Wriggling motion trajectory illusion

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In this paper, we report on a novel visual motion illusion. When hundreds of dots move in straight trajectories and random directions without colliding, the trajectories are perceived as wriggling rather than straight (Experiment 1). We examined the nature of this "wriggling motion trajectory illusion" via six separate experiments. The illusion was most pronounced when there were a large number of dots (Experiment 2). The illusion was independent of both the distance covered (Experiment 3) and the observer's eye movements (Experiment 4) as well as the dot types (Experiment 5). We also showed that the proximity among the moving dots plays a role in the illusion (Experiment 6).

Keywords: illusion, trajectory, wriggling, dot motion

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Introduction

Motion perception is one of the most fundamental aspects of visual perception, and, therefore, the mechanisms underlying it have long been of interest in the scientific community. Studies involving multiple moving dots have been widely conducted to examine the psychophysical and neurophysiological aspects of motion perception.

When multiple moving dots are used in vision experiments, each dot is assigned a specific speed and direction to achieve straight trajectories. The observation of such moving dots is known to elicit activities in the visual cortex. In particular, the middle temporal (MT) area in the visual cortex (Braddick et al., 2001; Huk, Dougherty, & Heeger, 2002) responds to dot speed (Newsome, Mikami, & Wurtz, 1986; Pack, Conway, Born, & Livingstone, 2006), dot coherency (McKeefry, Watson, Frackowiak, Fong, & Zeki, 1997; Rees, Friston, & Koch, 2000), and direction of motion (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996). The results of these neurophysiological studies are congruent with psychophysical observations (Britten et al., 1996; Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Britten, & Movshon, 1989; Newsome et al., 1986).

When moving dots are used as stimuli, their trajectories are, in most cases, set to be straight. In such cases, it is therefore logical to assume that they will be perceived as moving in straight lines. While the assumption seems to be valid in most cases, it is important to examine whether the perceived trajectories of the stimuli (dots) are always in accord with their actual physical trajectories.

There are several cases in which the perceived trajectory contradicts the actual physical trajectory. When a dot moves against a dark background, large discrepancies between the actual and the visually perceived trajectories have been observed (Fujii, 1943). In Fujii's experiment, the trajectory of a target moving in a square path was mislocalized towards inside when it was moving on the sides of the square, while the trajectory was accurately localized at around the corners. This type of misperceived trajectory was shown to be related to smooth pursuit eye movements (Festinger & Easton, 1974; Koga, Groner, Bischof, & Groner, 1998; Koga, Ohta, & Groner, 1996). Misperceiving trajectory length is another type of trajectory illusion. When judging the starting position of a moving stimulus, observers often mislocate the origin towards the direction of motion—the Frohlich illusion (Musseler & Aschersleben, 1998; Musseler & Neumann, 1992). Misperception of the path length has also been reported for spotlights along a circular trajectory (Sinico, Parovel, Casco, & Anstis, 2009). In these studies of misperceived trajectories, the perceived trajectory was examined with only one stimulus present, and the observer's attention was directed towards the moving stimulus.

When hundreds of dots moving in multiple directions are displayed on a screen, it is impossible to track the trajectory of each individual dot. Multiple moving dots give a perception of the whole and produce an integrated perception. In this paper, we report on a robust, novel visual illusion in which multiple dots move along straight trajectories without colliding, and yet their trajectories are perceived to be wriggling rather than straight. First, we demonstrated this illusion in Experiment 1. Then, the nature of this illusion was examined in five more experiments. The effects of speed and dot density on the illusion were evaluated in Experiment 2. In Experiment 3, we tested whether the robustness of the illusion is dependent on the speed or distance. In Experiment 4, the effects of the observer's eye movements on the illusion were examined. Experiment 5 involved a comparison between the illusion with filled dots and open dots. Finally, in Experiment 6, the role of the dots' proximity was examined by manipulating the distances between moving dots.

Experiment 1: Wriggling motion trajectory illusion

In Experiment 1, we introduced the wriggling motion trajectory illusion and demonstrated the robustness of its effect.

Subjects

Ten subjects with normal or corrected-to-normal vision participated in this experiment. Of the 10, five were male and five were female. The age range was 19–28 years, with a mean age of 23.1 years. All subjects were naïve to the purpose of the study and gave written informed consent for their participation in the experimental protocol, which was approved by the Institutional Review Board at Keio University.

Stimuli and procedure

The stimulus images were bitmap files generated by a Macintosh computer (model: MacMini, OS 10.7.4, Apple, Cupertino, CA) using C++ and OpenGL. The images were converted to QuickTime movies using QuickTime 7 Pro, and displayed on a 21-inch CRT monitor (EIZO, FlexScan T965) using Matlab 2010a with Psychtoolbox expansions (Brainard, 1997; Pelli, 1997). With their chins and foreheads fixed, the subjects viewed visual displays on a screen positioned 57 cm from their eyes. All experiments were conducted in a dimly lit room.

