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Revisiting motion repulsion: evidence for a general phenomenon?

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Abstract

Previous studies have found large misperceptions when subjects are reporting the perceived angle between two directions of motion moving transparently at an acute angle, the so called motion repulsion. While these errors have been assumed to be caused by interactions between the two directions present, we reassessed these earlier measurements taking into account recent findings about directional misperceptions affecting the perception of *single* motion (reference repulsion). While our measurements confirm that errors in directional judgements of transparent motions can indeed be as big as 22° we find that motion repulsion, i.e. the interaction between two directions, contributes at most about 7° to these errors. This value is comparable to similar repulsion effects in orientation perception and stereoscopic depth perception, suggesting that they share a common neural basis. Our data further suggest that fast time scale adaptation and/or more general interactions between neurons contribute to motion repulsion while tracking eye movements play little or no role. These findings should serve as important constraints for models of motion perception. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

When subjects are asked to estimate the direction of one of two spatially superimposed dot patterns or gratings moving at an acute angle they tend to misperceive the angle formed by the two directions. This phenomenon of motion repulsion between visual directions has been amply documented (Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Burke & Wenderoth, 1993; Hiris, 1995; Qian & Geesaman, 1995; Hiris & Blake, 1996; Kim & Wilson, 1996; Wishart, Braddick & Curran, 1998).

This overestimation occurs only for acute angles with the maximal error for relative angles between the two directions of 20–40°. The reported range of the largest repulsion (i.e. the deviation between the presented and perceived direction of *one* of the two motions) goes from 15° to over 20° (Marshak & Sekuler, 1979; Mather & Moulden, 1980; Snowden, 1989; Qian & Geesaman, 1995; Kim & Wilson, 1996). If the angle between the two directions exceeded 90°, the repulsion declined to zero or near zero (Patterson & Becker, 1996). If the angle between the two superimposed angles is very small, the percept is not one of transparent motion but rather only one motion in the direction of the vector sum is perceived (Williams & Sekuler, 1984; Yo & Wilson, 1992).

Motion repulsion has been interpreted as evidence for inhibition between direction-tuned channels or cells in the visual system (Blakemore, Carpenter & Georgeson, 1970; Wilson & Kim, 1994; Qian & Geesaman, 1995), and could serve as a powerful constraint for models of direction selectivity. But to serve as such a constraint, a good quantitative assessment of the magnitude of motion repulsion is needed.

We were concerned that previous studies did not provide such accurate measurements of motion repulsion because some of the experimental designs employed might have caused directional misestimations unrelated to motion repulsion.

First, some repulsion paradigms used repeated presentations of similar directions, which might be causing directional adaptation that can also lead to directional misjudgments (Levinson & Sekuler, 1976; Grunewald & Lankheet, 1996).

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Second, recent studies show that even the direction of *single* motions can be systematically misjudged (Blake, Cepeda & Hiris, 1997; Rauber & Treue, 1998). These misjudgments, termed reference repulsion, are as big as 9° and can be interpreted as a tendency by subjects to overestimate the angle between a direction of motion and a reference direction (e.g. the closest cardinal direction). This suggests that factors other than repulsion by the second direction might have contaminated previous studies.

Here, we attempted to design an experiment that minimizes the influence of reference repulsion to determine the misjudgment that is truly caused by the presence of the second motion. The influence of various stimulus parameters on this true motion repulsion is then investigated in an effort to understand the underlying mechanisms of this misjudgment.

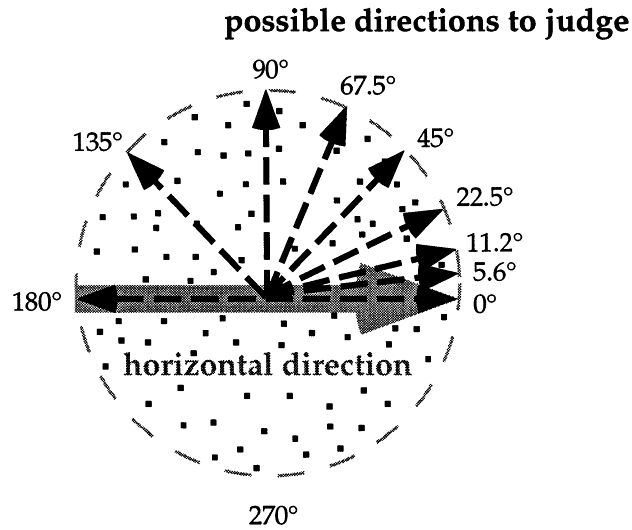

Fig. 1. Directions used for the control experiment and Experiment 1. In each stimulus, 200 points are moving horizontally from left to right (bold, pale arrow). Simultaneously, a second set of 200 points is moving in one of the directions indicated by the dashed arrows. Subjects have to report the direction of this second set.

