

Effects of attention on motion repulsion

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Abstract

Motion repulsion involves interaction between two directions of motion. Since attention is known to bias interactions among different stimuli, we investigated the effect of attentional tasks on motion repulsion. We used two overlapping sets of random dots moving in different directions. When subjects had to detect a small speed-change or luminance change for dots along one direction, the repulsive influence from the other direction was significantly reduced compared with the control case without attentional tasks. However, when the speed-change could occur to either direction such that subjects had to attend both directions to detect the change, motion repulsion was not different from the control. A further experiment showed that decreasing the difficulty of the attentional task resulted in the disappearance of the attentional effect in the case of attention to one direction. Finally, over a wide range of contrasts for the unattended direction, attention reduced repulsion measured with the attended direction. These results are consistent with the physiological finding that strong attention to one direction of motion reduces inhibitory effects from the other direction.

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1. Introduction

Motion repulsion is the overestimation of the angle between two stimuli moving in different directions (Marshak & Sekuler, 1979). This phenomenon reflects the interaction between neural representations of the two directions. Numerous physiological studies (Colby & Goldberg, 1999; Desimone & Duncan, 1995; Gottlieb, Kastner, & Reynolds, 2003; Kastner & Ungerleider, 2000; Treue, 2001) and psychophysical experiments (Alais & Blake, 1999; Lankheet & Verstraten, 1995;

von Grunau, Bertone, & Pakneshan, 1998) have demonstrated that attention can effectively alter stimulus interactions by enhancing the neural responses to the attended stimuli while simultaneously suppressing those to the unattended stimuli. We thus expect that motion repulsion should be strongly influenced by attention. More specifically, it has been proposed that inhibition between different directions of motion is responsible for motion repulsion (Hiris & Blake, 1996; Marshak & Sekuler, 1979; Wilson & Kim, 1994). Since attention to an MT cell's preferred direction of motion greatly reduces inhibition from the other direction of motion in the cell's receptive field (Treue & Maunsell, 1999), we expect that attention to one direction should reduce repulsive effects from the other, unattended direction.

Recent studies showed that even when a single direction is presented, human observers tend to overestimate the angle between that direction and the nearest cardinal

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axis, a phenomenon termed reference repulsion (Raubert & Treue, 1998, 1999). Therefore, only a part of motion repulsion originates from the interaction between the two directions, while the remaining comes from reference repulsion. In this study, we excluded reference repulsion from our measurements because only the portion of repulsion pertaining the interaction between two directions is expected to be strongly affected by attention. A recent abstract examined the effect of attention on repulsion (Alais, 2001). However, since a static marker (instead of a moving pattern) was used to measure repulsion in that study, reference repulsion was not excluded from the measurements (Chen, Matthews, & Qian, 2001; Rauber & Treue, 1998). In addition to focusing on the interactive portion of motion repulsion, we used demanding attentional tasks to further increase attentional effects. We also examined different attentional cues, attention to one or both directions of motion, the task difficulty, and the contrast dependence of attention. Preliminary results were reported previously in abstract form (Chen, Matthews, & Qian, 2002).

2. Experiment 1: Attending to speed-changes in one of two directions

2.1. Method

2.1.1. Observers

Three of the authors and two naive observers participated in this experiment. One of the authors (XM) was naive for this and the second experiments but not for the other experiments. All subjects had normal or corrected-to-normal vision. All experiments were undertaken with the understanding and written consent of each observer, and approval from our Institutional Review Board.

2.1.2. Apparatus and stimuli

The experiment was conducted on a 21 in. ViewSonic P817 monitor controlled by a Macintosh G4 500 MHz computer. The vertical refresh rate of the monitor was 120 Hz, and the spatial resolution was 1024×768 pixels. In a well-lit room, observers viewed the stimuli through a circular black tube with a diameter of 10 cm. A chin rest was used to stabilize head position at 76 cm from the monitor.

The screen had a constant veiling luminance of 47.2 cd/m^2 . The stimuli were random dot cinematograms (RDCs), seen as black dots (13.3 cd/m^2 , contrast 56.0%) translating within a virtual circular aperture (47.2 cd/m^2) that was 3° in diameter. Each dot was a 2×2 pixel square (approximately $3.6'$ on each side), and was generated with an anti-aliasing technique that set the luminance of a pixel in proportion to the area covered by the dot after linearizing the monitor. Dots that disappeared at one side of the aperture reappeared

at the opposite side. The fixation point had a diameter of $10.8'$ and was located at the center of the aperture. All stimuli were computed online. To save computing time, the stimuli were regenerated every 2 frames. Therefore, the effective stimulus refresh rate was 60 Hz.

Each trial consisted of a test RDC followed by a reference RDC. Two sets of 50 random dots were presented in the test RDC: one set moved in the upper-right direction, while the other moved in the lower-right direction. The initial speed for both sets of dots was $2^\circ/\text{s}$. At a random time from 400 to 800 ms after onset and in randomly mixed trials, the upper-right motion either slowed down, had no change, or sped up, for 200 ms, and then returned to the initial speed for 300 ms, while the speed of the lower-right motion was always constant. The amount of speed change in the upper-right motion depended on observers (see *Procedures*). The upper- and lower-right directions were chosen around 22.5° and -22.5° from the horizontal axis, respectively. To prevent observers from learning simply to report the same motion direction in every trial, a random angle uniformly distributed in $[-2.5^\circ, 2.5^\circ]$ was drawn in each trial; it was then added to one direction and subtracted from the other so that the mean direction of the two motions was always horizontal. Therefore, the physical directions for the upper-right motion and for the lower-right motion ranged from 20° to 25° , and from -20° to -25° , respectively.

