Perceived Shrinkage of Motion Paths

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We show that human observers strongly underestimate a linear or circular trajectory that a luminous spot follows in the dark. At slow speeds, observers are relatively accurate, but, as the speed increases, the size of the path is progressively underestimated, by up to 35%. The underestimation imposes little memory load and does not require tracking of the trajectory. Most importantly, we found that underestimation occurred only when successive motion vectors changed in direction. This suggests a perceptual rather than representational origin of the illusion, related to vector-sum integration over time of neural motion signals in different directions.

Keywords: motion integration, illusions, trajectory

Human observers are extremely precise in judging the size of stationary shapes. The accuracy of comparing shapes along one or two dimensions is extremely high, with Weber fractions of 2% to 6% (Laursen & Rasmussen, 1975). In the judgment of circularity, errors are remarkably small, ranging from 1% to 1.4% (Regan & Hamstra, 1992). Accuracy is also very high (2–3%) for motion-defined shapes (Regan, Hajdur, & Hong, 1996).

However, judging the size of the trajectory of a luminous spot that moves in the dark is an entirely different matter. Observers are accurate in perceiving straight-line trajectories but they are drastically hampered in their judgments when simple manipulations are made in the spatial and temporal arrangements of 100-ms trajectory segments (Verghese & McKee, 2002).

Inferring the size of a trajectory that a luminous dot has just completed is not easy either. To recover the direction and the amplitude of the trajectory, the visual system has to "fill it in" backwards, from the motion signal available at a given instant to those no longer there. Thus, observers have difficulty in localizing either the starting or the final position of a stimulus moving in continuous or apparent motion. For example, when judging the starting position of a moving object, observers often displace the judged onset in the direction of motion (the Fröhlich illusion) and

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in the direction opposite to the motion (onset repulsion effect). In addition, the judged final position is perceived as shifted in the direction of motion and, according to several authors, the forward displacement occurs because (Freyd & Finke, 1984; Hubbard, 1995) the mental system is unable to stop the cognitive representation of motion and this then continues after target offset. This is referred to as *representational momentum* and is an explanation in terms of internalized physical regularities. To avoid this reference to internalized physics, the more neutral term *mental extrapolation* is often used to refer to the high-level process that underlies the forward localization error (see also Finke & Freyd, 1989).

We shall now describe a motion illusion resulting from a light spot moving on a dark background, in which the amplitude of its two-dimensional motion is underestimated. We discovered that at slow speeds observers are relatively accurate. However, as the speed increases, the size of the path followed by the spot is progressively underestimated, by up to 35%, both when the trajectory is circular and when it is straight. It is tempting to relate this underestimation to the Fröhlich mislocalization illusion. Indeed, both phenomena occur whether the target moves on a linear or circular trajectory (Kerzel, 2003). In addition, the size of the Fröhlich effect depends on stimulus parameters such as movement speed and movement direction (Kerzel, 2002; Müsseler & Aschersleben, 1998; Müsseler, Stork, & Kerzel, 2002) and this suggests a perceptual basis for the Fröhlich effect. The results of five experiments are in favor of a perceptual explanation and suggest that the illusion arises from motion interpolation.

General Method

Participants

Twenty-one subjects with normal or corrected-to-normal vision participated. Three were the authors, and 18 were students of the University of Padua, naïve as the purposes of the experiments. There were six observers in Experiment 1, six in Experiment 2, six in Experiment 3a, five in Experiment 3b, and six in Experiment 4.

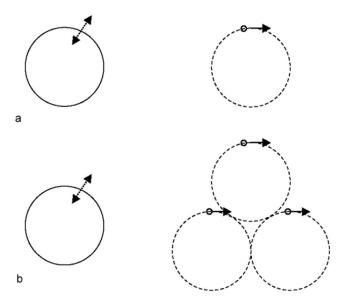


Figure 1. In a (top right) only one small spot moved clockwise along a circular trajectory. In b (bottom right) three spots moved clockwise along their circular trajectories, which were tangent to each other. On the left were static circles whose radii the observer adjusted to apparently match the trajectories. Dynamic demonstrations are available online at http://vision.psy.unipd.it/parovel.htm

Apparatus and Stimuli

The stimuli were created and the responses collected by an animation program written in True Basic 2.7. The stimuli were presented on a 31-cm (diagonal) screen of $1,024 \times 748$ pixels (horizontal by vertical) resolution of an Apple Power PC-G3/333 MHz I-Mac.

In the straight trajectory experiments (Experiments 1 and 2), the target stimulus was a 0.3° white spot moving back and forth along a vertical path with a speed either constant (Experiment 1) or varying sinusoidally [$y = \pm (1 \pm \sin 90-z)$] (Experiment 2). The subjective length of the perceived trajectory was matched with the length of an adjustable stationary line. The speed was randomly set to one of three values (2.2, 4.3, and 8°/s) within a block. The length of the trajectory was either fixed at 3° (Experiment 2) or was randomly set to one of five values (1.5, 2, 2.5, 3, 3.5°) within a block (Experiment 1).