2. General methods

The experiments were performed using an Apple Macintosh-Computer and a monitor with a frame rate of 74.5 Hz. The spatial resolution of the display was 33.3 pixels per degree of visual angle. The motion stimuli were moving random dot patterns (RDPs) presented behind a stationary virtual aperture, 9.2° (control experiment and Experiment 1) or 6° of visual angle (Experiment 2–8) in diameter. Unless otherwise noted each RDP consisted of 400 square black dots (3.6 min arc width) on a white background moving at 4° per second for 1 s. Dots that disappeared behind the aperture reappeared at the point opposite to their exit point. The subjects viewed the display binocularly, from a distance of 57 cm, maintained by a chin rest. A-priori we decided to compare the different amounts of misperception in Experiment 3–6 with a paired t-test. We therefore corrected for the use of multiple t-tests using the Bonferroni correction.

2.1. Control experiment

To make sure that the previously reported large amounts of motion repulsion were reproducible with our setup we replicated Marshak and Sekuler's (1979) classic experiment.

In their study one set of 200 dots moved coherently in the same direction (rightwards) in every trial and a second set of 200 dots moved in one of the nine directions shown in Fig. 1. Such a stimulus is perceived as two surfaces sliding across each other. In each trial the RDP was presented for 1 s, after which the subjects used a protractor scale ringing the CRT to report the perceived direction of the second set of dots. We used the same methods except for two small changes: First, the observer adjusted the orientation of a line presented on the monitor after the stimulus had been presented to report the perceived direction. Second, subjects were not instructed to maintain fixation (Marshak and Sekuler (1979) did not find a change in motion repulsion when comparing a free-viewing condition with one using a fixation point in the middle of the stimulus).

Marshak and Sekuler's original data are replotted in Fig. 2 (circles) as a function of the angle between the two surface directions. Positive values on the y-axis denote counterclockwise shifts of the perceived direction of the second set, i.e. repulsion away from the direction of the first set. Our results are also plotted in Fig. 2 (triangles), and show the same pattern, a misperception of more than 15 and as much as 22° for angles of 10–70° between the two directions. For larger interstimulus angles the misperception decreases and is gone for angles larger than 90°.

3. Part 1: contribution of adaptation and reference repulsion

If adaptation and reference repulsion contributed to the directional misperception, we should be able to measure misperceptions due to these effects, when presenting only the second surface. If the presence of the other set of dots is the only cause of the misperception it should disappear when only a single direction of motion is present.

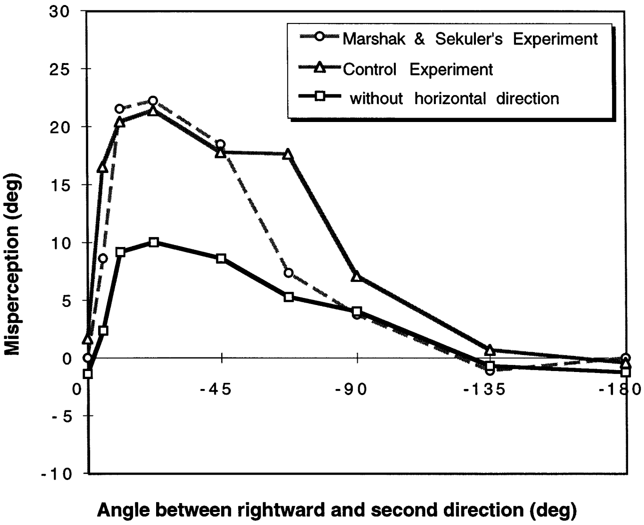

Fig. 2. Comparison of misperceptions between Marshak and Sekuler's (1979) classic experiment (circles), our repetition of it (triangles), and Experiment 1 without the first set (pale arrow Fig. 1), moving from left to right (squares). Positive values on the y-axis indicate counterclockwise misperceptions of presented directions. Marshak and Sekuler's (1979) classic experiment and the control experiment show the misperception of one direction in the presence of another direction. One set was always moving horizontally from left to right, the set whose direction the subject had to report was moving in one of the directions represented in Fig. 1 by the dashed arrows. The lower curve (squares) shows the reference repulsion, i.e. the misperception when the horizontally moving set of dots was removed.