The reference RDC served as a direction indicator, consisting of 50 dots moving in a upper-right direction only. Observers were required to adjust online this single direction to match the perceived direction of the upper-right motion in the test RDC of that trial, and press a key when done. The initial direction of the reference RDC was uniformly distributed in a 24° range centered at the upper-right, physical direction of the test RDC. It is important to use the reference RDC with moving dots, instead of a static marker, to measure motion repulsion because we did not want to include reference repulsion in the measurements (Chen et al., 2001; Rauber & Treue, 1998). Reference repulsion must work in a similar way in both the test and the reference RDCs with moving dots, and when motion repulsion in the test RDC is measured relative to the reference RDC in each trial, the reference repulsion is automatically discounted (Chen et al., 2001; Rauber & Treue, 1998).

The stimuli were generated in Matlab, using Psychophysics Toolbox extensions generously provided by Brainard (1997) and Pelli (1997).

2.1.3. Procedure

Each trial started with a fixation point that remained visible for the duration of the trial. Subjects were asked to fixate even though eye movements do not affect motion repulsion (Marshak & Sekuler, 1979; Rauber & Treue, 1999). After a key press, the test RDC was first

presented, followed by the reference RDC after a 1-s inter-stimulus interval. Three conditions were employed in this experiment: attentional condition and two controls—2-motion and 1-motion conditions. In the attentional condition, observers had to perform an attentional task—respond to the speed-change. They were instructed to press a key to terminate the test RDC if a speed-change was detected, or wait for the test RDC to disappear if no speed-change occurred. There was an equal number of trials for each of three speed-change cases (slow-down, no-change, and speed-up). The no-change trials, as well as the random onset time of speed change, help to prevent the subjects from using a simple timing strategy to report a change in every trial. They also help to rule out that the speed-changes per se affect motion repulsion. The duration from the actual speed-change to the observer's response was recorded as reaction time for the attentional task, usually around 400 ms. Observers were required to respond within a time window of 200–500 ms after the actual speed-change. A trial was aborted if subjects responded outside this time window, or responded when there was no actual speed-change. Audio feedback was provided for the aborted trials. The 2-motion condition was the normal motion repulsion paradigm. The stimuli were identical to those for the attentional condition, but subjects were instructed to ignore any speed-change. There was no requirement to report the speed-change and no audio feedback. The 1-motion condition was same as the attentional condition (including the detection of the speed-change) except that the lower-right motion in the test RDC was removed. Therefore, the attentional and 2-motion conditions employed same stimuli but different instructions, while the attentional and 1-motion conditions employed same instructions but different stimuli. For all conditions, subjects were required to adjust the direction of the reference RDC to match the perceived direction of the upper-right component in the test RDC in each trial.

Before data collection, we first determined each observer's sensitivity to the speed-change. We initially chose to measure the psychometric curves for the speed-up and slow-down cases with the constant stimulus method and a 2AFC procedure, and obtained the thresholds at 75% performance. However, we soon found that when the threshold speed-changes so measured were used in the main experiment, the observers' actual performances could be very different from 75%. The reason is that to obtain the psychometric curves, we had to use multiple speed increments and decrements, whereas in the main experiment, only a single increment and a single decrement were needed and a third of the trials had no speed-change. We therefore switched to the following staircase-like adjustment procedure. The stimuli were identical to the test RDCs in the attentional condition, with 20 trials for each speed-

change case (slow-down, no-change, or speed-up) in a block. Observers were only required to perform the attentional task without reporting the perceived directions. Audio feedback occurred on trials when the observer responded incorrectly. In the first block, the speed changes for each observer were initialized to -1 and $+1^\circ/\text{s}$ for the slow-down and speed-up cases, respectively. If an observer's performance to the slow-down or speed-up case was higher than 80%, the corresponding magnitude of speed-change was decreased by 0.2 or $0.25^\circ/\text{s}$ in the next block; if the performance was lower than 70%, the magnitude was increased by 0.2 or $0.25^\circ/\text{s}$. If the performance to the constant-speed case alone was higher than 80% (or lower than 70%), the magnitudes of speed-changes in the other two cases were both decreased (or increased) by 0.2 or $0.25^\circ/\text{s}$ in the next block. This procedure was repeated until the performance in each speed-change case was confined within 70–80% or until five blocks were run. Most observers reached this criterion in three blocks. One subject could not meet the criterion in five blocks, and the parameters for 65% correct were used. The final speed-change values were applied to all three experimental conditions. The mean test-RDC duration of the attentional condition from the pilot study was used as the duration of test RDCs in the 2-motion condition to ensure identical stimulation in the two conditions.

For data collection, the attentional, 2-motion, and 1-motion conditions were run in separate blocks of trials in a random order for each observer. Observers completed 30 trials for each speed-change case under each condition. Each condition usually took 30 min or less, including 30 practice trials and 1-min break every 30 trials. To minimize variations in observers' attentional state, we always ran the three conditions in a 2-h session on the same day for each observer. Although all but one observers showed performances between 70% and 80% in the pilot study, some of them failed to meet this criterion in the attentional condition of the main experiments due to day-to-day variations. Therefore, if an observer's performances were outside of 65–85% in the attentional condition, all three conditions were repeated after adjusting the speed changes one more time. The final speed-changes for the slow-down and speed-up cases were -0.5 and $+0.5$ (CQ), -0.75 and $+1.2$ (XM), -0.5 and $+0.5$ (YC), -0.75 and $+1.2$ (NQ), and -1 and $+1$ (XW) deg/s from the initial speed of $2^\circ/\text{s}$, for the five subjects, respectively. Their performances averaged over the three speed-change cases in the attentional condition were 79.9%, 69.2%, 71.3%, 83.3% and 65.6%, respectively, and those in the 1-motion condition were 68.9%, 81.7%, 75.1%, 79.0% and 64.4%, respectively. Although only the upper-right motion was presented in the 1-motion condition, there was no consistent trend that observers performed better in the 1-motion condition than in the attentional condition.