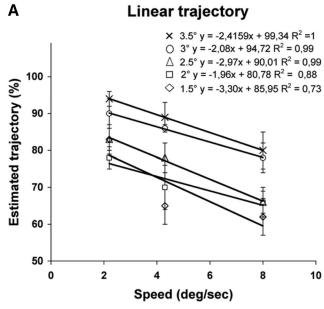
In the circular trajectory experiments (Experiments 3a, 3b, and 4), the target stimuli were either one or three light spots moving clockwise on a dark background along circular trajectories that had different radii in different experiments (Figure 1).

Three angular velocities (88, 157, 266 DegRot/s) were compared within a block in Experiment 3a, whereas one speed was used in Experiment 3b (198 DegRot/s) and Experiment 4 (157 DegRot/s). The luminance of the spot and that of the background were equal to 26.1 and to 3.07 cd/m², respectively. The environment was light to obscure possible persistence of the dot on the monitor.

Procedure

Participants sat 57 cm from the screen in a floodlit experimental room (300 lux) and received oral instructions. Using the method of

adjustment, observers had to match the perceived size of the trajectory. The target stimulus was presented on the right side of the screen, whereas the matching stimulus was simultaneously presented on the left side at a center-to-center distance of 10°. Observers had to adjust the matching stimulus (a stationary line or circle) setting it to the same size as the trajectory of the moving spot. The following instructions were given: "Please, adjust the



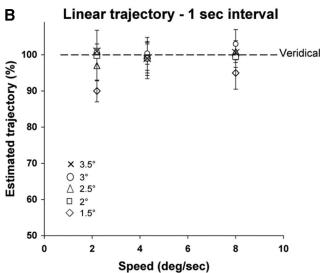
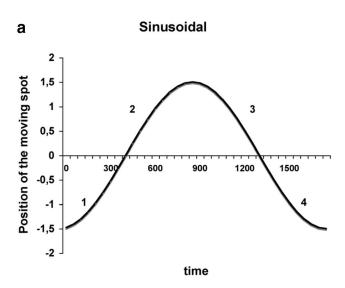


Figure 2. (A) Results of Experiment 1 for one dot moving back and forth along a vertical path, with no interval between sweeps. Estimates for five line lengths, expressed as % of physical length, are represented (rhombus = 1.5° ; squares = 2° ; triangles = 2.5° ; circles = 3° ; crosses = 3.5°). Equations of regression lines are shown in the legend. Errors bars represent standard errors. (B) Results of Experiment 1 for one dot moving back and forth along a vertical path, with 1-s interval between sweeps. Estimated lengths for five line lengths, expressed as % of physical length, are shown (rhombus = 1.5° ; squares = 2° ; triangles = 2.5° ; circles = 3° ; crosses = 3.5°). Errors bars represent standard errors.

length of the line (the size of the circle) until it looks identical to the trajectory of the moving spot(s). Use one key to gradually increase the size of the matching stimulus, and the other key to decrease it. When you are satisfied with the adjustment, press the third key to continue." The final settings were recorded for later analysis offline.

Data Analysis

Repeated measures ANOVAs were used to determine how underestimation of the trajectories depended on speed, stimulus, and eye movements. Post hoc *t* test with Bonferroni correction was used for pairwise comparisons. The Greenhouse-Geisser epsilon correction factor was applied where appropriate, to compensate for possible effects of nonsphericity in the measurements compared.



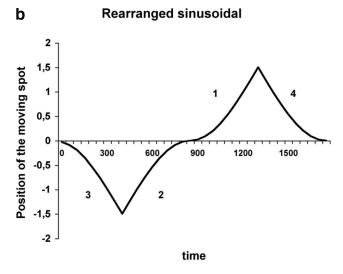


Figure 3. The position of the moving spot as a function of time. Mean speed was 3°/s. In Figure 3a the spot moves sinusoidally over time, the speed approaching to zero at the ends of the trajectory; in Figure 3b the four quadrants of the sinewave are rearranged to create a new waveform that was peaky at the ends of the trajectory and slowest in the middle.

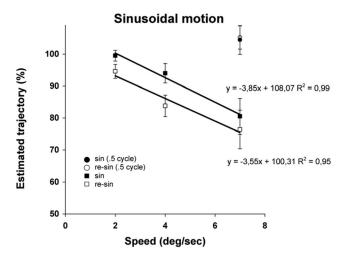


Figure 4. Results of Experiment 2. Estimated trajectory of one spot moving sinusoidally over time (sin: filled squares) or with a rearranged sinewave (re-sin: unfilled squares) fitted by regression lines. Filled (sin) and unfilled circles (re-sin) represent estimated trajectory in the control conditions with 1-s interval between half cycles. Errors bars represent standard errors.

Experiment 1: Straight-Line Paths

Observers matched the perceived length of the linear trajectory by adjusting the length of a static line. The adjustable line and the spot trajectory were presented simultaneously, side-by-side and randomly misaligned, to avoid spatial cues.

