

Vision Research 40 (2000) 2025-2036

Vision Research

www.elsevier.com/locate/visres

# The dependence of motion repulsion and rivalry on the distance between moving elements

Nestor Matthews<sup>a</sup>, Bard J. Geesaman<sup>b</sup>, Ning Qian<sup>a,\*</sup>

<sup>a</sup> Center For Neurobiology and Behavior, Columbia University, Room A730, 722 W. 168th Street, New York, NY 10032, USA <sup>b</sup> Department of Medicine, Massachussettes General Hospital, Cambridge, MA 02138, USA

Received 26 March 1999; received in revised form 27 January 2000

#### Abstract

We investigated the extent to which motion repulsion and binocular motion rivalry depend on the distance between moving elements. The stimuli consisted of two sets of spatially intermingled, finite-life random dots that moved across each other. The distance between the dots moving in different directions was manipulated by spatially pairing the dot trajectories with various precisions. Data from experiment 1 indicated that motion repulsion occurred reliably only when the average distance between orthogonally moving elements was at least 21.0 arc min. When the dots were precisely paired, a single global direction intermediate to the two actual directions was perceived. This result suggests that, at a relatively small spatial scale, interaction between different directions favors motion attraction or coherence, while interaction at a somewhat larger scale generates motion repulsion. Similarly, data from experiment 2 indicated that binocular motion rivalry was significantly diminished by spatially pairing the dots, which moved in opposite directions in the two eyes. This supports the recent proposal that rivalry occurs at or after the stage of binocular convergence, since monocular cells could not have directly responded to our interocular pairing manipulation. Together, these findings suggest that the neural mechanisms underlying motion perception are highly sensitive to the fine spatial relationship between moving elements. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Motion perception; Binocular rivalry; Attraction and repulsion

#### 1. Introduction

Both the perception of motion and the perception of spatial relationships are believed to be mediated by the dorsal stream of the primate visual system (Ungerleider & Mishkin, 1983; Felleman & Van Essen 1991). Consistent with this common-pathway scheme, motion information has been found to influence perceived relative position (Morgan, Watt & McKee, 1983; Welch & McKee, 1985; Nishida & Johnston, 1999) and conversely, appropriately positioned perturbing stimuli have been found to influence perceived motion (Bowne, McKee & Glaser, 1989; Welch, MacLeod & McKee, 1997). This study extends these findings by demonstrating that fine-scale spatial relationships significantly influence two well-known perceptual phenomena, motion repulsion and binocular motion rivalry.

\* Corresponding author. Tel.: +1-212-5435213; fax: +1-212-5435161.

E-mail address: qian@brahms.cpmc.columbia.edu (N. Qian)

Motion repulsion is the overestimation of the angle between two stimuli that move in different directions (Marshak & Sekuler, 1979). A stimulus parameter known to affect the magnitude of the phenomenon is the angle between the two directions. Motion repulsion is greatest when the presented directions differ by approximately 22.5°, but does not occur when the presented directions differ by 135° or more (Marshak & Sekuler, 1979). In the current study, we maintained a constant angle between two sets of dots that moved across each other, but manipulated the inter-dot distance using the spatial pairing procedure introduced by Qian, Andersen and Adelson (1994). Two dots are said to be paired to the extent that their trajectories spatially overlap. We varied the precision of pairing by systematically manipulating the vertical offset between dot positions in two spatially intermingled random dot patterns that moved in orthogonal directions. The data indicated that motion repulsion occurred only when the mean distance between moving elements was 21.0 arc



Fig. 1. Repulsion stimuli. Two L-shaped trajectories were simultaneously presented on each trial. One set of dots, represented by the broken line, moved downward-and-rightward ( $-22.5^{\circ}$ ) first, then upward-and-rightward ( $+67.5^{\circ}$ ). The other set of dots, represented by the solid line, always moved orthogonally to the first set. There were seven paired-dot conditions, and one unpaired-dot condition. The left and center panels depict the smallest and largest paired spatial offsets, for which the two dots in each pair were separated by a mean frame-to-frame Euclidean distance of 7.4 and 13.2 arc min, respectively. The distance between two unpaired dots (right panel) was random. Although the motion paths appeared perfectly smooth at the viewing distance of 57 cm, the trajectories are shown here in jagged lines to reflect the actual pixel-to-pixel displacements on the screen.

min or greater. As the distance between moving elements decreased motion repulsion was reduced, even when transparent motions were still clearly seen. With further decreases in the distance between moving elements, observers reported seeing motion coherence rather than transparency — consistent with previous work by Qian et al. (1994).

The second experiment was conducted to examine whether spatial pairing also affects motion rivalry the unstable, alternating percept that arises when different directions of motion are presented separately to the two eyes (Fox, Todd & Bettinger, 1975). As in the first experiment, we manipulated the precision of spatial pairing while keeping the directions of motion constant across stimulus conditions. The observers reported strong motion rivalry only when the dots presented to one eye were spatially independent from the oppositely moving dots presented to the other eye (i.e. the unpaired condition). When the dots were interocularly paired, motion rivalry was significantly reduced.

These results, together with the previously reported effect of pairing on motion transparency (Qian et al., 1994), strongly suggest that the neural mechanisms underlying motion perception are highly sensitive to the spatial relationship between moving elements. Some preliminary results were reported previously in abstract form (Qian & Geesaman, 1995; Matthews, Geesaman & Qian, 1999).

# 2. Experiment 1A: the effect of pairing on motion repulsion

#### 2.1. Method

#### 2.1.1. Observers

The observers were two of the authors and three individuals who were naive about the purpose of the study. All had normal or corrected-to-normal acuity, and had participated previously in other psychophysical experiments.