2.2. Results

Fig. 1 shows motion repulsion of five observers in the attentional, 2-motion, and 1-motion conditions. The motion repulsion is defined as the reported direction with the reference stimulus, minus the physical upper-right direction of the test stimulus. A positive value represents repulsion, while a negative value represents attraction. Since the reference stimulus contained moving dots (instead of a static marker), the reference repulsion is discounted from the results (Chen et al., 2001; Rauber & Treue, 1998). In each condition, we obtained motion repulsion for each observer under the three speed-change

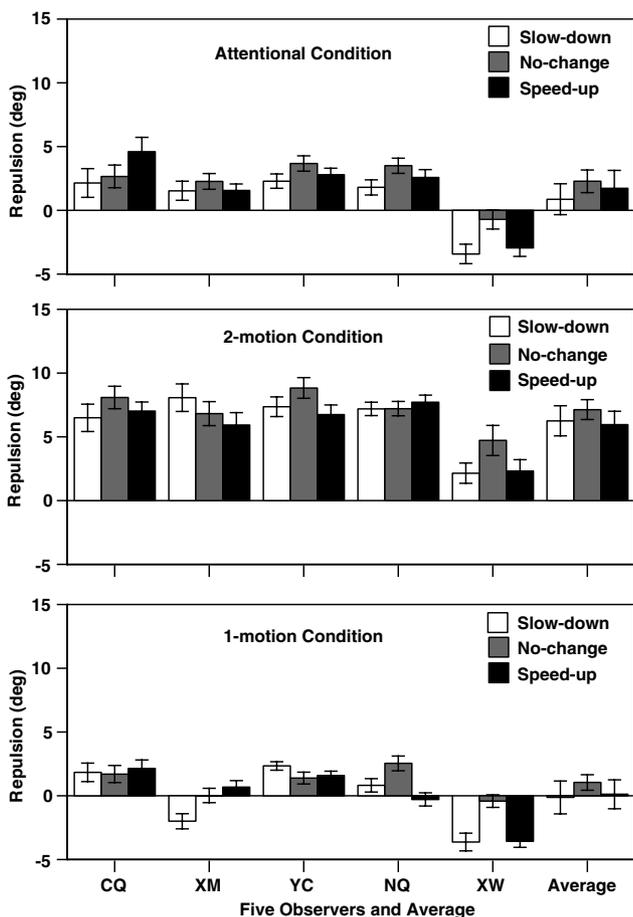


Fig. 1. Motion repulsion measured from the upper-right direction for five observers with speed-change detection as the attentional task. The three panels from top to bottom correspond to the attentional, 2-motion and 1-motion conditions, respectively. In each panel, the repulsion values for the three speed-change cases (slow-down, no-change, speed-up) are shown separately for each observer. The rightmost set of columns represents the average across observers. The positive and negative values indicate repulsion and attraction, respectively. Each error bar represents ± 1 SE (i.e., a total of 2 SEs). Note that for individual observers the standard errors were calculated from 30 trials, while for the “Average” the standard errors were obtained across the five observers. No significant difference was found among the three speed-change cases, while motion repulsion differed between each pair of conditions (see Fig. 2).

cases (slow-down, no-change, speed-up), represented by the bars with three different gray levels in Fig. 1. A within-subjects ANOVA revealed that there was no significant difference of repulsion among the three speed-change cases in each condition ($F(2,4) = 3.84, p = 0.07$ in the attentional condition; $F(2,4) = 2.36, p = 0.16$ in the 2-motion condition; $F(2,4) = 1.34, p = 0.32$ in the 1-motion condition). This result indicates that a brief speed-change per se does not influence motion repulsion. Therefore, we redrew Fig. 1 in Fig. 2 by averaging the repulsion values for each observer across the three speed-change cases in each condition.

Fig. 2 reveals the obvious difference among the three conditions. The mean repulsion values were $1.6^\circ, 6.4^\circ$ and 0.3° for the attentional, 2-motion and 1-motion conditions, respectively. The 2-motion condition measured the normal motion repulsion between two directions of motion. Motion repulsion in the 2-motion condition was significantly greater than that either in the attentional condition ($F(1,4) = 440, p < 0.001$) or in the 1-motion condition ($F(1,4) = 284, p < 0.001$). On the other hand, repulsion in the attentional condition was also greater than that in the 1-motion condition ($F(1,4) = 14.6, p = 0.019$), although the difference was not as large as the above two. This result indicates that attention to one of two directions indeed reduces motion repulsion, but does not eliminate it. It can be argued

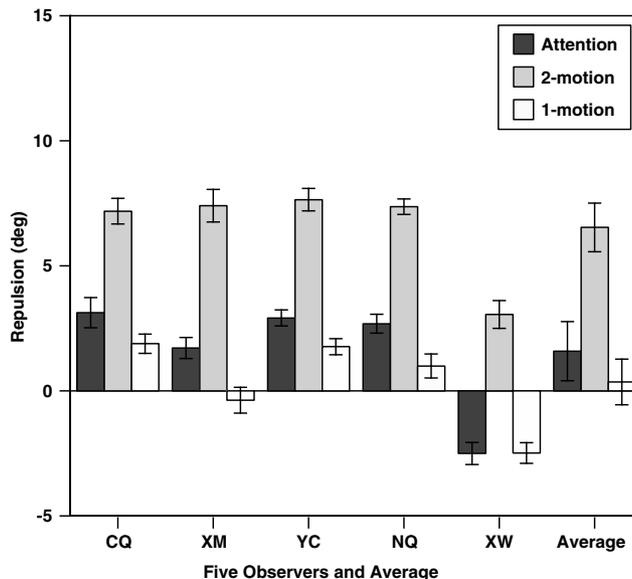


Fig. 2. Motion repulsion measured from the upper-right direction for five observers with speed-change detection as the attentional task. It is redrawn from Fig. 1 by averaging across the three speed-change cases for each observer in each condition. Note that the three bars for each observer represent the three experimental conditions, but not the three speed-change cases. The mean repulsion values were $1.6^\circ, 6.4^\circ$, and 0.3° in the attentional, 2-motion and 1-motion conditions, respectively. Motion repulsion was significantly greater in the 2-motion condition than that in the attentional condition, which was greater than that in the 1-motion condition.

that a certain amount of attention is always needed to perform any psychophysical task. However, it seems reasonable to assume that attention to the upper-right direction must be stronger in the attentional condition than in the 2-motion condition because of the demanding speed-change detection task. We believe that, since the stimulation was identical in these two conditions, it is this difference of the attentional load that is responsible for the different amounts of repulsion.

