot trajectory	Motion coherence threshold (S.E.)
2	0.2°	1.79 (0.35)
4	0.4°	1.73 (0.02)
2	0.1	6.42 (1.38)
4	0.2	2.97 (0.55)
1	0.2	2.16 (0.46)
2	0.4	1.32 (0.09)
1	0.1	6.69 (1.02)
2	0.2	1.79 (0.35)

3. Experiment 2

3.1. (a) Perceived speed of locally-paired stimuli

In this experiment subjects' perceived speed of locally-paired stimuli was estimated for three conditions, in which the paired dots differed in their directions by either 60, 90 or 120°.

3.1.1. Stimuli

Each trial consisted of the sequential presentation of a locally-paired test stimulus followed by an unpaired, random-dot comparison stimulus. Dots in the locally-paired test stimuli had a fixed velocity of 2°/s, and trajectory length of 0.2°. In the comparison stimulus all dots moved in the same direction and dot lifetime was identical to that of the test stimulus, but speed was varied. Movement of the comparison stimulus dots was in the vector average direction of the locally-paired dots. Dot density in both test and comparison stimuli was 2 dots/deg^2.

3.1.2. Procedure

After several practice trials the experiment proper began. The task of the observer was to judge whether the comparison stimulus moved faster or slower than the locally-paired test stimulus, using a two interval forced choice procedure (2IFC). A central fixation cross was presented 500 ms prior to stimulus presentation and was displayed for the stimulus duration. The test and comparison stimuli were presented for 1 s each, with an inter-stimulus interval of 500 ms. Stimuli were presented in blocks of 100 trials of the same direction-difference condition (in which the directions of dots within each pair differed by either 60, 90, or 120°). The speed of the comparison stimulus was chosen by adaptive probit estimation (described above). Stimulus direction was randomised from trial to trial. Two subjects were tested with four blocks of trials for each condition.

3.1.3. Results

Fig. 5 plots the results for two subjects. In this figure perceived speed of the locally paired stimulus is plotted as a function of the direction difference between paired dots in a locally-paired stimulus. The two lines without symbols depict the speeds of the vector sum and vector average for direction differences ranging from 60 to 120°. The data for both subjects show that, for all three direction differences tested, perceived speed is close to the vector average. In our next experiment we examined whether this vector averaging rule generalises to faster velocities than the 2°/s used here.

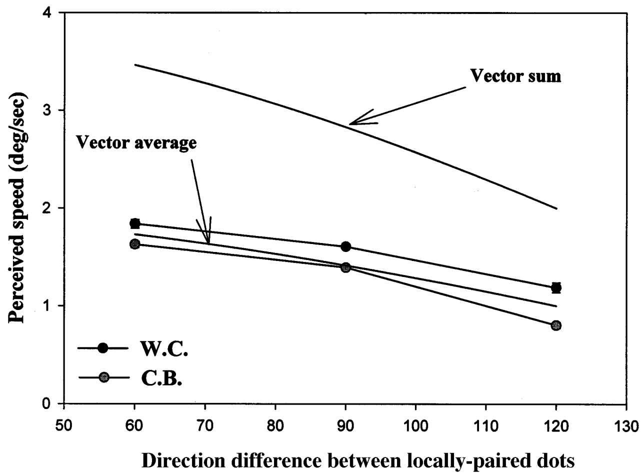

Fig. 5. Perceived speed of locally-paired dots as a function of direction difference. For both subjects tested perceived speed is close to the vector average.

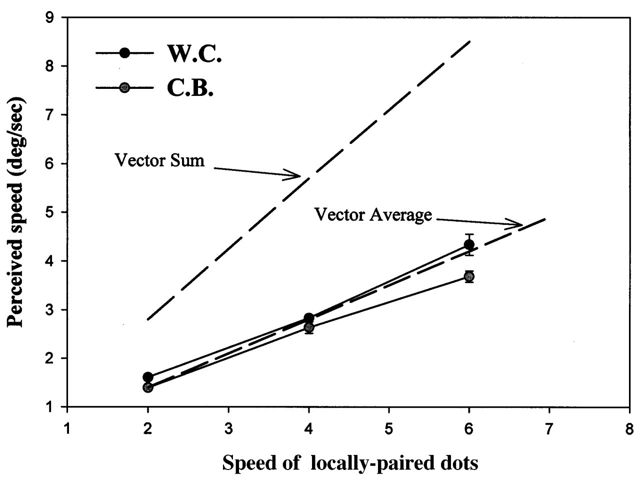

Fig. 6. Perceived speed of locally-paired dots as a function of dot speed.