#### 2.1.2. Apparatus and stimuli

The experiment was conducted on a 21 in. ViewSonic PT810 monitor that was controlled by a Macintoshcompatible PowerTower Pro 225 computer. The vertical refresh rate of the monitor was 100 Hz, and the spatial resolution was  $1024 \times 764$  pixels. In a well-lit room, observers viewed the monitor from a distance of 57 cm, using a chin rest to stabilize head position.

The screen had a constant veiling luminance of 47 cd/m<sup>2</sup>. Stimuli were presented at a lesser luminance, 0.7  $cd/m^2$ , to eliminate unwanted screen persistence. The stimulus-surround luminance contrast, -97%, was such that observers easily saw the stimuli as black dots moving within a white surround. Each stimulus contained 200 dots within a circular virtual aperture having a diameter of 7.4°. Therefore, the dot density was 4.65 dots/deg<sup>2</sup>. Each dot was a  $2 \times 2$ -pixel square (approximately 5 arc min on each side), and moved at a mean speed of 4.2 deg/s, traversing a path length of 0.72° during its 17 frame lifetime (170 ms). After completing a path, each dot was replotted in a randomly selected position and repeated the path. The cycle continued for 72 frames, making the total duration of each stimulus 720 ms. Dots moving out of the viewing area 'wrappedaround' to the opposite side. To prevent the entire display from blinking synchronously every 17 frames, the initial 'age' (i.e. the ordinal position within the 17-frame sequence) of the dots was randomized.

Half of the dots in each stimulus followed one Lshaped path (at random locations), and the remaining half followed a different L-shaped path. These two paths are shown schematically in Fig. 1. One of the paths, depicted in solid line, comprised upward-andrightward motion  $(+67.5^{\circ})$  for the first nine frames, then downward-and-rightward motion  $(-22.5^{\circ})$  for the last eight frames. Conversely, the other path, depicted in broken line, comprised downward-and-rightward motion  $(-22.5^{\circ})$  for the first nine frames, then upward-and-rightward motion  $(+67.5^{\circ})$  for the last eight frames. In this way, orthogonal directions of motion were present at any instant, and the L-shape of the paths provided a means to keep the dots near each other through the pairing process (see below).

The experiment consisted of eight different stimulus conditions, seven having paired dots, and one having unpaired dots. In all paired conditions, the two dots within each pair were initially (i.e. the first frame of the 17-frame sequence) constrained to have a 2-pixel horizontal separation. The vertical separation, on the other hand, was varied systematically across the paired conditions. Specifically, the vertical separation at the center of the two motion paths (i.e. the ninth frame of the 17-frame sequence) ranged between 6 and 12 pixels, inclusively, in 1-pixel increments. As a result, for any given paired condition, there was a single mean frameto-frame Euclidean distance separating the two dots in each pair. These paired offsets were 7.4, 7.7, 8.0, 8.9,



Fig. 2. The effect of pairing on perceived direction (averaged data). The observers' mean line-settings are plotted separately for the three stimulus conditions shown in Fig. 1. The line-settings represent the *perceived* direction of the more downward-moving stimuli on each trial. The dotted horizontal line at  $-22.5^{\circ}$  represents the *actual* direction of the more downward-moving stimuli. Error bars indicate one standard error of the mean after consistent individual differences were removed (Loftus & Masson, 1994). At the smallest paired offset (7.4 arc min, left bar), observers perceived a single global flow near the horizontal (i.e. near 0°). At the largest paired offset (13.2 arc min, center bar), observers perceived the more downward direction veridically (i.e. near  $-22.5^{\circ}$ ). Motion repulsion occurred in the unpaired condition (right bar), as observers overestimated the more downward direction.

10.1, 11.5 or 13.2 arc min. Examples of the smallest (7.4') and largest (13.2') paired offsets are drawn to scale in Fig. 1 (left and middle panels, respectively). An example of two unpaired dots is shown in the right panel of Fig. 1. By definition, the distance between two unpaired dots is random. Consequently, our unpaired condition differed from each paired condition in two ways. First, there was a comparatively large mean inter-dot separation in the unpaired condition. Given the dot-density of 4.6 dots/deg<sup>2</sup>, the mean Euclidean distance between unpaired dots was 27.8 arc min, approximately twice the distance of the largest mean paired separation. Second, within each paired condition, there was no variability associated with the mean distance between two paired dots, but in the unpaired condition, there was variability around the mean distance between dots (27.8'). This is because, within each paired condition, we uniformly constrained the distance between the two dots in every pair, whereas dot positions were always random in the unpaired condition.

#### 2.1.3. Procedure

Each trial began with a fixation cross that remained visible for the duration of the stimulus. Observers initiated the motion stimulus with a button press. After the fixation cross and motion stimulus disappeared, a line was presented in the center of the viewing area. Via the keyboard, observers rotated the line to indicate either the single direction of motion if a coherent flow was seen, or the lower direction of motion if separate transparent flows were seen. Observers were instructed to base their judgments on global motion directions. All observers first completed several practice blocks. Subsequently, every observer completed three 80-trial blocks, with each block comprising ten presentations from the eight stimulus conditions, in random order. To determine how the perceived direction was affected by the precision of pairing, we analyzed the observers' line-settings across stimulus conditions.

#### 2.2. Results (experiment 1A)

In Fig. 2, the five observers' mean line-settings, a measure of the perceived direction (see Section 2.1), are shown separately for each of the three stimulus conditions depicted in Fig. 1. As a within-subjects design was used, the error bars reflect one standard error after consistent individual differences were removed (Loftus & Masson, 1994). The dotted horizontal line at  $-22.5^{\circ}$  represents the lower of the two directions physically present on each trial. A perceived direction below the dotted line indicates repulsion between the two directions of motion. In the unpaired condition (right bar), the well-known motion repulsion effect was apparent:



Fig. 3. The effect of pairing on perceived direction (individual data). The average line-settings for each of the seven paired conditions ( $\square$ ) and the unpaired condition ( $\bigcirc$ ) are shown separately for each observer. Each error bar reflects one standard error of the mean, and the dotted line at  $-22.5^{\circ}$  represents the actual direction of the more downward-moving stimuli. The significantly fitting logarithmic function for each observer indicates that the line-settings became increasingly downward as the spatial offset between paired dots increased. The line-settings were consistently most downward in the unpaired condition (right side of each graph), suggesting motion repulsion. For each observer, the systematic change in perceived direction occurred despite the fact that the same physical directions ( $-22.5^{\circ}$  and 67.5°) were present across all conditions.