Note that observer XW showed a fairly large, negative value in the attentional condition. Since a similar negative value also exist in the 1-motion condition, this result suggests that the observer had a strong bias to underestimate the angle between the upper-right direction and horizontal axis. In other words, attention reduced motion repulsion, but did not reverse repulsion to attraction for that observer.

3. Experiment 2: Attending to luminance-changes in one of two directions

On the attentional task in Experiment 1, the requirement to detect speed-changes was motion-related, and may have directly affected the processing of motion direction. Therefore, in this experiment we introduced a motion-irrelevant attentional task—the detection of luminance change—to determine if the attentional effect depends on the specific attentional cue.

3.1. Method

The same five observers in the Experiment 1 participated in this experiment. The stimuli and procedures were same as those in Experiment 1 except that the speed-change was replaced with luminance change. In each trial, the initial luminance of the test RDC was 13.33 cd/m^2 , as in Experiment 1. After 400–800 ms, the luminance of the upper-right motion either turned dark, had no change, or turned bright for 200 ms, and then returned to the initial luminance for 300 ms. Again, the specific amount of luminance change for each observer was pre-measured to satisfy the criterion of 70–80% correct. In the turn-dark and turn-bright cases, the final luminance changes were -12.46 and $+10.46$ (CQ), -11.07 and $+10.46$ (XM), -11.07 and $+10.46$ (YC), -11.07 and $+10.46$ (NQ), and -12.46 and $+10.46$ (XW) cd/m^2 from the initial luminance of 13.33 cd/m^2 , for the five observers, respectively. Their performances in the attentional condition were 69.5%, 77.1%, 84.8%, 80.7%, and 67.2%, respectively, while those in the 1-motion condition were 81.4%, 92.8%, 88.2%, 89.1%, and 92.8%, respectively. Here, observers' performances were much better in the 1-motion condition than those in the attentional condition, in contrast with Experiment 1. Therefore, the lower-right direction appeared to affect

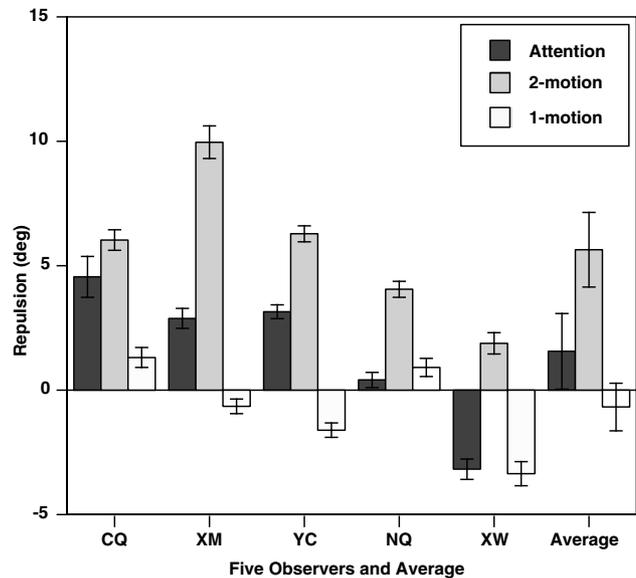


Fig. 3. Motion repulsion measured from the upper-right direction for five observers with luminance-change detection as the attentional task. The format is same as in Fig. 2. The mean repulsion values were 1.6° , 5.6° , and -0.7° in the attentional, 2-motion and 1-motion conditions, respectively. As in Fig. 2, motion repulsion was significantly greater in the 2-motion condition than that in the attentional condition.

the upper-right direction in the luminance-change detection task more than in the speed-change detection task.

3.2. Results

Fig. 3 shows motion repulsion of the same five observers with the luminance-change detection as the attentional task. Since no significant difference was found among the three luminance-change cases in each condition, only the mean values for each observer are shown here, with the same format as Fig. 2. Although there were some small variations, the result was very similar to that with the speed-change in Fig. 2. The mean repulsion values were 1.6 , 5.6 and -0.7° for the attentional, 2-motion and 1-motion conditions, respectively. Motion repulsion in the 2-motion condition was significantly greater than that either in the attentional condition ($F(1,4) = 18.7$, $p = 0.012$) or in the 1-motion condition ($F(1,4) = 23.0$, $p = 0.009$). Repulsion in the attentional condition was still greater than that in the 1-motion condition, but not significantly ($F(1,4) = 4.84$, $p = 0.093$). Taken together, the results from Experiments 1 and 2 indicate that attention reduces motion repulsion regardless of whether the attentional cue is motion relevant or not.

4. Experiment 3: Effect of attention to both directions

In the above experiments, subjects attended one of the two directions of motion. The reduced repulsion

under the attentional condition could be explained by the physiological notion that attention enhances the neural responses to the attended direction and suppresses the responses to the unattended direction, thus partially filtering out the inhibitory effects of the unattended direction on the attended direction. On the other hand, if subjects have to attend both directions of motion, neural responses to both directions should be somewhat enhanced, and repulsion should either stay the same, or even increase. This is tested in Experiment 3.

4.1. Method

Three (two authors and one naive) of five observers in Experiments 1 and 2 participated in this experiment. The speed-change of Experiment 1 was employed as the attentional cue, but different from Experiment 1, we introduced the speed-change to either one of the two directions in randomly mixed trials. Therefore, observers had to attend to both directions in order to perform well in this task. There were five possible speed-change cases: speed increment or decrement in the upper-right or lower-right direction, or no change at all. All five cases were randomly interleaved in each trial block. Since the 1-motion control condition was not necessary here, only the attentional and 2-motion conditions were run. In both conditions, observers were required to report the perceived upper-right direction by means of adjusting the reference stimuli, as in the first two experiments. In the attentional condition, observers had to respond if there was a speed change, regardless of the motion direction in which the change occurred. Observers were required to complete 30 trials for each speed-change case in each condition. The same speed-changes in Experiment 1 were employed here. Since attention was divided into both directions, this experiment should be more difficult than Experiment 1. However, the mean correct rates for the three observers were 80.0% (CQ), 78.2% (XM) and 83.1% (YC), respectively, better than those in Experiment 1. The reason is presumably that observers learned how to perform the attentional task from the previous two experiments.