3.1. Experiment 1

We repeated the control experiment with the presentation of only the second set of dots (again using the directions indicated by the dashed arrows in Fig. 1). The results are plotted in Fig. 2 (squares). Despite the absence of a second moving surface, the data show that except for very small and obtuse angles the direction of motion is misperceived away from the rightward direction. We measured a maximal misperception of about 10°. As in the control experiment, misperceptions are especially high for directions moving 11.2, 22.5, and 45° up from the horizontal. This pattern of results shows that the misperception in the control experiment did not arise solely because of the presence of a second set of dots. In fact, only about 10°, i.e. half of the misperception in the control experiment seems to be caused by the first direction.

There are at least two possible explanations for why subjects misperceived the single directions of motion presented in this experiment. The first possible cause is a build up of motion adaptation during the experiment. While using directions spaced evenly along 360° would result in the same level of activation for all direction-selective neurons, the use of unevenly spaced directions alters the distribution of activity and therefore presumably of directional adaptation. In the control experiment and Experiment 1, where mainly directions moving slightly upwards to the right were presented, the profile of activation peaks for directions of about 15° up from rightward. Presenting a direction with a steeper inclination than the center of adaptation might result in a counterclockwise shift of the perceived direction. If this effect contributed to the misperception, the amount of the shift counterclockwise should increase during an experiment since the anisotropy of adaptation would build up with more and more trials. We therefore looked for an increase in the misperception in the records of Experiment 1.

We did not find increasing amounts of misperceptions with increasing trial numbers. This means that either the timing of the experiment prevents a noticeable build up of adaptation or that its contribution to the observed misperception is small.

Another explanation for the misjudgment observed even in the absence of a second set of dots is the phenomenon of the so-called reference repulsion (Rauber & Treue, 1998). This phenomenon is a perceptual repulsion (i.e. for judgements of motion direction an overestimation of the angle) of a stimulus feature value from the nearest reference value. In motion perception the reference directions are the cardinal directions (upward, downward, leftward, and rightward motion). Especially directions moving slightly upwards from horizontal are affected. Reference repulsion can cause misperceptions of up to 9°. As many of the motions that had to be judged in this and the original (control experiment) experiment, were moving in these directions, reference repulsion is a likely contributor to the misperceptions observed.

3.2. Experiment 2 (main experiment)

Since reference repulsion does not seem to influence the perception of the cardinal directions themselves we designed an experiment in which the direction to be judged was aligned with the vertical.

To minimize adaptation, we balanced trials with stimuli containing upward motion with trials containing downward motion. If our interpretation is correct that the misperception measured in Experiment 1 is a combination of true motion repulsion and reference repulsion we expect to find a misperception of only about half the size found in the control experiment.

3.2.1. Methods

The two surfaces always moved at a relative angle of 30°. This value was chosen because it elicited strong misperceptions in the previous experiments. One experimental run consisted of 80 trials. Unlike in the previous experiments, observers did not adjust a line to the orientation of the perceived direction but had to report if the motion of the surface moving in a direction closer

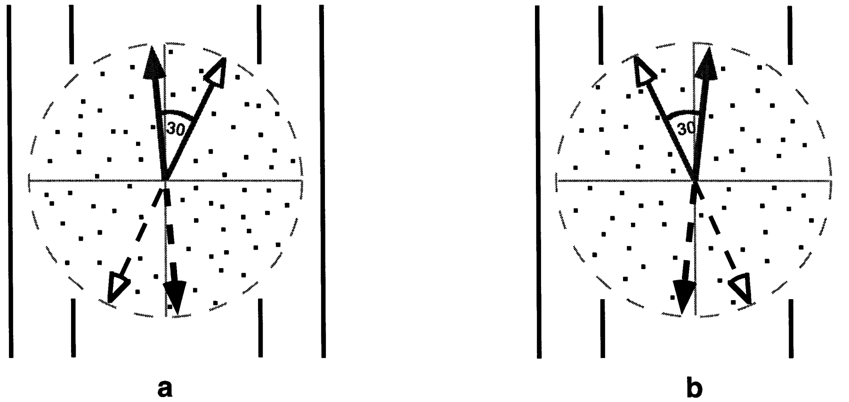

Fig. 3. These diagrams show the direction combinations presented in Experiment 2 a and b. Each direction combination consists of a direction to be reported (filled arrow heads) and another direction (empty arrow heads), which form an angle of 30°. Upward direction combination trials alternated with downward direction trials. The six vertical line segments appear after each presentation of a RDP to stabilize the impression of the vertical.

to the vertical pointed clockwise or counter-clockwise from the vertical (two-alternative forced choice). If the subject reported a clockwise tilt of the motion the next trial would contain a direction pair tilted more anti-clockwise and vice versa. This staircase method allowed a very accurate determination of the direction perceived as moving vertically.