The mean perceived direction was below the actual direction by approximately 15°. However, when the dot paths were precisely paired so that the average offset between the two paths was just 7.4' (left bar), the mean perceived direction was  $-1.85^{\circ}$ , well above the dotted line. In this condition, subjects reported perceiving a single unified global motion field, instead of two transparent flows, and the perceived direction was intermediate to the two actual directions  $(-22.5^{\circ} \text{ and } + 67.5^{\circ})$ . Finally, at the largest offset (13.2', middle bar) between the paired paths, the mean perceived direction was  $-25.24^{\circ}$ , very similar to the actual direction. A repeated measures, two-tailed *t*-test confirmed that the mean perceived directions in the three conditions differed significantly from each other (left and middle bars, t(4) = 7.65, P < 0.01; middle and right bars, t(4) = 2.95, P < 0.05). Thus, although the same directions of motion were physically present in all stimulus conditions, the data in Fig. 2 indicate that the perceived direction depended significantly on how the dots were spaced.

The effects seen in the mean data of Fig. 2 were also evident for each individual observer. These data are shown in Fig. 3 for the seven paired conditions (solid squares) and the unpaired condition (open circles). Every datum reflects the average of 30 observations, and error bars indicate one standard error. The leftmost and rightmost solid squares in each panel are data from the smallest (7.4') and largest (13.2') paired offsets, which, respectively correspond to the left and middle conditions in Figs. 1 and 2. As evidenced by the best-fitting logarithmic functions, the perceived direction for each observer changed significantly (P < 0.05) downward as the paired offsets became larger. The open circle on the right of each panel reflects the perceived direction for the unpaired dots,<sup>1</sup> the rightmost condition depicted in Figs. 1 and 2. Each observer showed significant repulsion in the unpaired condition as there is no overlap between the error bars on the open circles and the dotted horizontal line that represents the lower of the two physically present directions. This was true both before and after consistent individual differences were removed (Loftus & Masson, 1994). Thus, for individual observers, the data across Fig. 3 indicate that by systematically manipulating the spacing between dots, motion repulsion can be reduced.

<sup>&</sup>lt;sup>1</sup> Data from the unpaired condition were excluded from the regression analyses because, unlike the inter-dot distance in each of the paired conditions, there was variability around the inter-dot distance in the unpaired condition (see Section 2.1).

# 2.3. Experiment 1B: spatial relationship and transparency

In experiment 1A, observers informally reported seeing a single global flow when the separation between paired dots was smallest (7.4'), but two global flows at larger paired separations and in the unpaired condition. The purpose of experiment 1B was to determine more precisely the spatial relationships controlling the perception of coherence and transparency. Accordingly, the stimuli in experiment 1B were the same as in experiment 1A (seven paired conditions, and one unpaired condition), but now observers reported whether one (coherent) or two (transparent) global motions were seen. Stimuli from the eight conditions were chosen randomly across trials, with each stimulus condition being presented twenty times to each observer. The observers were the first author, one naive individual from experiment 1A, and two additional naive individuals.

#### 2.4. Results (experiment 1B)

The data from experiment 1B are shown in Fig. 4, where the probability of seeing two transparent motions is plotted as a function of the spatial relationship between moving elements. A similar pattern of responding is evident for all four observers. When the mean



Fig. 4. The effect of pairing on transparency (experiment 1B). For each observer, the probability of seeing transparent motion is plotted for the seven paired stimulus conditions ( $\bigcirc$ ) and the unpaired stimulus condition ( $\bigcirc$ ). For all observers, coherence was seen reliably at the smallest paired offsets. Transparency was seen reliably at the largest paired offset (13.2') and in the unpaired condition. Intermediate offsets were associated with intermediate probabilities of transparency.

spatial offset between paired dots (solid squares) was less than 8.0', observers reliably reported seeing a single coherent motion, rather than two global motions. As the mean spatial offset between paired dots increased, the probability of seeing two global motions also increased — a pattern consistent with that reported previously by Qian et al. (1994). Additionally, Fig. 4 indicates that transparency was reported reliably both at the largest paired offset (13.2') and when the dots were spatially unpaired (open circles). Therefore, although both repulsion and transparency depend on how precisely the elements are paired (compare the right and center bars of Fig. 2), a lack of repulsion does not necessarily imply a lack of transparency. This suggests that the difference between repulsion and veridical perception in experiment 1A reflects something other than a breakdown in transparency at the largest paired offset (13.2'). The stimulus attribute(s) that may have generated repulsion in the unpaired condition and veridical perception in the largest paired condition are examined in the control experiment that follows.

#### 2.5. Experiment 1C: control

As mentioned in Section 2.1, the paired-dot conditions differed from the unpaired condition in two ways. First, the average distance between unpaired dots (27.8') was more than twice the average distance at even the largest paired offset (13.2'). Second, within any given paired condition, there was no variability in the mean distance separating the two dots in each pair. This contrasts sharply with the unpaired condition, where there was much variability in the distance between dots. Therefore, since repulsion occurred only in the unpaired condition, it is possible that the repulsion depended on the large spatial variability, rather than the large average distance between moving elements. Accordingly, experiment 1C was designed to determine the extent to which the repulsion in experiment 1A was owing to spatial variability or to the average inter-element distance. Specifically, experiment 1C consisted of the unpaired stimulus from experiment 1A (mean interelement distance = 27.8'), and three paired conditions having a mean inter-element distances of either 7.4' (as before), 21.0' or 29.7'.2 Observers rotated a line to indicate the perceived direction of motion. If spatial variability were necessary for repulsion, one would expect repulsion to occur only in the unpaired condition. Alternatively, if the average inter-element distance were critical to repulsion, one would expect repulsion to occur even in the paired conditions, so long as the average inter-element distances were sufficiently large.