4.2. Results

Fig. 4 shows motion repulsion for the three observers with the five speed-change cases in the attentional and 2-motion conditions. Similar to the result in Fig. 1 of Experiment 1, there was no significant difference in repulsion among the five speed-change cases in each condition ($F(4, 2) = 0.94$, $p = 0.49$ in the attentional condition; $F(4, 2) = 0.85$, $p = 0.53$ in the 2-motion condition). Interestingly, the repulsion did not depend on which motion direction the speed-change occurred as long as subjects had to pay attention to both directions.

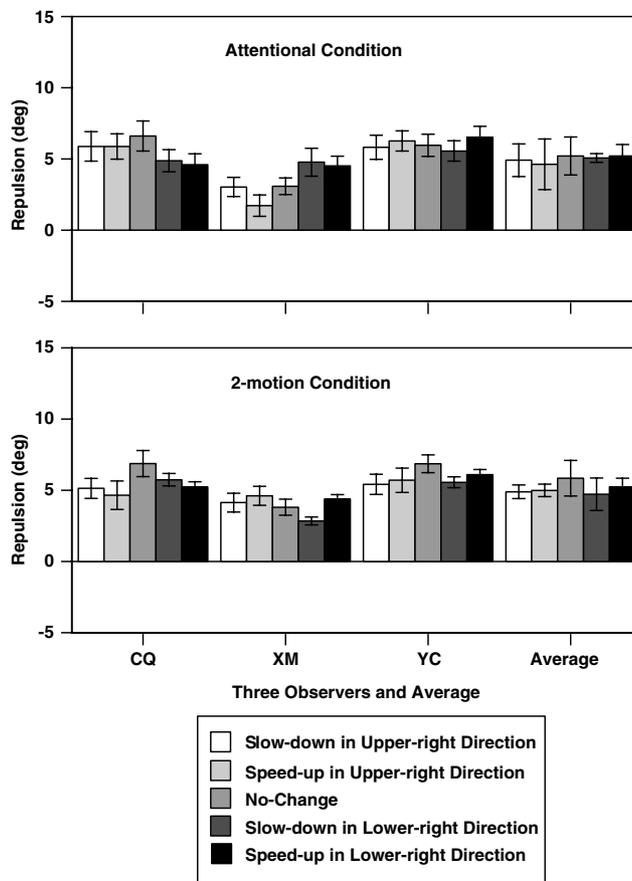


Fig. 4. Motion repulsion measured from the upper-right direction for three observers attending to both directions. The two panels represent the attentional and 2-motion conditions, respectively. In each panel, the repulsion values for the five speed-change cases are shown separately for each observer. The rightmost columns represents the average across observers. No significant difference was found among the five speed-change cases, or between the two conditions (see Fig. 5).

Since observers were required to respond to the speed-change—which was a salient event—it is possible that attention was automatically attracted to the direction with the speed change for a short period of time after the change. Therefore, our result suggests that a transient attentional shift, if any, did not affect motion repulsion when attention was directed to both directions overall.

Another important feature in Fig. 4 is that with attention to both directions, there was little difference between the attentional and 2-motion conditions. To show this more clearly, we redrew Fig. 4 in Fig. 5 by averaging the repulsion values for each observer across the five speed-change cases in each condition. The mean repulsion values were 4.7° and 5.2° for the attentional and 2-motion conditions, respectively. There was no significant difference between them ($F(1, 2) = 0.74$, $p = 0.48$). Since only three observers participated in this experiment, a lack of statistical power may be a reason for the insignificant difference. However, the same three observers showed a significant difference between the two conditions in Experiment 1 ($F(1, 2) = 215$,

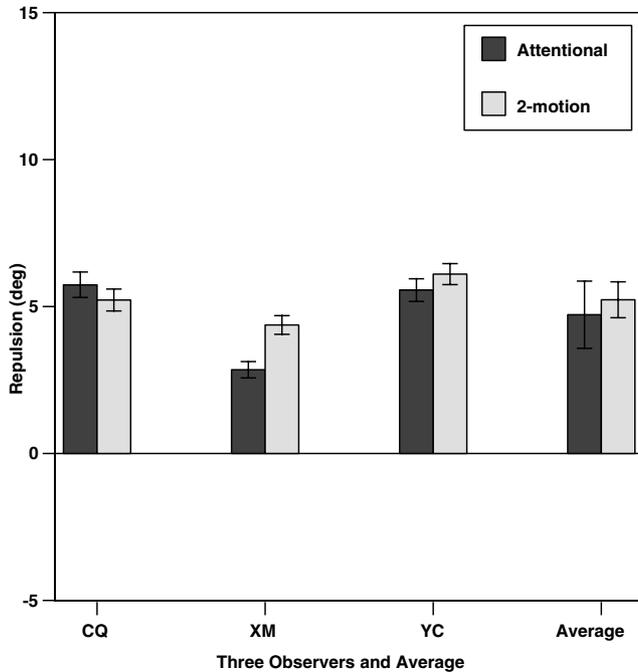


Fig. 5. Motion repulsion measured from the upper-right direction for three observers attending to both directions. It is redrawn from Fig. 4 by averaging across the five speed-change cases for each observer in each condition. The average repulsion values were 4.7° and 5.2° in the attentional and 2-motion conditions, respectively, and were not significantly different from each other.

$p = 0.005$). We therefore conclude that attention to both directions did not reduce motion repulsion as attention to one of the two directions did.