Table 3
Speed (°/s) values used in Experiment 2c

Speed 1 (trajectory, °)	Speed 2 (trajectory, °)	Ratio
2 (0.2)	4 (0.4)	1:2
4 (0.2)	6 (0.3)	1:1.5

3.2. (b) Does the vector averaging rule occur over a range of speeds?

In this experiment the locally-paired dots had a speed of either 4 or 6°/s, and a direction difference of 90°. As in the previous experiment, each dot's lifetime was restricted to a trajectory of 0.2°. The paired dots moved in trajectories orthogonal to each other in both speed conditions. Apart from speed the stimulus parameters and experimental procedure were identical to those of Experiment 2a. The same two subjects were tested with four blocks of 100 trials in each velocity condition.

3.2.1. Results

Fig. 6 plots perceived speed as a function of dot speed, for each subject. Data from the 90° direction-difference condition of Experiment 2a, in which dot speed was 2°/s, are also included in the graph. The data clearly show that perceived speed of locally-paired stimuli lies close to the vector average for dot speeds ranging from 2 to 6°/s.

We have shown the vector averaging rule for directions and speeds of paired dots moving at the same speed, and for directions of dots moving at different speeds. In our final experiment we address whether the perceived speed of mixed-speed stimuli also follows the vector average.

3.3. (c) Perceived speed of locally-paired, mixed-speed stimuli

The stimuli and procedure in this experiment were similar to those in Experiment 2b, except that the orthogonally moving paired dots in the test stimulus differed in speed, as shown in Table 3.

3.3.1. Results

Fig. 7 shows the perceived speed of these mixed-speed stimuli, for the two subjects. In each case the perceived speed lies close to the vector average, and well below the vector sum. Thus the findings of Experiments 2a–b that locally paired RDK's give perception of the vector average speed, extend to the case where the component speeds are not equal.

4. Discussion

Qian et al. (1994) reported that locally-paired dot stimuli appear as directionless flicker when the component dot directions differ by 90° or more. They concluded that inhibitory effects between directionally-tuned mechanisms are not restricted to opposite directions of motion, but extend at least to direction differences of 90°. However, Experiments 1a–c described in this paper show that such stimuli, with direction differences of 60, 90, or 120° and various speed combinations, can yield the perception of unitary, coherent motion, in the vector average direction of the component motions.

These results contrast sharply with the reports of Qian et al., which used stimuli overlapping with ours in speed, trajectory length, and direction difference. Transparency was effectively abolished in our displays, as evidenced by subjective appearance, subjects' ability to make quantitative direction and speed judgements, and the relation of the dot trajectories used to previous experiments. The only parameter that differed significantly was dot density (2 dots/deg^2 in our displays, approximately half the lowest dot density used by Qian et al.). Although it has not been ruled out, it is unlikely that this difference in dot densities can account for the differing results.

Qian et al. (1994) interpret the absence of apparent coherent motion in locally-paired stimuli as evidence of inhibitory interactions between directionally-tuned mechanisms. If this interpretation is correct, then the results from Experiments 1a–c suggest that inhibitory effects between directionally-tuned mechanisms do not suppress motion signals over as wide a range of direction differences as proposed by Qian et al., but allow signals from directions 120° apart to contribute together to motion perception. We did not test for direction differences larger than 120°. However, given the directional bandwidth of MT/V5 neurones for random dot kinematograms (Albright, 1984; Snowden, Treue & Andersen, 1992), we would expect larger direction differences to significantly activate neurones tuned to opposite directions and thus to yield mutual suppression. Of course, our results do not necessarily imply the absence of inhibitory interactions between detectors tuned within 120°; such interactions might contribute to shaping the distribution of activity which leads to a unitary perception of the average vector, but they do not lead to suppression of motion perception.

We found that the direction of apparent motion in locally-paired stimuli was the vector average of the component motions. Thus it appears that the visual system applies some type of pooling operation for responses from neurones tuned to the two directions. This operation acts appropriately to yield the vector average even when speeds in the two directions are different, implying either that it acts on signals which are linear with speed, or that it takes account appropriately of the speed sensitivity of the direction-tuned mechanisms.

Combination of direction vectors has also been reported for non-locally-paired stimuli. Williams and Sekuler (1984) report that a global motion percept in the vector average direction occurs for a dot pattern containing a range of local motion vectors, when these are drawn from a distribution restricted to less than 180°. While motion in the vector average direction occurs in both cases, it is clear that perceived direction for these stimuli and for locally-paired stimuli is derived from different processes. Williams and Sekuler report that the percept of coherent motion with their stimuli was all but abolished if motions in a 60° range around the mean were removed from the distribution. Our stimuli comprised motion vectors whose directions differed by at least 60°, but still gave a clear percept of coherent motion in the vector average direction. In the Williams and Sekuler stimuli, the perception of global motion co-exists with the individual motion directions being readily perceived, and in fact distributions of local motions can be optionally parsed into global components in different ways (Zohary, Scase & Braddick, 1996). In contrast, in our locally-paired stimuli, the individual motion directions are not apparent. The global motion in the Williams and Sekuler type of display is the result of pooling motion vectors over a large area, while the interaction we are studying is limited to a range of about 0.25°. In short, the processes for global vector combination in experiments like Williams and Sekuler's are different from those in ours or Qian et al.'s, which operate to produce locally combined vectors.