 $<sup>^{2}</sup>$  Note that the two larger paired conditions (21.0' and 29.7') in experiment 1C were considerably larger than the largest paired condition in experiment 1A (i.e. 13.2').



Fig. 5. Data from control experiment 1C. The observers' mean perceived direction is plotted for each of four dot configurations. Error bars indicate one standard error of the mean after consistent individual differences were removed (Loftus & Masson, 1994). Upper panel: The physical directions ( $+67.5^{\circ}$  and  $-22.5^{\circ}$ ) are shown in heavy dotted lines, and the average of these directions  $(+22.5^{\circ})$  is shown in faint dotted line. Observers reported either the single direction of motion if a coherent flow was seen, or the more upward direction of motion if separate transparent flows were seen. At the smallest paired offset (7.4'), a single flow was seen, and the perceived direction departed from the average direction, toward the horizontal axis (0°). Repulsion occurred at the larger paired offsets and in the unpaired condition. Lower panel: The physical directions were changed to  $+22.5^{\circ}$  and  $-67.5^{\circ}$  (heavy dotted lines), making the average direction  $-22.5^{\circ}$  (faint dotted line). Observers reported either the single direction of motion if a coherent flow was seen, or the more *downward* direction of motion if separate transparent flows were seen. As in the panel above, the coherent flow seen at the smallest paired offset appeared to move in a direction that departed from the average direction, toward the horizontal axis. Repulsion occurred at the larger paired offsets and in the unpaired condition.

We also note that at small paired offsets in experiment 1A, observers saw a single global flow moving *more downward* than the average of the two physical directions (i.e. closer to  $0^{\circ}$  than to  $+22.5^{\circ}$ ). There are two possible causes for this finding. First, our instruction to report the more downward direction on each trial could have introduced a downward response bias. Second, the downward departure from the mean direction could reflect an interaction with the horizontal axis, since directional sensitivity for human observers is greatest along the cardinal axes (Ball & Sekuler, 1987; Matthews & Welch, 1997; Matthews & Qian, 1999). Thus, in experiment 1A both the effect of task-instruction and cardinal-axis would have influenced responses in the same direction — downward. We therefore designed experiment 1C such that the factors of task-instruction and cardinal-axis would have diverging influences, thereby revealing the relative contributions of each. Specifically, in one condition, we presented the same directions of motion as in experiment 1A ( $+67.7^{\circ}$ and  $-22.5^{\circ}$ ), but now required the observers to report the more upward direction. Under this condition, the perceived direction should be more upward than  $+22.5^{\circ}$  (the physical average) if the instructional influence were dominant, but more downward than  $+22.5^{\circ}$ if the cardinal influence were dominant.

In a further test, we changed the physical directions to  $-67.5^{\circ}$  and  $+22.5^{\circ}$ , and required observers to report the more downward direction. Under this condition, the perceived direction should be more downward than  $-22.5^{\circ}$  (the physical average) if the instructional influence were dominant, but more upward than  $-22.5^{\circ}$  if the cardinal influence were dominant.

In brief, experiment 1C was designed to determine the relative influences of task-instruction and cardinalaxis when the paired offset is small (7.4'), and whether repulsion is seen when the paired offset is large (i.e. greater than 21.0'). Three naive observers were recruited for experiment 1C.

#### 2.6. Results (experiment 1C)

The data from experiment 1C are shown in Fig. 5. The relative contributions of task-instruction and cardinal-axis can be evaluated at the smallest paired offset (7.4'), which generated coherent motion for all observers (consistent with Fig. 4). The top panel shows the condition in which the physical directions were  $+67.5^{\circ}$ and  $-22.5^{\circ}$  (depicted in heavy dotted lines) and observers were required to report the more upward direction. The mean perceived direction was  $+15.0^{\circ}$ , slightly *above* the horizontal (0°). When the same stimuli were presented in experiment 1A and observers were required to report the more downward direction, the mean perceived direction was  $-1.85^\circ$ , slightly below the horizontal (Fig. 2, left). This change in the mean perceived direction suggests that the task instructions may have influenced the observers' responses, at least

partially. However, as we mentioned above, experiment 1C was designed so that the influence of the task instructions would always be opposite to the influence of the cardinal axis. Specifically, the instruction to report the more upward direction would be expected to bias the perceived direction upward from the average physical direction, whereas an interaction with the horizontal axis would be expected to bias the perceived direction downward from the average physical direction. The top panel of Fig. 5 indicates that the mean perceived direction was more downward than the average of the physical directions ( $+22.5^\circ$ , depicted in faint dotted line). This downward departure toward the cardinal axis occurred even though the task instructions were to report the more upward direction. Therefore a bias toward perceiving a direction near the cardinal axis was larger than any bias attributable to the task instructions. Indeed, the comparatively large influence of cardinal-axis is also evident in the bottom panel of Fig. 5. This panel corresponds to the condition in which the physical directions were  $-67.5^{\circ}$  and  $+22.5^{\circ}$ (depicted in heavy dotted lines) and observers were required to report the more downward direction. Now, the instruction to report the more downward direction would be expected to bias the perceived direction downward from the average physical direction, whereas an interaction with the cardinal axis would be expected to bias the perceived direction upward from the average physical direction. Once again, the mean perceived direction,  $-12.4^{\circ}$ , departed from the average physical direction (faint dotted line at -22.5) toward the horizontal. This upward departure from the average physical direction is contrary to what would be expected if responses had been biased by the instruction to report the more downward direction. The data in Fig. 5 (left bars) therefore suggest that when a single global flow was seen, the perceived direction was influenced more by the cardinal axis than by the task instructions.