5. Experiment 4: Effect of attention during an easy task

If the reduced repulsion in Experiments 1 and 2 was indeed due to the attentional modulation of neuronal responses to the two motion directions, instead of due to some other aspects of the attentional task, then diminishing the attentional load by making the task easy should decrease the modulation (Beauchamp, Cox, & DeYoe, 1997; Spitzer, Desimone, & Moran, 1988) and thus attenuate the attentional effect. To test this prediction, we repeated the attentional and 2-motion conditions in Experiment 1 with decreased task difficulty.

5.1. Method

The same three observers in Experiment 3 participated in this experiment. The stimuli and procedures were same as those in Experiment 1 except that the amount of speed-change was made larger such that each observer reached the 90% correct rate in the pilot measurement of sensitivity to speed-change. The final speed-changes for the slow-down and speed-up cases were -1 and $+1$ (CQ), -1.3 and $+1.3$ (XM), and -1.3

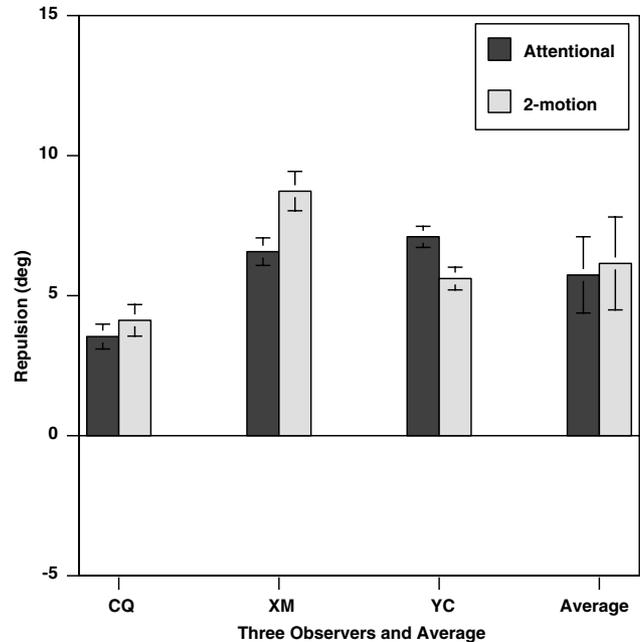


Fig. 6. Motion repulsion measured from the upper-right direction for three observers under the easy task. The format is same as in Fig. 5. The average repulsion values were 5.7° and 6.2° in the attentional and 2-motion conditions, respectively, and were not significantly different from each other.

and $+1.3$ (YC) deg/s from the initial speed of 2° /s, for the three observers, respectively. The corresponding correct rates in the attentional condition were 87.6%, 96.9%, and 95.4%, respectively.

5.2. Results

Fig. 6 shows motion repulsion of the three observers during the easy task. Again, since no significant difference was found among the three speed-change cases in each condition, only the mean values for each observer were shown, with the same format as in Fig. 5. The mean repulsion values were 5.7° and 6.2° for the attentional and 2-motion conditions, respectively. There was no significant difference between them ($F(1,2) = 0.15$, $p = 0.73$). Compared with the data for the same three observers in Experiment 1, motion repulsion under the easy attentional task was either unaffected by attention or was reduced by a much smaller amount. This result indicates that the effect of attention on motion repulsion depends on the difficulty of the attentional task.

6. Experiment 5: Contrast titration of attentional effect

In this experiment, we studied how attentional effects in Experiment 1 depended on the contrast of the unattended direction.

6.1. Method

Two of the authors and three naive observers participated in this experiment. The stimuli and procedures were the same as those in Experiment 1 except that the dot contrasts were different.

The contrast for the lower-right (unattended) direction was randomly varied among six values (0%, 5.5%, 10.0%, 20.6%, 41.3%, or 82.4% in different trials). These six values were achieved by altering the dot luminances on a fixed background luminance of 42.0 cd/m². The contrast for the upper-right (attended) direction was fixed at 20.6%. The reason we varied the contrast of the unattended direction, but not the attended direction, is that the difficulty of the attentional task (speed-change detection) decreases with increasing contrast of the attended direction. Since we wanted to isolate the effect of contrast in this experiment, we had to keep the task difficulty constant for each observer instead of letting contrast and task difficulty covary. Like Experiment 1, we included the three speed-change cases for the upper-right motion: slow-down, no-change and speed-up. However, while we ran the attentional and the 2-motion conditions, we did not run the 1-motion condition. This is because, when the contrast of the unattended direction is zero, the attentional condition is identical to the 1-motion condition. Trials for the attentional condition were run separately from those for the 2-motion condition in randomly interleaved blocks. In each of those conditions, each observer com-

pleted 30 trials for each combination of speed-change and contrast.

Since some observers were new and the contrast of the attended direction (20.4%) was lower than that (56.0%) in Experiment 1, the speed-changes for each observer had to be re-measured. Since the adjustment procedure in Experiment 1 is time consuming and since it is not critical to keep the performances of all observers within a narrow range, we applied the method of constant stimuli to obtain the psychometric curves for the speed-up and speed-down cases, and used the 75% threshold values of the curves as the speed-changes in the main experiment. As expected, the observers' actual performances in the main experiment had a larger scatter than in Experiment 1: the mean performances were 91.3% (AA), 49.7% (CQ), 84.8% (QX), 72.3% (XM), and 73.3% (YC) for the five observers, respectively. For each observer, the performance did not change much with the contrast of the unattended direction, except for observer YC. When the contrast of the unattended direction was 82.4%, the performances were 96.0%, 53.3%, 85.7%, 72.6%, and 80.9% for the five observers, respectively. When that contrast was 0% (i.e., the 1-motion condition), the performances were 90.7%, 48.8%, 82.4%, 69.6%, and 63.6%, respectively.