Our second series of experiments demonstrate that local vector combination determines the perceived speed as well as direction of a range of locally-paired

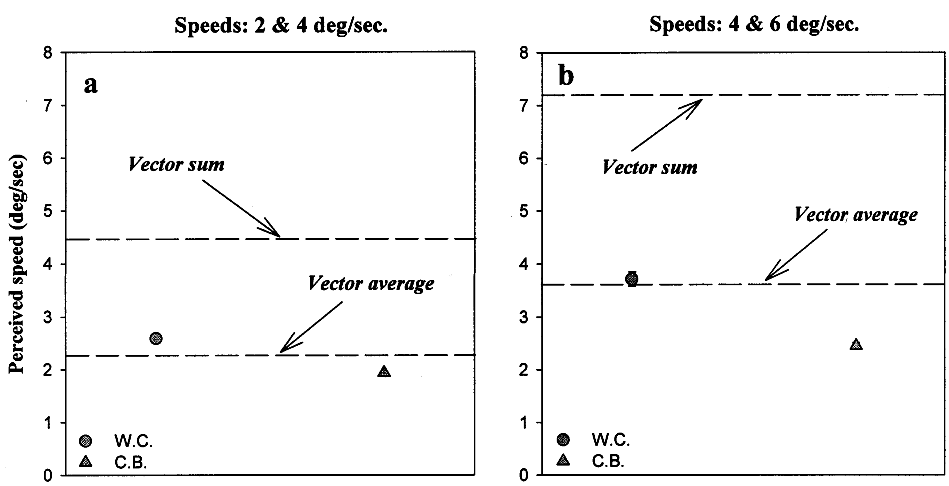

Fig. 7. Perceived speed of locally-paired, mixed-speed stimuli, in which paired dots moved at speeds of either (a) 2 and 4°/s or (b) 4 and 6°/s. In both cases, subjects' perceived speed lies closer to the vector average than the vector sum.

stimuli. Similarly, in the speed domain, Watamaniuk and Duchon (1992) report that the perceived speed of random dot kinematograms comprising dots moving at different speeds is equal to the average speed of the dots, suggesting that the visual system averages speed information. As in Williams and Sekuler's experiments, the phenomenon described by Watamaniuk and Duchon operates at a global level (in their stimuli dots are not locally paired and are seen to be moving at different speeds).

van Doorn and Koenderink (1982b, 1983) investigated the ability of human observers to detect the non-uniformity of a random dot pattern containing different motions in two regions. This is the inverse of the vector-combination question; if differently moving regions are not seen as distinct, presumably their motions are being combined into a single global motion. van Doorn and Koenderink measured the smallest vector difference for which observers could detect the non-uniformity, and find that this value (for motions differing in either direction or speed) gives a Weber ratio (defined as the magnitude of the difference vector divided by the magnitude of the vector average of the two motions, at threshold) of around 0.6–0.9. They state that this corresponds to the limit on the relationship between motions which can be seen as transparent (van Doorn & Koenderink, 1982a). In our experiments, however, the minimum value of this ratio is 1.15 (for equal speeds 60° apart) and it ranges up to 3.48 (equal speeds 120° apart). Thus we are working in the range where Koenderink and van Doorn expect discrimination, not pooling of the two motion vectors. Indeed, this would be expected from the observation that, when the dots are not locally paired, all our velocity combinations appear transparent. We conclude then, that as for the studies of Watamaniuk and Duchon (1992) and Williams and Sekuler (1984), the effects studied by Koenderink and van Doorn reflect global pooling of local motion signals, whereas the vector averaging of locally paired motions reflects different processes operating only over a very short spatial range.

The precision of the vector averaging in our experiments raises the question of whether this local process does in fact represent an interaction between different local direction-tuned units. An alternative view is that vector averaging represents the detection of motion energy due to the two dots of a pair, *within* the receptive fields of individual local motion detectors. Such an argument could also cover the abolition of motion perception with locally-paired opposed motions, since in this case the net motion energy within a receptive field would be zero. Psychophysically, our experiments do not distinguish this possibility from that based on interaction between units. The principal argument against it comes from the physiological experiments of Qian and Andersen (1994, 1995) who found that the suppression resulting from locally balanced stimuli was found in the responses of MT/V5 neurones, but *not* in V1 neurones. Thus, at the earliest stage of elementary motion detection, the paired signals are encoded separately and directional combination does not occur. If this argument applies to the psychophysical results, then they imply a process, within subunits of receptive fields at the V5 level, which can compute the vector average direction of two motions differing in both direction and speed. There is a need, however, for more evidence, including interactions between directions other than 180°, which can distinguish interaction between the signals of elementary directional detectors from interaction in the initial generation of these signals.