Observers were free to track the target and to move their eyes between the matching and target stimuli. In each block, every pairing of the three speeds (2.2, 4.3, and 8°/s) and five trajectory lengths (1.5, 2, 2.5, 3, 3.5°) was presented once each in random order. To avoid response bias, the initial length of the stationary line was not fixed but varied randomly on each trial from 0 to \pm 80% of line length. Each observer repeated the block three times. Two stimulus conditions were compared within a block: the dot moved up and down cyclically at constant speed, either with no interval (Condition 1) or with 1-s interval between the two directions (Condition 2). During the interval the dot remained visible and stationary.

Results and Discussion

In Figure 2, the data points, fitted by regression lines, indicate estimated length as a function of speed and trajectory length. When the direction of motion reversed with no time interval, the length of the linear trajectory was underestimated. Mean underestimation was 22%. Underestimation linearly increased with speed but decreased for longer trajectories. Repeated measures ANOVA showed a significant effect of line length (F(4, 20) = 31.8, p < .0001) and speed (F(2, 10) = 63.3, p < .0001). Post hoc comparison showed that lengths 1.5, 2, and 2.5° differed significantly from both 3 and 3.5° (p < .01) and that all speed pairs differed significantly (p < .01). The length × speed interaction was not significant (F(8, 40) = 1.9, p = .051). Indeed, the difference between the lowest and highest level of speed was significant at all lengths (p < .05) and the slopes of the functions describing the

relationship between length and speed are very similar (mean slope = $-2.544 \pm .57$). However, with the shortest line the best fit was not linear ($R^2 = .71$) but logarithmic ($R^2 = .97$), suggesting that a factor intervened to increase the perceived length of the line and reduce underestimation at the highest speed. This factor could be visual persistence that, with an estimated duration of 50 ms (Kerzel, 2000), would increase the perceived length maximally for the shortest and fastest line.

On the other hand, the estimate was generally accurate in Condition 2, when the motion stopped for 1 s before reversing direction. Neither main factor, length (F(4, 20) = 1.6, p > .05) nor speed (F(2, 10) = 2.1, p > .05), nor the interaction length \times speed (F(8, 40) = .7, p > .051) was significant. The fact that this pause in Condition 2 cancels the illusion, indicates that the underestimation requires a crucial parameter present in Condition 1 only: reversal of motion direction with no time delay. This is different from other mislocalization errors (Finke and Freyd, 1989; Hubbard, 1995; Kerzel, 2002, 2003; Müsseler & Aschersleben, 1998; Müsseler et al., 2002), which instead occur for unidirectional trajectories and rather show overestimation.

Our results, that trajectories were underestimated only when they reversed in direction without pausing, suggest a perceptual integration of the motion signals within a relatively fixed temporal window.¹

Experiment 2: Sine and Rearranged-Sine Motion

The disappearance of the illusion when the spot pauses, directed our attention to the end of the trajectory where the direction reverses. One possibility is that the visual system takes short cuts in virtue of its hypothetical "integrating time" t; the perceived motion of the moving spot is averaged or integrated over this time t by means of vector summation. Thus, a spot moving steadily up or down shows no illusion, but if it abruptly reverses, its final upward motion and initial downward motion should summate and cancel out, so that the extreme part of its trajectory is not perceived and the spot's total path is underestimated. If the spot pauses longer than the integration time before reversing, this underestimation will not happen.

So, to test the model, we arranged that when the spot reached the ends of its trajectory it was moving either at very low speed, which should minimize the underestimation, or else at maximum speed, which should enhance the underestimation. We made the spot move back and forth along the same vertical trajectory at the same mean speed, but we used two different velocity profiles on different trials. In one condition, the velocity profile was sinusoidal. The spot moved back and forth sinusoidally, which meant that its velocity slowed to almost zero at the two ends of its trajectory. In the other condition, we rearranged the parts of a sinewave so that the spot had maximum velocity at the ends of its trajectory, and minimum velocity in the middle of its path. We predicted, correctly as it turned out, that the latter case would give more underestimation. To rule out the possibility that the highest speed of the spot at the end of its trajectory may introduce end point position uncertainty as a new factor, we added two control conditions in which there was 1-s interval, with the screen dark, between half cycles of the sine and rearranged-sine trajectories: at the end of its motion in one direction the spot disappeared and reappeared one second later moving in opposite direction.

Figure 3 shows the position of the moving spot as a function of time. In Figure 3a the spot moves sinusoidally over time; note that at the ends of the trajectory (top and bottom) the velocity approaches zero, like a pendulum at the extrema of its swing. However, in a second condition (Figure 3b) we rearranged the four quadrants of the sinewave to create a new waveform that was peaky (fastest) at the ends of the trajectory and slowest in the middle. We argued that the faster the motion at the ends, the more the moving spot would change its position during the integrating time t and the greater the underestimates would be.

Method

The spot moved back and forth along a vertical trajectory 3° long, at the three speeds. The six conditions (three speeds \times sine or rearranged-sine velocity profile) were randomly intermingled. In the control conditions with 1-s interval between half cycles of sine and the rearranged-sine motion only the highest speed was tested.