6.2. Results

Fig. 7 shows motion repulsion of the upper-right direction as a function of the contrast of the lower-right

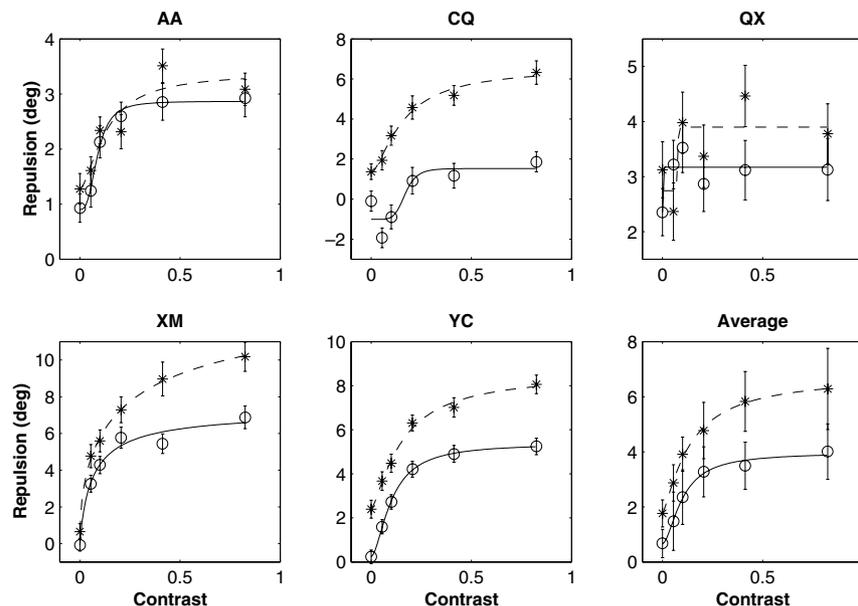


Fig. 7. The contrast dependence of repulsion. Data from five observers (first five panels) and their average (last panel) are shown. In each panel, the repulsion measured from the upper-right direction is plotted against the contrast of the lower-right direction, for the attentional condition (circles and solid curve) and the 2-motion condition (stars and dashed curve). The fitted curves have the functional form of $r = r_{\max} * C^n / (C^n + C_{50}^n) + r_0$, where the variables r and C are the repulsion value and the contrast of the unattended direction, respectively, and the parameters r_{\max} , n , C_{50} , and r_0 are the maximum repulsion, exponent, contrast at half-maximum, and baseline repulsion, respectively. With the average data in the last panel, these parameters are 3.31°, 1.70, 10.0%, and 0.65° for the attentional condition, and 5.01°, 1.27, 13.7%, and 1.75° for the 2-motion condition.

direction for each observer (first five panels). The circles and stars in each panel represent results from the attentional and 2-motion conditions, respectively. Since no significant difference was found among the three speed-change cases at each contrast and in each condition, only the mean values over the speed-change cases are shown. By comparing the attentional and 2-motion conditions, we see that attention generally reduced motion repulsion of the attended (upper-right) direction at all contrasts of the unattended (lower-right) direction. The main exception is observer AA who had virtually identical results under the two conditions. This may be explained by his high performance (91.3%) for the attentional task, indicating that the task was easy and the attentional demand was low for him. In the last panel of Fig. 7, we show the average results of all five observers. At relatively low contrast of the lower-right direction, the effect of attention to the upper-right direction can be compensated by increasing the contrast of the lower-right direction. For example, when the contrast of the lower-right direction was 7.0%, attention to the upper-right direction reduced repulsion from 3.3° to 1.9°. This reduction can be compensated by increasing the contrast of the lower-right direction to 20.6%. However, such trade-off between contrast and attention does not hold at high contrast because the two curves show different maximum repulsion values. Indeed, the two curves are related better by a scaling factor along the vertical axis than by a translation along the horizontal axis.

7. Discussion

In this paper, we studied the effect of attention on motion repulsion under a few different conditions. When observers only attended one direction (that was also used for measuring repulsion) in a stimulus with two motion directions, repulsion was significantly reduced by attention. This reduction did not depend on whether the visual cue for the attentional task was a speed-change or a luminance change (Experiments 1 and 2). However, when the task required attending to both directions simultaneously, the impairment to motion repulsion was non-significant (Experiment 3). In addition, the effect of attention on repulsion was diminished when the attentional task was made easy (Experiment 4). Finally, the attentional effect was titrated by varying the contrast of the unattended direction (Experiment 5). We found that attention scaled down repulsion over all tested contrasts of the unattended direction. Therefore, only at low contrast of the unattended direction, can the attentional effect be compensated by increasing the contrast. For all experiments, the interleaved catch trials with no speed or luminance change ensured that the reduced repulsion (when found) was due to attention instead of to the speed or luminance change per se.

Our results are largely consistent with physiological studies on attention. First, recent experiments have demonstrated that the response of an MT neuron is dominated by the attended direction when two directions simultaneously appear within the neuron's receptive field (Treue & Maunsell, 1999). Attention to one direction strongly reduces the inhibitory effect from the other, unattended direction. Since motion repulsion likely reflects the inhibitory interactions between different directions of motion (Hiris & Blake, 1996; Marshak & Sekuler, 1979; Wilson & Kim, 1994), our finding that attention to one of two directions significantly impairs motion repulsion is consistent with MT physiology. Second, attention has been found to affect both ventral and dorsal pathways in the brain (Desimone & Duncan, 1995; Gottlieb et al., 2003; Kastner & Ungerleider, 2000; Raymond, 2000; Treue, 2001), and when one feature of an object is attended, other features of the object are automatically selected as well (O'Craven, Downing, & Kanwisher, 1999; Valdes-Sosa, Cobo, & Pinilla, 1998). In Experiments 1 and 2, speed-change or luminance change was combined with the directional feature into the upper-right motion. When speed-change or luminance change was attended, the corresponding direction must also be attended. This could explain our finding that the attentional effect on motion repulsion did not depend on the specific visual cue for attention. Finally, some studies have shown that attentional modulation of neuronal responses depends on the task difficulty (Beauchamp et al., 1997; Rees, Frith, & Lavie, 1997; Spitzer et al., 1988). This is consistent with our finding that repulsion was unaffected by an easy attentional task.