We used four stimulus conditions, which we divided across two trial runs (Experiments 2 a and b). In each run we alternated between trials containing two directions moving upward and trials containing two directions moving downward. In Experiment 2 a, the subject had to determine the direction of the set of dots which was moving more counterclockwise. In Experiment 2 b, the subject had to determine the direction of the set of dots which was moving more clockwise. Since subjects had to judge motion direction relative to the vertical, we presented six vertical lines outside the stimulus circumference after each stimulus presentation to aid the subjects in maintaining a stable vertical reference (Fig. 3).

A total of 14 subjects participated in this experiment, 12 were paid volunteers, naive to the purpose of the research, two were from our laboratory. All had normal or corrected-to-normal visual acuity.

3.2.2. Results and discussion

Each of the four stimulus conditions used resulted in one measurement of motion repulsion. The average across these four measurements for all subjects was a misperception of only 7.1° ($\pm$3.4°, 99% confidence interval). This value is not significantly different from the 10° estimate for true motion repulsion in the previous experiment and reinforces our interpretation that the misperception exceeding 20° in the Sekuler and Marshak experiment was a combination of motion repulsion and reference repulsion.

4. Part 2: the influence of different parameters on the amount of motion repulsion

To get an insight to the underlying mechanisms of motion repulsion, it is important to know which parameters influence motion repulsion. Using the previous experiment as a starting point we investigated the effect of changing different parameters on the amount of motion repulsion. We concentrated on four parameters namely the stimulus duration, the point density, the point lifetime, and the stimulus speed.

4.1. Experiment 3 (varying stimulus duration)

Humans are able to discriminate directions of motion for stimulus durations as short as 50 ms (Kelly, 1979; McKee & Welch, 1985). Motion repulsion might already be present when judging such brief stimuli or it might be a phenomenon requiring extended stimulus durations to build up. We therefore measured motion repulsion for a range of different stimulus durations.

4.1.1. Methods

Using a stimulus diameter of 6° we repeated Experiment 2 with presentation times of 1000, 500, 250, 200, and 150 ms. A total of 14 subjects participated in this experiment.

4.1.2. Results and discussion

Motion repulsion decreased with increasing presentation time. This was significant in a two-factor ANOVA (factors: subjects and stimulus duration) [F (4, 52) = 12.8, $P < 0.01$] (Fig. 4 left histogram).

There are at least two possible causes of the decrease of motion repulsion with decreasing stimulus duration: A reduced temporal build up of repulsion and/or a reduction in pursuit eye movements.