Observers struck keys to change the length of the static line until it looked identical to the trajectory drawn by the spot that was moving up and down on the other side of the screen. With one key they gradually increased the length of the matching stimulus, with another key they decreased it. When satisfied with their adjustment, they pressed a third key to record the results for later analysis offline and continue. Observers made 10 readings of each of the six conditions.

Results

Figure 4 shows the results of Experiment 2. As predicted, the underestimates were greater for the rearranged-sine than for the sine conditions. In addition, the underestimates always increased with stimulus speed, as we already found in the first experiment. Repeated-measures ANOVA revealed significant differences between sine and rearranged-sine motion (F(1, 5) = 17.86, p < .01) and between the three speed levels (F(2, 10) = 8.48, p < .01). The motion \times speed interaction was not significant (F(2, 10) = 1.07, p > .05). Nevertheless, pairwise comparison showed that the difference between the two conditions was significant only at intermediate speed (p < .005). The lack of a significant difference between the two low-speed conditions is expected. At the highest speed, visual persistence, which increased perceived duration of about 50 ms (Kerzel, 2000), may have restored a more accurate length estimate, so that the final judgment may have resulted from a balance between the underestimation effect, because of motion integration over time, and the effect of retinal persistence. In the control conditions, where the spot disappeared for 1 s between half cycles of the trajectory, there was no underestimation, rather a slight overestimation was found (4.7% \pm 4 SE), in agreement with the representational momentum effect (Hubbard, 1995). This rules out the possibility that the higher underestimation with the

¹ We are happy to acknowledge that Rick Cai (personal communication) has independently done some experiments closely similar to ours. He moved a horizontal line up and down through a distance equal to its own horizontal length, thus sweeping out a square. However, the motion looked shorter than it really was, so the swept area looked not square but like a wide, low rectangle.

rearranged-sine motion was because of position uncertainty with very high speed.

The results obtained at intermediate speed support the integrating time hypothesis. They suggest that the perceptual mechanism underlying underestimation of motion operates within a relatively fixed temporal window.

Experiment 3: Circular Paths

Model Applied to Circular Paths

Whereas a linear trajectory reverses at its end, in a circular orbit the trajectory is continuously changing, although to a milder degree. A set of hypothetical neurons at early stage of motion analysis, responding to linear motion, with their receptive fields positioned along the trajectory, would 'view' the circular motion trajectory as made up of small segments along a many sided polygon. Individual linear motion segments could lie inside the arc (as the motion along a chord) or outside the arc (as the motion along the tangent). In the first case, one would expect underestimation, in the second case overestimation. Coren, Bradley, Hoenig, & Girgus (1975) reported a shrinking circle illusion that could possibly be related to the shrinking line illusion we showed in Experiments 1 and 2. In the following experiments we checked whether a circular trajectory, as well as a linear trajectory, was misperceived and in which direction.

Method

In independent blocks, the target stimuli were either one or three spots following a circular orbit (Figure 1). The three circular orbits were tangential. The radius of the trajectories was 1.4° .

In one block, for each of the stimuli, the angular velocity was 88, 157, or 266 DegRot/s (= 0.24, 0.44 or 0.74 rev/s). The tangential speed was respectively 2.14, 3.83, and 6.49° /s.

In each condition observers were required to track the spot trajectory and match the circular path of the spot(s) by adjusting the size of a single stationary circle. Each observer made three settings for each speed and for both stimuli. To avoid response bias the initial radius of the matching circle was $1.4^{\circ} \pm 0.3^{\circ}$ on each trial.

Results and discussion

Results are shown in Figure 5. Repeated measures ANOVA revealed that underestimation was larger with three spots (F(1, 5) = 73.9, p < .0001) and increased with speed (F(2, 10) = 21.4, p < .001). The interaction was not significant (F(2, 10) = 4.1, p > .05).

First, we found that the size of the trajectory was underestimated, so that the circle appeared to shrink. This replicates Coren and coworkers' results and is consistent with a recovery of the trajectory size by integrating linear motion segments lying inside the arc. Indeed, integration along the tangent would produce overestimation.

Second, we found that trajectories looked 5.4% smaller for three spots than for one. Possibly, the increased underestimation with three spots might arise from division of attentional resources when the moving dots were tracked attentively (Cavanagh & Alvarez, 2005). However, this is unlikely for several reasons. First, our

Circular path (1 vs 3 spots)

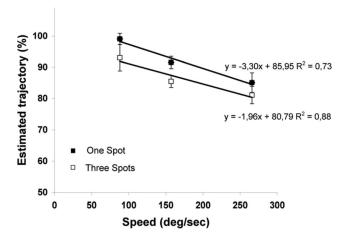


Figure 5. Results of Experiment 3a. Data points referring to the estimation of the radius of one spot (filled symbols) and three spots (unfilled symbols) circular trajectories are fitted with regression lines. Errors bars represent standard errors.

subjects were allowed to inspect the display with no time limit. Second, even assuming that total attentional capacity was shared among the three spots, whether they were attended concurrently (multiple attention) or sequentially (switched attention), one may expect higher misjudgments of the size of the trajectory but there is no reason to think that the misjudgments should be biased towards underestimation. Third, multiple tracking of three spots could have been made possible by grouping them into a higher order object (Yantis, 1992). Indeed, our subjects reported the three spots to group into a triangular shape that moved along a circular trajectory, but this would lead to no difference between one and three spots. Instead, it is interesting to speculate that the shape or the size of the object moving along a circular trajectory may affect the perceived size of its trajectory.