The data in Fig. 5 also demonstrate that repulsion can occur in spatially paired displays, provided that the average distance separating the dots within a pair is sufficiently large. As can be seen in the top panel, when the mean paired offsets were 21.0' and 29.7' (center bars), observers overestimated the more upward physical direction  $(+67.5^\circ$ , shown in heavy dotted line), indicating repulsion. The magnitude of this repulsion was virtually identical to that demonstrated in the unpaired condition (right bar). Additionally, similar results are evident in the bottom panel of Fig. 5, which corresponds to the condition in which observers judged the more downward direction ( $-67.5^\circ$ , shown in heavy dotted line). Here again, repulsion occurred with virtually equal magnitude when paired dots were separated by 21.0' and 29.7' (center bars), and when the dots were unpaired (right bar). The data in Fig. 5, therefore, suggest that repulsion can be equally salient in paired

and unpaired displays, even though these two types of displays differ in the amount spatial variability between moving elements (as discussed above). The critical factor is the distance between moving elements.

Having found evidence that the distance between moving elements affects motion repulsion, we next considered whether an interocular version of this manipulation would affect binocular motion rivalry.

# 3. Experiment 2: the effect of pairing on motion rivalry

# 3.1. Method

# 3.1.1. Observers

The four observers in experiment 2 consisted of the first author, two naive observers who had participated in our repulsion study, and one additional naive observer who had no previous experience in psychophysical experiments. All had normal or corrected-to-normal spatial acuity, normal color vision (Ishihara, 1973), and stereo acuity finer than 1.25 arc min (Randot Stereotests, 1988).

### 3.1.2. Apparatus and stimuli

The monitor, computer, viewing distance, and dotsize were the same as described in the Section 2.1 for experiment 1. The main difference was the dichoptic viewing condition required for this experiment. In a dark room, observers wore red/blue stereo glasses and viewed two spatially intermingled sets of dots. To the naked eye, one set of dots appeared red and the other appeared blue. These two sets of dots were presented at the same luminance  $(0.1 \text{ cd/m}^2)$ , although for some observers the luminance of one set had to be adjusted slightly to make the two colors appear equally bright. The veiling luminance was just  $0.02 \text{ cd/m}^2$ , rendering the dots clearly visible at all times. Each stimulus consisted of 75 dots of each color and was presented in a circular virtual aperture 2.5° in diameter.<sup>3</sup> Therefore, the dot density was 15.3 dots/deg<sup>2</sup> for each eye. Dots of different colors moved in opposite horizontal directions, and the assignment of the red/blue color and the left/right direction was random within each trial block. All dots moved at a speed of 3.7 deg/s, traversing a 0.41° path in 11 frames (110 ms) before being replotted in a new random position. To prevent global blinking after every 11 frames, initial dot ages were asynchronized. Dots moving out of the viewing area 'wrappedaround' to the opposite side. There was no fixation point within the display. The display was viewed foveally.

<sup>&</sup>lt;sup>3</sup> The aperture used in our rivalry experiment was smaller than the aperture used in our repulsion experiment because we found that exclusive dominance was more easily obtained with the smaller aperture.



Fig. 6. Schematic presentation of motion rivalry stimuli. Dot trajectories are shown for each stimulus condition in the motion rivalry experiment. The black, white, and gray dots shown here respectively correspond to dots that appeared red, blue, and purple to the naked eye. All data were collected with observers wearing red/blue stereo glasses. In the exclusive-dominance-report paradigm, observers viewed either an unpaired stimulus (A), or a paired stimulus in which the oppositely moving dots had no vertical offset (B). In the two alternative-forced-choice paradigm, the 'standard' stimulus was unpaired (A) while the paired 'test' stimuli had vertical offsets of 0', 6.6' or 13.2' (B, C, D, respectively). In the binocular control condition, the 'test' was an unpaired stimulus and each dot was drawn with both the 'red' and 'blue' guns of the monitor. To the naked eye these dots appeared purple, signified here by gray dots (E).

The integrity of the red/blue glasses was verified in a control experiment, which required the observers to view moving stimuli through one filter only. When the red filter was covered and observers monocularly viewed the stimuli through the blue filter, two motion stimuli were shown sequentially. One stimulus contained only blue dots moving in one horizontal direction. The other stimulus contained blue dots moving in one horizontal direction and red dots moving in the opposite horizontal direction. Observers were required to identify the interval ('first' or 'second') that contained two directions of motion. Performance was at chance levels, indicating that the red dots could not be seen through the blue filter. Similarly, performance was at chance levels when the dot colors were switched (red to blue, and vice versa) and observers monocularly viewed the displays through the red filter. Therefore, the observers' performance in the control experiment indicated that any residual 'leakage' from the filters was not sufficient to influence behavior.

Unlike experiment 1, the spatial pairing in experiment 2 was between dots presented to different eyes. The 'unpaired' stimulus contained red and blue dots whose positions were spatially independent of each other, whereas in the completely 'paired' stimulus, dots of different colors were constrained to have spatially overlapping trajectories (with 0 vertical offset). We also considered two less precisely paired stimuli by introducing 6.6' and 13.2' vertical offsets between the dots in each pair, respectively. The unpaired and the three paired stimuli are shown schematically in Fig. 6A-D.

#### 3.1.3. Procedure

To examine the effect of the interocular spatial pairing on motion rivalry, we used two different paradigms; an exclusive-dominance-report paradigm, and a two alternative-forced-choice paradigm (2-AFC). In the exclusive-dominance-report paradigm, observers viewed either the unpaired (Fig. 6A), or the completely paired (Fig. 6B) stimuli continuously for 60 s. The observers' task was to depress a button when one of the two directions was exclusively visible (i.e. during exclusive dominance; Blake, Yu & Lokey, 1998), and to release the button whenever two directions were simultaneously visible. Each observer completed, in random order, five trials in each of the two stimulus conditions. A repeated-measures *t*-test was used to determine whether the mean duration of exclusive rivalry depended on spatial pairing.