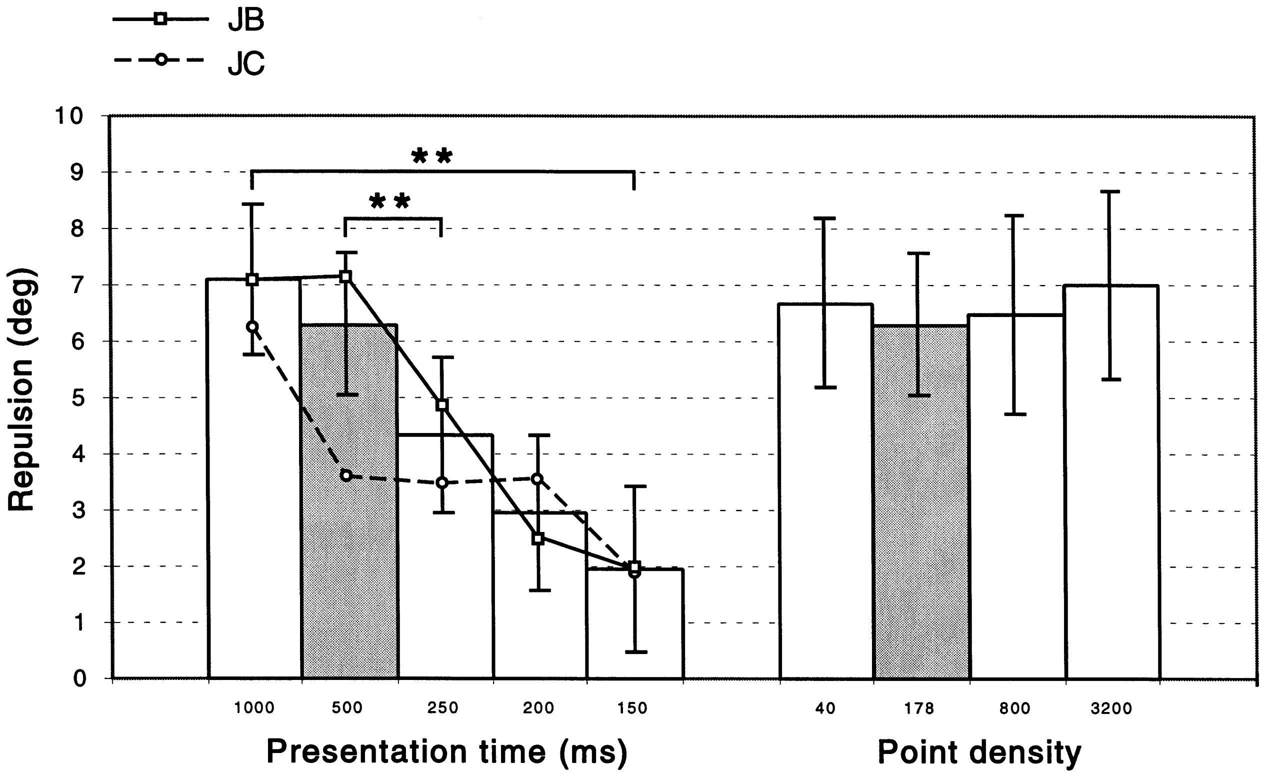

Fig. 4. The y-axis plots motion repulsion in degrees (averaged across subjects). The left histogram shows motion repulsion at different presentation times (1000, 500, 250, 200, and 150 ms). The right histogram shows motion repulsion at different point densities (20, 89, 400, and 1600 points for each of the two sets). The error bars represent the standard error for the 14 subjects. Asterisks show a significant decrease of misperception with decreasing presentation time from 1000 ms to 150 ms [F (4, 25) = 12.8, $P < 0.01$, two-factor analysis of variance] or significant differences between the magnitude of motion repulsion at different presentation times. Using a paired t-test with Bonferroni correction, motion repulsion was significantly higher ($P < 0.01$) at 500 ms compared to a presentation time of 250 ms. The solid and dashed lines in the left graph show data of subjects JB and JC. A total of 12 of the 14 subjects showed the effect (eight were significant ($P < 0.05$) individually in a regression analysis of repulsion vs. log of presentation time).

Pursuit eye movements can contribute to repulsion if the visual system does not compensate for their effect on the retinal image motion. Tracking one of the two surfaces will result in an increased angle between the two directions of motion on the retina. Humans need about 200 ms presentation time of a moving target to initiate eye pursuit (Robinson, 1965). Ferrera and Wilson (1990) used this fact to conclude that eye movements played no role in their experiments since shortening the presentation from 1 s to 200 ms, had no significant effect on the directional misjudgment. But they provided no further details concerning the amount of bias for the 200 ms stimulus duration. On the other hand, the increasing amount of motion repulsion with increasing stimulus duration in our experiment indicates that an incomplete compensation of eye pursuit might contribute to the misperceptions. At a presentation time of 150 ms, where pursuit eye movements do not happen, motion repulsion is only about 2°. In the next experiment, we tried to reduce eye movements during extended stimulus durations by using eccentric fixation to gain a better understanding of the role of eye movements in motion repulsion.

Our results are also in agreement with the possibility that motion repulsion is a phenomenon which builds up slowly, possibly because of adaptation to the stimulus itself or because of neuronal interactions that take hundreds of ms to build up.

4.2. Experiment 3a

In the previous experiment, we demonstrated an increasing motion repulsion with increasing presentation time. This increase might be due to more pursuit eye movements during the longer stimulus durations. If this is the case then reducing tracking eye movements, without a shortening of the stimulus duration should also generate reduced motion repulsion. We therefore measured the amount of motion repulsion with eccentric fixation and compared the results with the data, when the subjects were allowed to make eye movements. If eye movements indeed increase the amount of motion repulsion, we expect a larger motion repulsion without fixation.

4.2.1. Methods

The experiment was identical to Experiment 2 except that subjects were instructed to maintain fixation on a small cross formed by two lines, presented 5° left of the stimulus' center. We used the same nine subjects as in Experiment 2.

4.2.2. Results and discussion

Using a paired t-test, we did not find a significantly ($P = 0.35$) higher amount of repulsion without fixation (6.8°) compared to the result with 5° eccentric fixation (6.3°). This is in agreement with Marshak and Sekuler (1979) and Mather and Moulden (1980) who failed to find a change in motion repulsion when comparing a free-viewing condition with one using a fixation point in the middle of the stimulus. As a stimulus duration of 500 ms did not significantly change the amount of motion repulsion, we used it in all following experiments.

4.3. Experiment 4 (varying point density)

Applying different experimental designs, previous studies investigated the influence of dot density on motion repulsion. Qian and Geesaman (1995) presented two transparently moving sets of dots with short life times. Every point of a set formed a pair with a corresponding point in the other set. The trajectories of pairs would cross in the middle of their life times (see Qian, Andersen & Adelson, 1994 for details). This kind of experimental design ensured an equilibrium of motion vectors from both sets in every region of the stimulus. Increasing the point density, they measured an increasing amount of motion repulsion suggesting that interactions between different directions of motion at larger spatial scales favor motion repulsion. Here we tested if the point density in the absence of paired dots influences the amount of motion repulsion.