Note however that the enhanced underestimation with three spots should not occur if it resulted from tracking eye movements because observers can only track one trajectory at the time (Coren et al., 1975; Kerzel, 2002), and indeed Experiment 4 shows that eye movement cannot be the only explanation.

Third, we found that the circular trajectory was perceived veridically when the spot moved slowly, and subjectively shrank in size with increasing speed. The slopes of regression lines are similar with one and three spots, suggesting similar effect of speed in the two conditions.

Why does underestimation depend on velocity? The classical view is that eye movements can alter perceived velocity (Aubert, 1886; Fleischl, 1882; Harris, 1994). However, eye movements may not be causing the underestimates (Kerzel, 2000). Previous work showed that several mislocalization errors along the path of motion depend upon velocity (i.e. Fröhlich illusion, Kerzel and Gegenfurtner, 2004; onset repulsion effect (ORE), Thornton, 2002; flash-lag, Brenner & Smeets, 2000; representations of centripetal forces, Hubbard, 1996) but unlike our effects, these do not require any change in motion direction.

Here we attribute our underestimation phenomena to changes in direction that are integrated over a short visual integration time, rather than to mislocalization errors.

Experiment 3b: Null Method for Circular Paths

In a cleaner demonstration that circular trajectories are underestimated, we repeated the three-circle condition, using a nulling method that required no matching circle. Three dots arranged in a rigid equilateral triangle moved along a circular path. Observers adjusted the amplitude of this path until the circular trajectories of the three dots appeared to be tangential to one another. As we shall see, they underestimated the sizes of the trajectories and actually set them so that they overlapped considerably.

Results

Observers viewed three overlapping black outline circles on a mid-grey surround on a computer screen, with their centers lying at the apices of an equilateral triangle. Each circle subtended a visual angle of 4°, 50% larger than that used in the previous experiment. A white spot ran clockwise around the perimeter of each circle at a rate of 198 DegRot/s (0.55 rev/s, tangential speed = 6.9° /s). The three spots were always locked in step, such that they all passed (say) 2 o'clock or 6 o'clock at the same instant. All three circles could be moved bodily inwards and outwards toward and away from each other, without changing their radii, with a single shift of the computer mouse. Stated differently, the three spots lay at the corners of an unchanging upright equilateral triangle, and the observer adjusted the circular trajectory of this triangle. The observers were invited to adjust the positions of the circles until they just touched tangentially. This task was trivially easy and all settings made were virtually correct. Where 100% was the true separation between the centers of the circles, the mean settings were 98.3% \pm 0.2 (mean of three readings \times 5 Ss \pm 1

The background was then changed from mid-grey to black. This left the moving spots visible but completely hid the static circles. The observers now repeated the same task, but they were now obligated to base their judgments on the perceived amplitudes of the three circular paths instead of on the diameters of the now invisible static circles. The main result was that observers greatly underestimated the amplitudes of the motion paths and set the circles too close together, with a mean underestimation of $35.8\% \pm 4.1$. In other words, instead of separating the centers by the correct distance of one diameter (=100%) observers separated them by only two thirds of a diameter, so that when the circular paths were judged to be tangential they actually overlapped considerably. Figure 6b is a scale drawing of their actual mean setting.

Two control conditions examined the effects of landmarks. The three spots circled around as before, but now the background consisted of dense random grey-scale dots. These were either static, providing a wealth of static textural landmarks, or else twinkled dynamically. For the static dots, estimates of the circling spots were fairly accurate (92.2% \pm 4.3), and observers acknowledged that they "cheated" by lining up the circling spots with stationary background dots or clumps that served as landmarks. However, the twinkling dots provided no reliable fixed landmarks,

and once again, the circular trajectories were considerably underestimated (mean underestimation $31.4\% \pm 4.4$).

Discussion

Our results show that trajectories were underestimated over a wide range of configurations and psychophysical methods. We found earlier that only two factors abolished the underestimation: low speed, and long pauses when motion signals change direction. The absence of landmarks was also necessary. These results suggest that the illusion occurs when the visual system is forced to integrate motion signals over time within a short integration time.

Experiment 4: The Role of Eye Movements

The integration of motion signals is a relatively low level operation that would not require observers to track the moving targets. This is not what previous work showed. Coren et al. (1975) reported a shrinking illusion very similar to that we described in Experiment 3. However, they found, at the speed we used, very little underestimation when observers fixated the center of the circle. On the other hand, Hubbard (1996) reported an apparent displacement of the judged position toward the center of the orbit, a phenomenon that may account for the shrinking illusion, and Kerzel (2003) found that this displacement was larger with motionless eyes than with ocular pursuit of the target. Because different studies offer conflicting evidence on the part played by eye movements in the shrinking illusion, we shall now further examine the role of eye movements.