We next used a 2-AFC paradigm to investigate whether motion rivalry is systematically altered by the precision of spatial pairing. On every trial, a 'standard' and a 'test' stimulus were sequentially presented for 3 s each, with a 500 ms inter-stimulus interval. The 'standard' was always the unpaired stimulus (Fig. 6A) and the 'test' was one of the three paired stimuli, having a vertical offset of 0', 6.6' or 13.2' (Fig. 6B-D). The observers' task was to indicate which of the two intervals appeared more motion rivalrous (i.e. produced greater directional dominance). Within each 50-trial block, the order of 'standard' and 'test' stimuli was random, and just one level of paired precision (either 0' or 6.6' or 13.2') was presented. Each observer completed five 50-trial blocks in each of the three 'test' conditions, presented in random order. The data were

analyzed by plotting the percentage of trials on which the variously paired 'tests' appeared more motion-rivalrous than the unpaired 'standard'.

In principle, it was possible for an observer to show a dependence on spatial pairing without ever experiencing motion rivalry. This is because a rivalry-blind observer could have employed a strategy by which the stimulus containing the greater mean vertical distance between the red and blue dots would be selected as 'more rivalrous' on each trial. To investigate this possibility we added a binocular control condition. The 'standard' in the control condition was, as always, the unpaired stimulus presented dichoptically. The 'test' also comprised spatially unpaired dots, however, *all* 'test' dots were presented to *each* of the eyes. This was achieved by drawing every dot in the 'test' stimulus with both the 'red' and the 'blue' guns of the monitor<sup>4</sup> so that the dots appeared purple to the naked eye.<sup>5</sup>





Fig. 7. The effect of pairing on the duration of motion rivalry. Data from the exclusive-dominance-report paradigm are plotted. On the left ordinate, the duration of motion rivalry is shown as a percentage of the 60-s viewing duration. The right ordinate reflects the duration in seconds. For individual observers, each bar reflects the mean and standard error from five 60-s trials in the unpaired (black bars) and paired (white bars) conditions. The two bars on the right reflect the average across observers and one standard error after consistent individual differences were removed (Loftus & Masson, 1994).

Thus, on control trials, the vertical distance between the dots in each pair was the same in 'standard' and 'test' stimuli, yet only the 'standard' stimulus would be expected to produce motion rivalry. Indeed, a strategy based on motion rivalry would lead one to choose the 'standard' on all control trials, whereas a strategy based on spatial cues would lead one to choose the 'standard' on just half the control trials.

### 3.1.4. Results (experiment 2)

The effect of interocular spatial pairing on motion rivalry can be seen in Fig. 7, which contains the data from the exclusive-dominance-report paradigm. For each observer, the mean duration of exclusive rivalry was much greater when the dots were spatially unpaired (black bars) than when the dots were spatially paired (white bars). The two bars on the far right indicate the averages across the four observers and one standard error after consistent individual differences were removed (Loftus & Masson, 1994). A repeated-measures t-test revealed that the observers saw exclusive dominance for a significantly longer duration in the unpaired condition (mean = 36 s) than in the paired condition (mean = 4.4 s) (t(3) = 5.1, P < 0.05, two-tailed). This was true despite the fact that opposite directions of motion were physically present in both the unpaired and paired conditions.

In the above exclusive-dominance paradigm only the unpaired and the completely paired stimulus conditions were tested. The results from the 2-AFC paradigm indicated that motion rivalry also depended on the precision of interocular pairing. This dependence can be seen in Fig. 8, where the percentage of trials on which the 'test' appeared more rivalrous than the 'standard' is plotted for each level of paired-precision. The white and the two differently hatched columns, respectively, correspond to 'test' stimuli that had vertical offsets of 0', 6.6' and 13.2'. For each observer, the percentage of trials on which the 'test' was seen as more rivalrous than the 'standard' increased monotonically as the vertical offset between oppositely moving dots in the two eyes increased. Averaging across the four observers produced the bars on the far right, where the standard error is also shown after consistent individual differences were removed (Loftus & Masson, 1994). The means increased from 5.2% when there was no vertical offset, to 10.2 and 23.75% when the vertical offset was respectively increased to 6.6' and 13.2'. This monotonicity suggests that motion rivalry can be systematically altered by the precision of spatial pairing.

It is unlikely that the data in Fig. 8 can be explained by a strategy in which observers based their judgments directly on the vertical offset, rather than on motion rivalry. Such a strategy would have produced a 50% responding rate in the binocular control condition (illustrated in Fig. 6E), since both the 'test' and 'standard'

<sup>&</sup>lt;sup>4</sup> The intensity of the 'red' and 'blue' guns was adjusted so that resultant binocular-control stimuli appeared as bright as the dichoptically presented stimuli.

<sup>&</sup>lt;sup>5</sup> Although the 'test' dots appeared purple to the naked eye, observers viewed all stimuli while wearing red/blue glasses. As a result, the 'test' dots did not appear purple during actual trials, thereby precluding the perception of purple dots as a basis for employing a unique strategy in this control condition.