4.3.1. Methods

We repeated Experiment 2 using four different point densities (40 points, i.e. 1.4 points per degree square, 178 points, i.e. 6.3 points per degree square, 800 points, i.e. 28.3 points per degree square, and 3200 points, i.e. 113.2 points per degree square). A total of 14 subjects served in this experiment.

4.3.2. Results and discussion

We found no significant influence of dot density on motion repulsion. Therefore, within the range of densities tested motion repulsion does not seem to depend on local interactions between individual dot motions. Rather, the perception of the two motion directions seems to be based on the integration over larger scales.

4.4. Experiment 5 (varying point lifetime)

The direction of a homogeneously moving RDP can be recovered from the direction of the individual point but such measurements might be noisy. Especially when the information provided by the individual dots is limited, spatial integration of many or all dots will improve direction discrimination (Williams & Sekuler, 1984; Lorenceau, 1996). We wanted to know if such increased demand for spatial integration will affect motion repulsion. To increase the demand for spatial integration we reduced the lifetimes of the individual dots in the pattern.

4.4.1. Methods

We repeated Experiment 2 using four different point lifetimes (500, 200, 107, and 53 ms). Every point would disappear after its lifetime expired and a new point would appear at a random location within the stimulus boundaries. The lifetime phases of individual points were shuffled relative to each other such that an equal number of dot lifetimes would expire a every given stimulus frame. A total of 11 subjects served in this experiment.

4.4.2. Results and discussion

We did not find a significant effect of point lifetime on the amount of motion repulsion (Fig. 5 left histogram). This suggests that subjects might already perform a spatial integration across the whole stimulus for long lifetimes and therefore no further effect of reducing lifetime is observed or motion repulsion is not affected by the changes in spatial and temporal integration over the range tested here.

4.5. Experiment 6 (varying point velocity)

Two surfaces in transparent random dot patterns are more readily segmented when they move at higher velocities (van Doorn & Koenderink, 1982). To test if such improved segmentation leads to reduced repulsion we investigated the influence of stimulus velocity.

4.5.1. Methods

We repeated Experiment 2 using four different point velocities (2, 4, 8, and 16 deg/s). A total of 11 subjects served in this experiment.

4.5.2. Results and discussion

Motion repulsion decreased with increasing velocity. This was significant in a two-factor ANOVA (factors: subject and velocity) [$F(3, 30) = 10.33$, $P < 0.01$]. (Fig. 5 right histogram).

Perceptually it is easier to segment the two surfaces in transparent RDPs if they move at higher velocities. It is possible that this improved segmentation decreases