Method

Using the circular trajectory paradigm of Experiment 3a and a speed of 157° DegRot/s (0.44 rev/s), we asked observers either to track the moving spot, or to fixate steadily on the center of the circular path for at least three rotation periods. Then, they had to move their gaze to the center of the comparison circle and, without moving their eyes, adjust its size by either increasing or decreasing it until satisfied. These two tasks were performed twice, once with a red fixation cross in the center of each of the two stimuli and once without the fixation crosses. We added the no-cross condition because we introspectively had the impression that the fixation

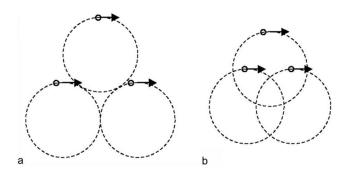


Figure 6. Three dots forming a rigid equilateral triangle moved along circular paths at 198 DegRot/s. Observers adjusted the path amplitude, attempting to set the three circular paths to be tangential to each other, as in a. However, they underestimated the path sizes and actually set them as in b (compare Figure 1). Note that b is an accurate scale drawing.

Eye movements effect

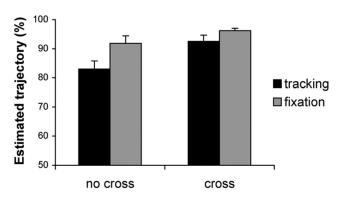


Figure 7. Results of Experiment 4 with and without eye movements in two conditions: with and without fixation cross in the center of the circular trajectory. Errors bars represent standard errors.

cross favored the strategy of judging the distance between two symmetrical points of the trajectory instead of its size. Indeed, Experiment 3b showed that the presence of static landmarks reduced the illusion. When the cross was absent, observers were required to maintain fixation on an imaginary fixation point in the center of the trajectory, and during 20 practice trials observers were trained to do this.

Eye movements were recorded with of a video-based eye monitoring system (Tobii 1750, Tobii) with Clearview 2.7.0 software. Tobii 1750 integrates the camera and infrared lighting into a TFT 17" monitor (1,024 \times 768 resolution). The system has an accuracy of 0.5°, a sampling frequency of 50 Hz and a reacquisition time shorter than 100 ms. We continuously recorded the position of the user's gaze, expressed as x and y coordinates on the stimulus screen. We used the following criterion to evaluate fixation: we rejected those trials (less than 5%) in which the eyes wandered more than 0.7° away from the fixation point during the 5 s before moving the eyes to the comparison stimulus.

Results and discussion

The effect of eye movements was significant (F(1, 5) = 12.3, p < .02) and showed that fixation reduced underestimation (Figure 7). When the cross was present, underestimation decreased but not significantly (F(1, 5) = 5.0, p < .08). The eye movements \times stimulus interaction was also not significant (F(1, 5) = .7, p = .4), indicating a similar effect of eye movements in the two conditions.

To summarize, shrinkage was greater with smooth tracking eye movements than without, and was greater without the fixation cross, during both tracking and fixation.

Our finding that eye movements are not necessary to have underestimates differs from Kerzel (2003), who found that inward subjective displacement is larger with motionless eyes. However, the inconsistency is only apparent because both his findings and ours indicate that the illusory effect cannot be because of eye movements. Mateeff and Mitrani (1979) also disproved possible influence of "overtracking" on mislocalization phenomena.

The fixation cross also reduced underestimation, perhaps by acting as a landmark and providing positional cues. Eye move-

ments introduce other important differences: fixation lets the spot fall on successive retinal positions, whereas tracking holds the spot on the fovea so that the visual system has to integrate the motion signal available at a given instant with those no longer there to recover the trajectory. Therefore, during fixation, the observer could have adopted the strategy of judging the distance between symmetrical points of the trajectory. Moreover, there are crucial aspects of Coren et al.'s method that may explain why they found fixation to drastically reduce (but not to abolish) the illusion. Their trajectories were much larger than ours and the retinal image was more peripheral. We do not know whether eccentricity plays a role but if it does, it is not the same during tracking and fixation. Even most importantly, the task was different. They asked observers to estimate the circle's diameter and this, together with the presence of a fixation cross, could have induced a different strategy during fixation.

Conclusion

To summarize, our results show that (a) underestimation occurs even if the visual task involves little memory, (b) both straight and circular trajectories are underestimated, (c) the underestimation increases linearly with speed, and (d) eye movements are important but not crucial to the illusion. We found only two factors capable of drastically abolishing underestimation: low speed and long pauses when motion signals change direction.