The result in Experiment 4 also raises an alternative interpretation of the finding in Experiment 3 that attention to both directions did not impair repulsion. Our original interpretation was that when both directions were attended, the neuronal responses to the two directions should be equally enhanced. There was thus no response bias or inhibition suppression introduced by attention, and the repulsion between the two directions should either remain the same or even increase. Alternatively, if attention is assumed to be a limited resource, then a weaker attentional influence would be expected in Experiment 3 than in Experiment 1, since the former required dividing attention across two directions while the latter did not. The null attentional effect in Experiment 3 may be a consequence of weak attentional modulation of neuronal responses. The weak attention may also explain why the repulsion was not increased in Experiment 3. A combined psychophysical and physiological study may be needed to resolve this issue.

In Experiment 3, we mentioned that the three observers showed higher performances on the attentional task than they did in Experiment 1, although the

speed-changes were kept the same for each observer in the two experiments. The observers presumably improved their performance through learning over the course of the experiments. It is possible that the learning effect contributed to the disappearance of attentional effect in Experiment 3. To rule out this possibility, we repeated Experiment 1 for those three observers. Although the performances for the attentional task increased slightly, the differences in repulsion among the three conditions remained the same as in Experiment 1 (results not shown). Therefore, the learning effect, if any, did not affect our conclusion.

In a previous study, we reported that motion repulsion was significantly attenuated during binocular rivalry (Chen et al., 2001), similar to the current case of attention to one of two directions. A common feature of the two cases was that one direction dominated the other at a given time. In the case of attention, observers focused on the upper-right direction in order to perform the attentional task, while the unattended lower-right direction was largely ignored. In fact, most observers reported not noticing the lower-right direction in the attentional condition of Experiments 1 and 2. This is also why we did not measure motion repulsion of the unattended direction. In the case of binocular rivalry, one direction eventually dominated perception while the other was suppressed. The two studies together lead us to speculate that the directional perception of the dominant stimulus is largely unaffected by the suppressed stimulus, no matter whether the suppression results from attention or binocular rivalry.

We argued in the previous study (Chen et al., 2001) that motion repulsion and the motion aftereffect (MAE) might involve different neuronal events based on their different dependence on disparity. In contrast, attention appears to affect motion repulsion and the MAE in a similar way. Chaudhuri (1990) found that pulling attention away from an adapting motion stimulus considerably reduced the MAE. At first glance, this result seems to be the opposite of our finding that putting attention on one of two motion directions significantly impaired motion repulsion. However, considering that the MAE originated by adapting to the moving stimulus itself, and that motion repulsion of one direction came from a different direction, the attentional effects were actually similar in the two cases. Specifically, unattending the adapting stimulus reduced its MAE (von Grunau et al., 1998); likewise, unattending one direction reduced its repulsive effect on the attended direction. A related finding is that without attention, adaptation to two (transparent) motion directions results in an MAE in a direction opposite to the average of the two adapting directions. With attention to one of the two adapting directions, however, the MAE is opposite of the attended direction (Lankheet & Verstra-

ten, 1995). This result again indicates that the MAE of the attended stimulus is largely unaffected by the unattended stimulus, consistent with our finding on motion repulsion.

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References

- Alais, D. (2001). The influence of noise and attention on motion repulsion. *Investigative Ophthalmology and Visual Science Supplementary (ARVO)*, 42(4), 871.
- Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience*, 2(11), 1015–1018.
- Beauchamp, M. S., Cox, R. W., & DeYoe, E. A. (1997). Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *Journal of Neurophysiology*, 78, 516–520.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature*, 344, 60–62.
- Chen, Y., Matthews, N., & Qian, N. (2001). Motion rivalry impairs motion repulsion. *Vision Research*, 41, 3639–3647.
- Chen, Y., Matthews, N., & Qian, N. (2002). Attention affects motion repulsion. *Investigative Ophthalmology and Visual Science Supplementary (ARVO)*, 43, 3780, E-Abstract.
- Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience*, 22, 319–349.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- Gottlieb, J., Kastner, S., & Reynolds, J. (2003). Attention. In L. R. Squire (Ed.), *Fundamental neuroscience* (pp. 1249–1274). San Diego, London: Academic Press.
- Hiris, E., & Blake, R. (1996). Direction repulsion in motion transparency. *Visual Neuroscience*, 13, 187–197.
- Kastner, S., & Ungerleider, L. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341.
- Lankheet, M. J. M., & Verstraten, F. A. J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research*, 35(10), 1401–1412.
- Marshak, W. M., & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science*, 205, 1399–1401.
- O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, 401, 584–587.
- Pelli, D. G. (1997). The video toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.
- Rauber, H.-J., & Treue, S. (1998). Reference repulsion when judging the direction of visual motion. *Perception*, 27, 393–402.
- Rauber, H.-J., & Treue, S. (1999). Revisiting motion repulsion: Evidence for a general phenomenon? *Vision Research*, 39, 3187–3196.

- Raymond, J. E. (2000). Attentional modulation of visual motion perception. *Trends in Cognitive Science*, 4(2), 42–50.
- Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, 278, 1616–1619.
- Spitzer, H., Desimone, R., & Moran, J. (1988). Increasing attention enhances both behavioral and neuronal performance. *Science*, 240, 338–340.
- Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Neurosciences*, 24(5), 295–300.
- Treue, S., & Maunsell, J. H. R. (1999). Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *Journal of Neuroscience*, 19(17), 7591–7602.
- Valdes-Sosa, M., Cobo, A., & Pinilla, T. (1998). Transparent motion and object-based attention. *Cognition*, 66(2), B13–B23.
- von Grunau, M. W., Bertone, A., & Pakneshan, P. (1998). Attentional selection of motion states. *Spatial Vision*, 11(4), 329–347.
- Wilson, H. R., & Kim, J. (1994). A model for motion coherence and transparency. *Visual Neuroscience*, 11, 1205–1220.