**Data from 2-AFC Rivalry Paradigm** 



Fig. 8. Motion rivalry changes with the precision of pairing. Data from the 2-AFC paradigm are plotted. The ordinate indicates the percentage of trials on which the 'test' stimulus was judged to be more rivalrous than the 'standard' stimulus. For individual observers, the bars represent the mean and standard error of five 50-trial blocks. 'Test' stimuli appeared increasingly rivalrous as the vertical offset between moving elements increased from 0' (white columns), to 6.6' (45° hatched columns) and 13.2' (135° hatched columns). The cluster on the far right reflects the mean of the four observers, and one standard error after consistent individual differences were removed (Loftus & Masson, 1994). In the control condition (small solid bars), the binocularly presented 'test' stimuli were never seen as more rivalrous than the 'standard'. The solid bars should therefore be plotted at zero, but are plotted slightly above zero here so as to be visible.

control stimuli were spatially unpaired. To the contrary, we found that each observer identified the 'standard' as being more rivalrous than the binocularly presented 'test' on every trial. Thus, the percentage of trials on which the binocular 'test' was seen as more rivalrous than the 'standard' was zero. For the purpose of illustration, these zero scores are represented as very short solid bars in Fig. 8.

It is also unlikely that the data in Fig. 8 can be explained by the possibility that the oppositely moving dots in the more precisely paired stimuli had been stereoscopically fused. If this were the case, one would expect the observers to have seen motion in depth. Instead, when rivalry was not seen the stimuli appeared to contain locally opposite directions of motion, and to flicker globally. Therefore, the data in Fig. 8 are not easily explained by stereoscopic fusion. Additionally, this absence of motion in depth is consistent with an earlier report (Regan, Erkelens & Collewijn, 1986) which suggested that motion in depth is not seen in multi-dot displays containing no optical expansion cues and no central fixation point.

Finally, we considered the possibility that the data in Fig. 8 reflected the operation of a general binocular mechanism, rather than a specific motion mechanism. Accordingly, we created displays in which the interocular positional information was the same as before, but the dots flickered in place rather than moving coherently. A general binocular mechanism would presumably respond to this stimulus, whereas a motion mechanism would not. Under this condition, when the vertical interocular offset was zero a volume of flickering dots was perceived — an unsurprising percept since the horizontal distance between the red and blue dots in a pair was random across the display. When a vertical interocular offset was added to the interocularly paired dots or when the dots were interocularly unpaired, the flicker became flat, and more importantly, no rivalry was seen. This is in sharp contrast to the rivalry that had been seen when opposite directions of motion were presented to the two eyes. The absence of rivalry in the flicker conditions may have been owing to the fact that the two monocular flickering images could not be discriminated.6 Indeed, under binocular viewing conditions, even the first author was unable to correctly judge beyond chance levels whether the two monocular flickering images were the 'same' or 'different'. This was

<sup>&</sup>lt;sup>6</sup> As Verhoeff (1935) noted, if an image presented to one eye first dominates, and is then suppressed by an identical (or a sufficiently similar) image presented to the other eye, the observer would not experience the change. Similarly, an observer would not likely experience a change if a randomly varying stimulus presented to one eye first dominates, and then is replaced by a randomly varying stimulus presented to the other eye.

true for both two-spatial-interval and two-temporal-interval paradigms. In summary then, the absence of a rivalrous percept in our flicker experiment implies that different directions of motion were necessary for the rivalry reflected in Fig. 8. This in turn suggests that a motion mechanism, rather than a general binocular mechanism, was responsible for the rivalry data in experiment 2.

### 4. Discussion

The purpose of this study was to determine whether the distance between moving elements affects two well known motion phenomena — motion repulsion, and binocular motion rivalry. These phenomena were studied separately, and we will discuss each in turn.

Experiment 1 was designed to determine whether the pairing of dots in spatially intermingled random dot patterns affects motion repulsion. When dots were precisely paired so that the average spatial offset between dots in each pair was only 7.4 arc min, observers perceived a single global flow moving near the horizontal axis. When the paired spatial offset was increased to 13.2 arc min, however, two global flows were reliably seen and the more downward direction was perceived veridically. Finally, we found the well-known motion repulsion when the dots were unpaired or when the average distance between paired dots was 21.0 arc min or greater. Thus, the spatial offset between dots moving in different directions significantly affected perceived direction. Similar findings were obtained in a preliminary study in which the two motion directions differed by only 45° (Qian & Geesaman, 1995).

We note that the coherent motion seen in our most precisely paired displays can be conceptualized as the most extreme case of motion attraction — an underestimation of the angle between two directions. Accordingly, the systematic change from underestimating directional differences to overestimating directional differences with the increase of spatial separation appears to be qualitatively similar to stereoscopic attraction and repulsion (Westheimer, 1986; Westheimer & Levi, 1987): Attraction is observed at the smallest separations, while repulsion is observed at larger separations. This raises the possibility that the phenomena in both visual submodalities could be caused by similar mechanisms.

Rauber and Treue (1998) have recently examined the notion that motion repulsion is an interaction between two directions. They found that when just a single direction of motion was presented, observers systematically overestimated the angle between the presented direction and the nearest cardinal (i.e. horizontal or vertical) direction;<sup>7</sup> a phenomena dubbed reference repulsion. It is possible, therefore, that some of the repulsion observed in the present unpaired condition can be attributed to reference repulsion, rather than an interaction between the two motions. However, since we presented the same two physical directions within each trial block, the systematic changes in perceived direction could not be entirely attributed to reference repulsion. Accordingly, we suggest that the phenomena of motion repulsion may be largely determined by the following stimulus factors: (1) the angle between the direction of motion being judged and the nearest cardinal direction (Hiris & Blake, 1996; Rauber & Treue, 1998); (2) the angle and speed difference between the presented directions of motion (Marshak & Sekuler, 1979); and (3) the precision with which dots in the two presented directions are spatially paired.

In experiment 2 of the present study, we used two different paradigms to examine the effect of interocular spatial pairing on binocular motion rivalry. In the first paradigm, motion rivalry was seen for significantly longer durations when the stimulus comprised interocularly unpaired dots than when the stimulus comprised interocularly paired dots. In the second paradigm, we found that motion rivalry also depended on the precision of pairing. Specifically, the stimuli could be made to appear increasingly rivalrous as the interocular vertical offset between oppositely moving elements was increased from 0' to 13.2'. Thus, although the same directions of motion were physically present across our stimulus conditions, motion rivalry was systematically altered by changes in the distance between moving elements presented to the two eves.