We have considered the most popular explanation of misperceived trajectories. A high-level explanation is that the end-point is displaced forwards because the mental system is unable to stop the cognitive representation of motion and this then continues after target offset (Freyd & Finke, 1984). This cognitive representation of motion is referred to as "mental extrapolation" or, when thought to be based on internalized physical regularities, as "representational momentum" (see also Finke & Freyd, 1989). The high-level interpretation in terms of mental extrapolation is under debate (see also Bertamini, 2002) mainly because low-level mechanisms of eye movements may contribute to misperception errors with smooth stimulus motion (Baldo, Kihara, Namba, & Klein, 2002; Kerzel, 2000; Kerzel, 2006; Kerzel, Jordan, & Müsseler, 2001; Whitney & Cavanagh, 2002; Whitney, Murakami, & Cavanagh, 2000). According to this low-level explanation, the observer's eyes are likely to pursue a smooth stimulus motion. After target disappearance, the smooth pursuit eye movements would overshoot the final target position, such that the point of fixation would be shifted in the direction of motion during the retention interval. Thus, end-point errors may result from eye movement overshoots, in combination with some known distortions of visual space such as the persistence of the target's image after target offset (Kerzel, 2000), and a bias to localize the target toward the fovea (Kerzel et al., 2001).

Both low-level and high-level explanations have been offered for various mislocalizations of moving objects: the flash-lag effect, in which a flash adjacent to a continuously moving object is perceived to lag behind it (Nijhawan, 1994); the Fröhlich effect (Fröhlich, 1923), in which the judged onset of a moving target is displaced in the direction of target motion; the onset repulsion effect, in which the error in the judgment of the initial target position is always back along the observed path of motion (Thornton, 2002)—the opposite of the Fröhlich effect; and the inward

displacements with circular trajectories (Hubbard, 1995). Two of these effects are comparable to ours. Our illusion could be well assimilated to apparent displacement of the judged final position inward the center of the orbit (Hubbard, 1996) that may have its cause in perceptual factors (Kerzel, 2003). The Fröhlich effect also resembles ours even though the mechanism cannot be the same since our illusion affects the whole trajectory not its starting point. In all three cases—the Fröhlich effect, Hubbard's inward shift, and our underestimation phenomenon—misperception increases with velocity. This speed effect is compatible with both high-level (Hubbard, 1996) and low-level (Kerzel, 2003) accounts of misperception errors.

The shrinkage illusion applies to the trajectory of a bright spot moving on a dark background, and it occurs only when the linear trajectory changes direction without a pause. Whether the spot moves up and down or in a circle, the motion system can recover the trajectory only by integrating each present position with the previous positions that are no longer present. That is, to reconstruct the trajectory, the visual system has to integrate local segments of it over time. The trajectory would be unambiguously underestimated if the visual system attempted to reconstruct a path in which the direction changes in time by interpolating of local segments of the trajectory within successive short integration times. One way this interpolation may occur for both linear and circular trajectories is by vector sum of successive straight motion signals (Smith, 1994) and this could lead to shrinking of overall trajectory size.

For motion along a linear trajectory, the model predictions are straightforward. Indeed, two motion vectors of equal magnitude and opposite direction cancel each other out. Of course, this cancellation will only occur for those parts of the trajectory where the direction reverses. Because the amount of cancelled trajectory is fixed, the perceived estimate of the trajectory length should decrease as length increases, which is exactly what we found. We propose that a vector sum applied to circular trajectories could also shrink the perceived size of the circular trajectory. In Figure 8a, the trajectory of a moving spot (black dot) is represented by an arc (A) of length proportional to angular velocity of the spot $(v_1 \text{ and } v_2)$. The invisible ongoing trajectory segment can be recovered by averaging (vector summation), within a short temporal window, of successive neural local motion signals as v_1 and v_2 , corresponding to chords of successive arcs. The perceived position of the moving spot will be at the average of its physical positions during time t, at the midpoint of the vector sum (p), and it is shown by the white dot. The space between the arc and p, hence the amount of underestimation (D), will increase with vector length, that is with speed.³ Indeed, as vector length increases with increasing speed, the angle α increases. Equation (a) allows us to calculate the value of D. For a unit radius h, we have:

a) D =
$$(h - \cos \alpha/2)$$

Because the length of p, that is related to α , depends on the length of motion vectors, the outcome is that D also depends on the length of motion vectors. To fit this model to the data we need to adjust only one parameter. We assume an integrating time no longer than a fixation duration: 250 ms. In Figure 8b, linear (dark grey), sinusoidal (light grey), and rearranged-sinusoidal (black) trajectories are superimposed. The dotted rectangle represents the integrating time, and the horizontal lines shows the average position of the spot that moves along the trajectories: linear (66.6%),