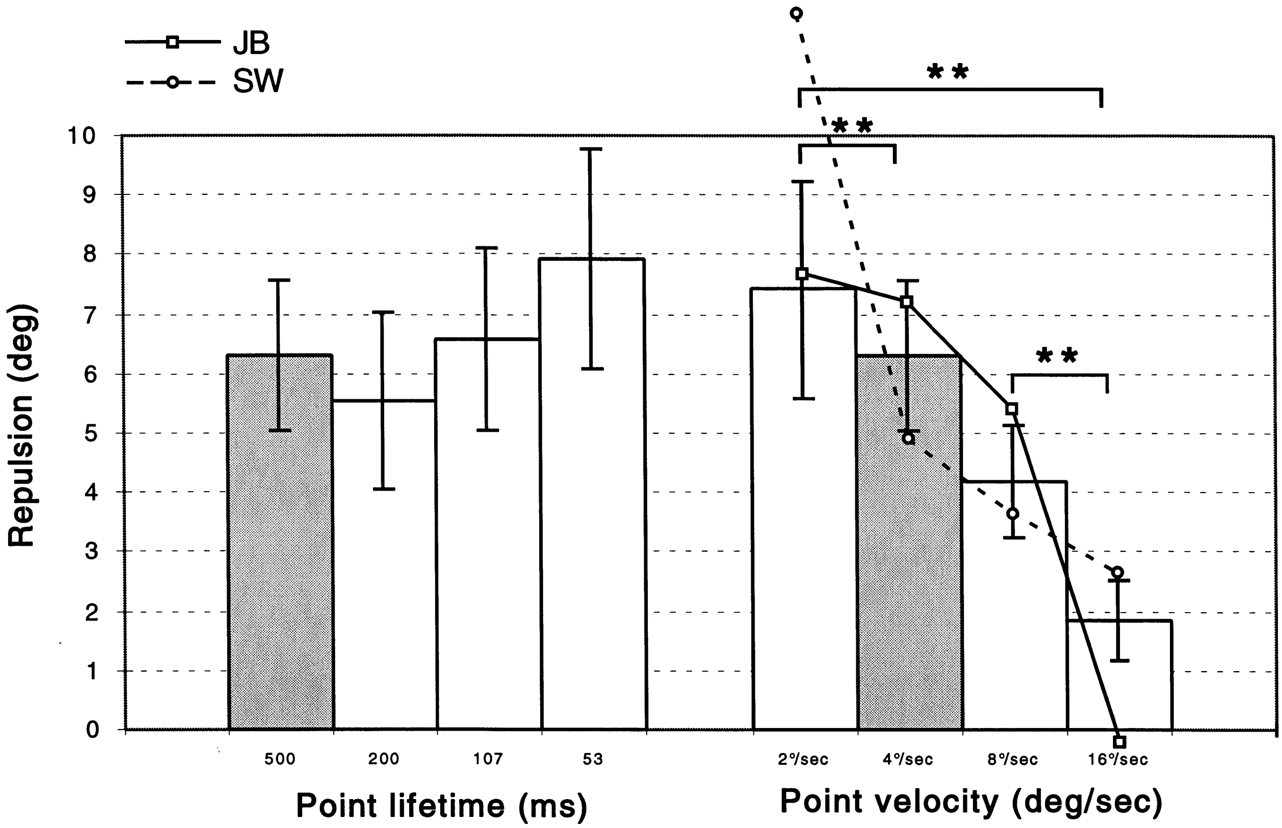

Fig. 5. The y-axis plots motion repulsion in degrees (averaged across subjects). The left histogram shows motion repulsion at different point lifetimes (500, 200, 107, and 53 ms). The right histogram shows motion repulsion at different stimulus velocities (2, 4, 8, and 16 deg/s). The error bars represent the standard error for the 11 subjects. Asterisks show a significant decrease of motion repulsion with increasing point velocity from 2 to 16 deg/s [F (3, 32) = 10.33, $P < 0.01$, two-factor analysis of variance] or significant differences between the magnitude of motion repulsion at different point velocities. Using a paired t-test with Bonferroni correction, motion repulsion was significantly higher ($P < 0.01$) at 2 deg/s compared to a point velocity of 4 deg/s and motion repulsion was significantly higher for a point velocity of 8 deg/s ($P < 0.01$) compared with a point velocity of 16°/sec. The solid and dashed lines in the right graph show data of subjects JB and SW. Nine of the 11 subjects showed the effect (two were significant ($P < 0.05$) individually in a regression analysis of repulsion vs. log of velocity)

the influence of one surface on the perceived direction of the other surface. While this effect suggests an influence of the ease of surface segmentation on motion repulsion there is another possibility for the observed reduction in repulsion with increasing point velocity: Even when using dark dots on a bright computer monitor, moving dots are perceived as having trailing tails. With increasing stimulus velocity, this impression intensifies. The direction of motion can now also be judged from the orientation of the tails. It is possible that for the higher velocities used in this experiment subjects performed an orientation judgement rather than judging the direction of motion directly. While repulsion also exists for orientation judgements it peaks at a value of about 4°, an amount comparable to the one we measured with velocity of 8 and 16 deg/s.

5. General discussion

Motion repulsion, the overestimation of acute angles between transparently moving patterns has been reported to be as big as 25° for each of the two motions (Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Burke & Wenderoth, 1993; Qian & Geesaman, 1995; Hiris, 1995; Hiris & Blake, 1996; Kim & Wilson, 1996; Wishart et al., 1998). Here, we reevaluated these assessments under more controlled conditions, taking into account the recent finding that even the direction of single motions can be misestimated (reference repulsion, Rauber & Treue, 1998). We find true motion repulsion to peak at only about 7° (with most stimulus conditions causing an even smaller repulsion).

5.1. Perceptual repulsion occurs in several systems

Repulsion is not a perceptual phenomenon restricted to the realm of visual motion processing. It has been reported for stereoscopic depth perception, using random-dot stereograms of overlapping transparent surfaces. Here repulsion peaks at about 1 min arc for surfaces with separations of about 6–8 min arc (Steven-son, Cormack & Schor, 1991). Repulsion has also been shown using patterns made up from two groups of oriented lines. Estimating the orientation of such stimuli when the two orientations form acute angles, a peak repulsion of about 4° has been reported for angles of about 10° (Blakemore et al., 1970; Campbell & Maffei, 1971; Carpenter & Blakemore, 1973; Wallace & Moulden, 1973). Even when estimating the orientation of elongated random patterns composed of short line segments repulsion between the overall orientation and the local orientation of the comprising lines has been reported (Lánsky, Yakimoff & Radil, 1988).