In summary, locally-paired motions yield perception of the vector average motion. If indeed this reflects interactions between local motion detectors, then these interactions (a) do not take the form of a suppressive interaction, for direction differences up to at least 120°; (b) reflect the speed as well as the direction of the component motions.

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References

Albright, T. D. (1984). Direction and orientation selectivity of neurones in visual area MT of the macaque. *Journal of Neurophysiology*, *52*, 1106–1130.

Braddick, O. J. (1997). Local and global representations of velocity: transparency, opponency, and global direction perception. *Perception*, *26*, 995–1110.

Clarke, P. G. H. (1977). Subjective standstill caused by the interaction of moving patterns. *Vision Research*, *17*, 1243.

de Bruyn, B., & Orban, G. A. (1993). Segregation of spatially superimposed optic flow components. *Journal of Experimental Psychology*: *Human Perception and Performance*, *19*, 1014–1027.

Mulligan, J. B. (1992). Motion transparency is restricted to 2 planes. *Investigative Ophthalmology and Visual Science*, *33*(4), 1049.

Qian, N., Andersen, R. A., & Adelson, E. H. (1994). Transparent motion as detection of unbalanced motion signals I: Psychophysics. *Journal of Neuroscience*, *14*, 7357–7366.

Qian, N., & Andersen, R. A. (1994). Transparent motion as detection of unbalanced motion signals II: Physiology. *Journal of Neuroscience*, *14*, 7367–7380.

Qian, N., & Andersen, R. A. (1995). V1 responses to transparent and nontransparent motions. *Experimental Brain Research*, *103*, 41–50.

Qian, N., & Geesaman, B. J. (1995). Motion repulsion depends on the distance between the moving elements. *Investigative Ophthalmology & Visual Science*, *36*, S50.

Smith, A. T., & Curran, W. (1998). Global motion segregation does not depend on detection of steep motion gradients. *Perception*, *27*, 196.

Smith, A. T., Curran, W., & Braddick, O. J. (1999). What motion distributions yield global transparency and spatial segmentation? *Vision Research*, *6*, 1121–1132.

Snowden, R. J., Treue, S., Erickson, R. E., & Andersen, R. A. (1991). The response of area MT and V1 neurones to transparent motion. *Journal of Neuroscience*, *11*, 2768–2785.

Snowden, R. J., Treue, S., & Andersen, R. A. (1992). The response of neurones in area V1 and MT of the alert rhesus monkey to moving random dot patterns. *Experimental Brain Research*, *88*, 389–400.

van de Grind, W. A., van Doorn, A. J., & Koenderink, J. J. (1983). Detection of coherent motion in peripherally viewed random-dot patterns. *Journal of the Optical Society of America*, *73*, 1674–1683.

van Doorn, A. J., & Koenderink, J. J. (1982a). Temporal properties of the visual detectability of moving spatial white noise. *Experimental Brain Research*, *45*, 179–188.

van Doorn, A. J., & Koenderink, J. J. (1982b). Visibility of movement gradients. *Biological Cybernetics*, *44*, 167–175.

van Doorn, A. J., & Koenderink, J. J. (1983). Detectability of velocity gradients in moving random-dot patterns. *Vision Research*, *23*, 799–804.

Verstraten, F. A. J., Fredericksen, R. E., & van de Grind, W. (1994). Movement after effect of bi-vectorial transparent motion. *Vision Research*, *34*, 349–358.

Watamaniuk, S. N. J., & Duchon, A. (1992). The human visual system averages speed information. *Vision Research*, *32*, 931–941.

Watt, R. J., & Andrews, D. P. (1981). APE: adaptive probit estimation of psychometric functions. *Current Psychological Reviews*, *1*, 205–214.

Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, *24*, 55–62.

Wishart, K. A., & Braddick, O. J. (1997a). Performance-based measures of motion transparency. *Investigative Ophthalmology & Visual Science*, *38*, S75.

Wishart, K. A., & Braddick, O. J. (1997b). Performance based measures of transparency in locally-balanced motions. *Perception* (*Suppl.*), *26*, 86.

Zohary, E., Scase, M. O., & Braddick, O. J. (1996). Integration across directions in dynamic random-dot displays: Vector Summation or Winner-Take-All? *Vision Research*, *16*, 2321–2331.