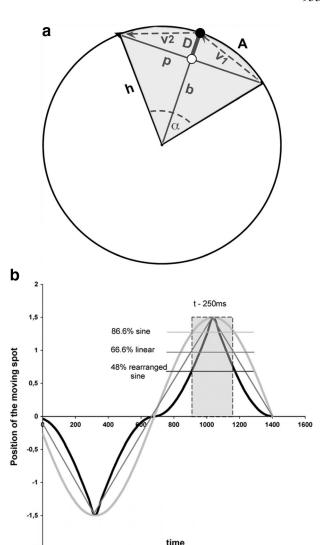


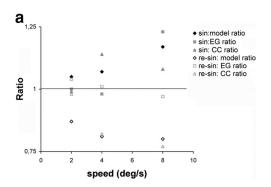
Figure 8. The trajectory of a moving spot (black spot) is represented by an arc (A) of length proportional to angular velocity of the spot (Figure 8a). The invisible ongoing trajectory is recovered, within an integrating time t no longer than fixation duration (250 ms, grey sector) by a vector sum (p) of successive straight local motion signals (v_1, v_2) corresponding to the chord of A. The length of p increases with α . The perceived position of the moving spot will be at the average of its physical positions during time t, and is shown by the white dot. In Figure 8b, linear (dark grey), sinusoidal (light grey) and rearranged-sinusoidal (black) trajectories of a line (3° long) moving at 4°/s are superimposed. The horizontal lines show the average position of the spot that moves along the trajectories: linear (66.6%), sinusoidal (86.6%) and rearranged-sinusoidal (48%) of maximum.

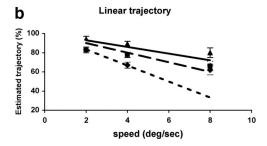
sinusoidal (86.6%), and rearranged sinusoidal (48%) of maximum. The black line is much lower than the light-grey line because the

² Kerzel and Gegenfurtner (2004) were able to explain also the onset repulsion effect on the bases of this model, assuming that the constant spatial distortion was negative.

³ Note that even if v1 and v2 were tangent to their respective arcs, the vector sum would still correspond to a chord.

black curve falls off much more sharply from the peak. To be more accurate, at a speed of 4°/s, the average position of the light grey lies about halfway between 86.6% and 100%, namely at 93.3%, the average position of the black spot lies about halfway between 48% and 100%, namely at 76%, whereas the average position of the dark grey spot lies halfway between 66.6% and 100% namely 87%. The ratios between both sinusoidal and linear trajectories and between rearranged-sinusoidal and linear trajectories as predicted by the model (black symbols) are compared, in Figure 9a, with the corresponding ratios (grey symbols) obtained by two subjects (CC and EG). Individual data reflect the two important predictions from the model: (a) ratios larger and smaller than 1 are found with sinusoidal and rearranged-sinusoidal respectively. In other words,





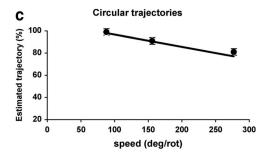


Figure 9. Figure 9a shows the ratios between both sinusoidal and linear trajectories (filled symbols) and between rearranged-sinusoidal and linear trajectories (unfilled symbols) resulting from the model (black) and from individual data (CC, grey triangles, and EG, grey squares). Figure 9b shows estimation as a function of speed as predicted by the model (lines) and mean experimental data points in three line length conditions: 1.5° (continuous, triangles), 2.5° (broken, squares) 3.5° (dotted, rhombus). Figure 9c compares, for the case of circular trajectories, the estimated trajectory as a function of speed predicted by the model (continuous lines) and that resulting from average experimental data (black circles).

a sinusoid gives less shrinkage than a linear motion, whereas a rearranged-sinusoid gives more, (b) these increase with speed.

Figure 9b shows the mean estimates made as a function of speed, together with the lines predicted by the model, for 1.5° (dotted), 2.5° (broken), and 3.5° (continuous) trajectories. In all three cases, the fit is good because underestimation increases as length decreases. However, the model also predicts that underestimation should increase with speed, more for the shortest lines. The data do not indicate this relationship. We have discussed in Experiment 1, which with the shortest line the best fit is not linear but logarithmic, suggesting that a factor intervenes, probably visual persistence, to reduce underestimation. There is evidence for the role of visual persistence (Kerzel, 2000) that would account for reduced underestimation particularly with the shortest line moving at the highest speed.

Finally, Figure 9c compares the estimated trajectory as a function of speed for circular trajectories, either predicted by the model (continuous line) or resulting from average experimental data. When the trajectory is circular, and the angular speed is 266 DegRot/s, the time required for the entire trajectory (360°) is 1.3 s. Within the 250-ms temporal window, the dot rotates through 70°. The value of α decreases to 39° and 22° as speed decreases to 156 and 88 DegRot/s. The line in Figure 9c represents these predicted values. Again, the fit with the data is very good. Thus, overall, the model provides a good fit of experimental data.

We predict that visual persistence plays a role also with circular trajectories. We might speculate that the perceived size of the trajectory would continue to shrink with speed, but at some higher speeds the trajectories would start to look like circles and their perceived size would start to rise again.

In conclusion, it is interesting to speculate how general this mechanism is. Whereas it does not explain the Fröhlich effect and other mislocalization errors, since the trajectory does not change direction, it seems compatible with the well-known phenomenon of displacement of the judged final position inward the center of the orbit (Hubbard, 1996). Indeed, the phenomenal reports of some of our subjects were spectacular: upon increasing the speed, the path becomes an apparent spiral, directed toward the center of the orbit, and this is well predicted by vector sum model.

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