5.2. Why do we find motion repulsion to be so much smaller than previously reported?

Except for a recent report by Hiris and Blake (1996), all studies of motion repulsion reported motion repulsion peaking at about 20°.

If this large effect would truly represent repulsion by the second direction (and not a combination of reference repulsion and motion repulsion, as we suggest here) it would make motion repulsion an unusual case of perceptual repulsion, since in both stereoscopic depth perception and orientation perceptual repulsion effects are much smaller when expressed as multiples of discrimination thresholds or as fractions of physical separation. Both orientation and stereoscopic repulsion effects are about five to eight times larger than their respective discrimination thresholds (Discrimination threshold for depth is 10–20 s arc (Westheimer & Levi, 1987) and orientation discrimination threshold is about 0.3–0.8° (Westheimer, Shimamura & McKee, 1976; Burbeck & Regan, 1983; Orban, Vandenbusche & Vogels, 1984; Regan & Beverly, 1985; Westheimer & Beard, 1998)) while a motion repulsion exceeding 20° represents a factor of about 15 over the discrimination threshold (1–2°, De Bruyn & Orban, 1988; Watamaniuk & McKee, 1998). Both orientation and stereoscopic repulsion effects also result in a maximal error of about 10–40% of the physical stimulus (4° of orientation repulsion for angles of about 10° and about 1 min arc stereoscopic depth repulsion for surfaces separated by about 6–8 min arc). A motion repulsion exceeding 20° would represent an error of 60–100% of the physical separation. While it is difficult to compare repulsions in different domains quantitatively it is noteworthy that the discrepancy between the magnitude of motion repulsion on one side and orientation and stereoscopic depth perception on the other disappear with the smaller motion repulsion we report here.

5.3. What causes repulsion?

Earlier studies focused on descriptions of motion repulsion with only a few suggestions as to its cause. The most discussed possibility are inhibitory interactions among direction-selective neurons (Marshak & Sekuler, 1979; Mather & Moulden, 1980; Wilson & Kim, 1994; Hiris, 1995; Qian & Geesaman, 1995). Other possible causes of motion repulsion include adaptation and pursuit eye movements.

5.3.1. Is repulsion caused by eye movements?

With longer presentation times, we found significantly increased motion repulsion (Experiment 3). This points to a possible influence of pursuit eye movements which, because of their onset latency, only come into play with longer stimulus durations. If the subjects track the direction of a group of dots the retinal image motion of the other pattern would form a larger angle than present in the stimulus. Incomplete compensation for this effect of eye-movements (such as suggested by the Filehne illusion; Filehne, 1922; Haarmeier & Thier, 1996) would lead to motion repulsion. But note that such an effect would not show the pronounced dependence on the angle between the two directions observed in motion repulsion. We repeated our Experiment 2 with eccentric fixation (Experiment 3 a) and, like Mather and Moulden (1980), found no significant difference to the results obtained with foveal presentation without fixation. These findings as well as the existence of repulsion in other domains (where eye movements could not account for the effect) make it very unlikely that eye movements are a major contributor to motion repulsion.

5.3.2. Adaptation and repulsion

Adaptation can profoundly influence perception. This includes changes in perceived direction (Levinson & Sekuler, 1976; Patterson & Becker, 1996). Such direction-selective adaptation is thought to shift the distribution of activity among a population of directionally selective cells away from adapted mechanisms which alters perceived direction of the moving test patterns (e.g. Burke & Wenderoth, 1993). The largest adaptation in our experiment would occur for those neurons which are selective for motion directions *between* the two directions presented and might thus account for the increasing motion repulsion with extended presentation time. It should be noted that such an adaptation effect would have to be fast acting (i.e. happen within a single stimulus presentation) since we did not find evidence for a stronger repulsion in later trials in our Experiment 1.

5.3.3. Lateral inhibition and repulsion

Another possible mechanism could be other interactions between neurons that also build up only with prolonged stimulus duration. Part of such a mechanism may be excitatory and inhibitory interactions between directionally-tuned cells, such as lateral or recurrent inhibition proposed by Wilson and Kim (1994).

In summary, our results confirm the existence of motion repulsion between visual directions moving at acute angles, but demonstrates that previous measurements of this phenomenon have greatly overestimated it, likely because of the confounding influence of reference repulsion. The more accurate estimate of motion repulsion represented here does not only suggest that it reflects a common mechanism across visual dimensions but should also serve as a powerful constraint for models of motion perception.

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