We believe that the results from experiment 2 may provide useful information about the neural locus of binocular rivalry. In particular, the results suggest that motion rivalry may be mediated by neural responses at or after binocular convergence. This follows from the fact that monocular neurons would be incapable of directly sensing our interocular pairing manipulation. Of course, our psychophysical experiments cannot rule out the possibility that monocular cortical neurons responded indirectly to the binocular pairing via interactions with binocular neurons (Blake, 1989). Nevertheless, the most straightforward interpretation of our data is consistent with earlier physiological (Leopold & Logothetis, 1996) and psychophysical (Logothetis, Leopold, & Sheinberg, 1996) reports suggesting that rivalry correlates with the responses of binocular neurons.

 $<sup>^{7}</sup>$  Using random dot patterns that contained two directions of motion, Hiris and Blake (1996) also found direction repulsion to be considerably reduced when the direction to be estimated was one of the four cardinal directions.

The present findings are reminiscent of those reported previously for motion transparency. Qian et al. (1994) found that the percept of global transparent motion could be much reduced by spatially pairing dots moving in different directions. Likewise, the present data indicate that by decreasing the spatial offset between paired dot trajectories both motion repulsion and binocular motion rivalry can be largely eliminated. Taken together, these studies demonstrate that the spatial relationship between moving elements can significantly affect how the visual system integrates different directions of motion. Indeed, it might be that the motion system uses spatial relationship as the basis for integrating or segmenting individual features, such as motion direction. These psychophysical findings are consistent with the physiological and anatomical data indicating that a common pathway in the primate visual system mediates motion perception, binocular vision, and the perception of spatial relationships.

#### Acknowledgements

We are grateful for the suggestions made by Dr Leslie Welch, and two anonymous reviewers. This work was supported by the N.I.H. and the Sloan Foundation.

#### References

- Ball, K., & Sekuler, R. (1987). Direction specific improvements in motion discrimination. *Vision Research*, 27(6), 953–965.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145–167.
- Blake, R., Yu, K., & Lokey, M. (1998). Binocular rivalry and motion perception. Journal of Cognitive Neuroscience, 10(1), 46–60.
- Bowne, S. F., McKee, S. P., & Glaser, D. A. (1989). Motion interference in speed discrimination. *Journal of the Optical Society* of America, 6(7), 1112–1121.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1(1), 1–47.
- Fox, R., Todd, S., & Bettinger, L. A. (1975). Optokinetic nystagmus as an objective indicator of binocular rivalry. *Vision Research*, 15, 849–853.
- Hiris, E., & Blake, R. (1996). Direction repulsion in motion transparency. Visual Neuroscience, 13, 187–197.

- Ishihara, S. (1973). Tests for colour-blindness. Tokyo: Kanahara Shuppan.
- Leopold, D. A., & Logothetis, N. A. (1996). Activity changes in early visual cortex reflect monkey's percept during binocular rivalry. *Nature*, 279, 549–553.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, 1(4), 476–490.
- Logothetis, N. A., Leopold, D. A., & Sheinberg, S. L. (1996). What is rivaling during binocular rivalry? *Nature*, 380, 621-624.
- Marshak, W. M., & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science*, 205, 1399–1401.
- Matthews, N., Geesaman, B. J., & Qian, N. (1999). Spatial pairing affects motion rivalry and repulsion. Society for Neuroscience Abstracts, 25(1), 1052.
- Matthews, N., & Welch, L. (1997). Velocity-dependent improvements in single-dot direction discrimination. *Perception & Psychophysics*, 59(1), 60–72.
- Matthews, N., & Qian, N. (1999). Axis-of-motion affects direction discrimination, not speed discrimination. *Vision Research*, 39(13), 2205–2211.
- Morgan, M. J., Watt, R. J., & McKee, S. P. (1983). Exposure duration affects the sensitivity of vernier acuity to target motion. *Vision Research*, 23(5), 541–546.
- Nishida, S., & Johnston, A. (1999). Influence of motion signals on perceived position of spatial pattern. *Nature*, 397(6720), 610–612.
- Qian, N., Andersen, R. A., & Adelson, E. H. (1994). Transparent motion perception as detection of unbalanced motion signals. I. Psychophysics. *The Journal of Neuroscience*, 14, 7357–7366.
- Qian, N., & Geesaman, B. J. (1995). Motion repulsion depends on the distance between the moving elements. *Investigative Ophthal*mology and Visual Science (supplement), 36, 50.
- Randot Stereotests (1988). Stereo Optical Company, Chicago.
- Rauber, H. J., & Treue, S. (1998). Reference repulsion when judging the direction of visual motion. *Perception*, 27, 393-402.
- Regan, D., Erkelens, C. J., & Collewijn, H. (1986). Necessary conditions for the perception of motion in depth. *Investigative Ophthal*mology and Visual Science, 27(4), 584–597.
- Ungerleider, L. G., & Mishkin, M. (1983). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield, *Analysis of visual behavior*. Cambridge, MA: MIT Press.
- Verhoeff, F. H. (1935). A new theory of binocular vision. Archives of Ophthalmology, 13, 152–175.
- Welch, L., & McKee, S. P. (1985). Colliding targets: evidence for spatial localization within the motion system. *Vision Research*, 25(12), 1901–1910.
- Welch, L., MacLeod, D. I., & McKee, S. P. (1997). Motion interference: perturbing perceived direction. *Vision Research*, 37(19), 2725–2736.
- Westheimer, G. (1986). Spatial interaction in the domain of disparity signals in human stereoscopic vision. *Journal of Physiology*, 370, 619–629.
- Westheimer, G., & Levi, D. M. (1987). Depth attraction and repulsion of disparate foveal stimuli. *Vision Research*, 27, 1361–1368.