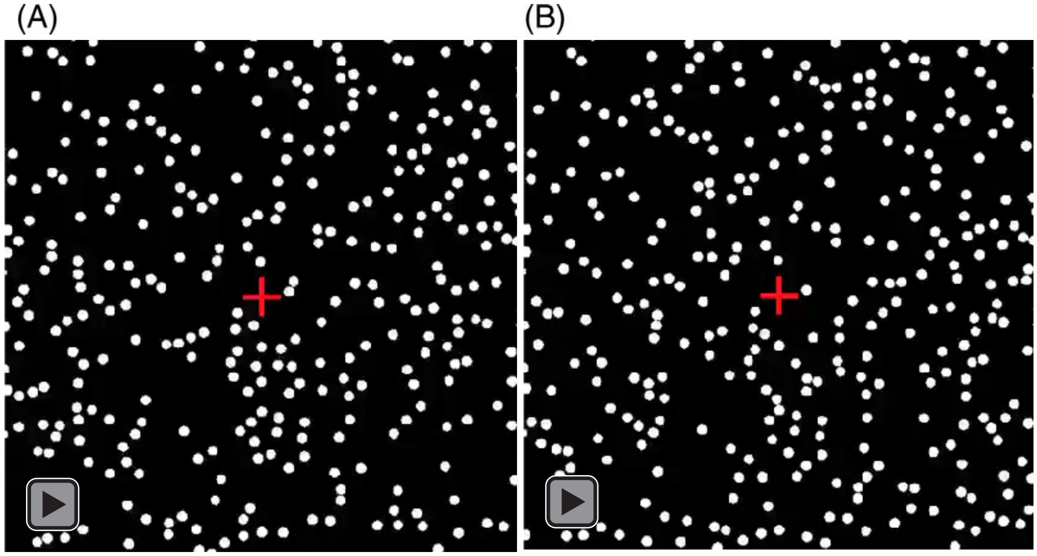
The stimulus movies consisted of white round dots moving in random directions against a black background. The diameter of each dot was 0.4°, and the dots were displayed inside a square window with dimensions of $20° \times 20°$. The movies were displayed at 30 frames per second (fps).

In the stimulus movies, 300 dots moved at a constant speed of 3°/sec. Each stimulus movie met one of two conditions. In the collision condition, the moving dots were allowed to overlap while moving in straight lines (Movie 1A). In the no-collision condition, the directions and positions of the moving dots were arranged so that no dots overlapped while moving in straight lines (Movie 1B). In each trial, a red fixation cross subtending 1° was displayed against a black background for 500 ms, followed by a movie of the moving dots for 3 sec. The red cross was displayed throughout the movie, and the subjects were asked to fix their eyes on it while observing the moving dots. After the presentation, the subjects were asked whether the dot motion appeared to be straight or wriggled and responded by pressing a button (Figure 1). The two experimental conditions were each tested 20 times with 20 different stimulus movies presented in random order. Note that we named the collision condition to denote the dots' overlapping on their paths. The moving dots in the collision condition were actually perceived as streaming rather than colliding.

Results and discussion

The percentage of the dot motion perceived as wriggling rather than straight was calculated for each condition and plotted in Figure 2. When all dots moved in straight trajectories, whether the dots collided resulted in a clearly different perception of their trajectories. In the collision condition, in which the moving dots collided in their paths, the dot motion was perceived as straight. However, in no-collision condition, in which the moving dots did not collide, the motion was perceived as wriggling. A paired sample t-test confirmed a significant difference between the two conditions, $t(9) = 20.4$, $p < 0.001$. After the experiment, all 10 subjects reported that they saw the dots wriggling, and that they were not aware that all dots were actually moving in straight lines.

As demonstrated in this experiment, when dots are moving in straight lines in random directions without



Movie 1. Samples of the stimulus movies used in Experiment 1. (A) Collision condition. All dots are moving in random directions in straight trajectories, and the dots are allowed to collide with each other on their paths. (B) No-collision condition with wriggling motion trajectory illusion. All dots are moving in random directions in straight trajectories without colliding with each other.

colliding, the dot motion was perceived as wriggling. We named this the "wriggling motion trajectory illusion."

Experiment 2: The role of speed and dot density

In Experiment 2, we examined the nature of the wriggling motion trajectory illusion by evaluating the effects of dot speed and dot density.

Subjects

Seven subjects with normal or corrected-to-normal vision participated in this experiment. Of the seven, five were male and two were female. The age range was 19–31 years, with a mean age of 24.4 years. None of these subjects participated in Experiment 1, and all were naïve to the purpose of the study. The subjects gave written informed consent for their participation in the experimental protocol, which was approved by the Institutional Review Board at Keio University.

Stimuli and procedure

This experiment was similar to Experiment 1 except for the following. The three stimulus features of speed, number of dots, and whether the dots collided were manipulated in this experiment. A combination of dot speed (1°, 2°, or 3°/sec), number of dots (100, 200, or 300), and dot collision or no-collision resulted in 18

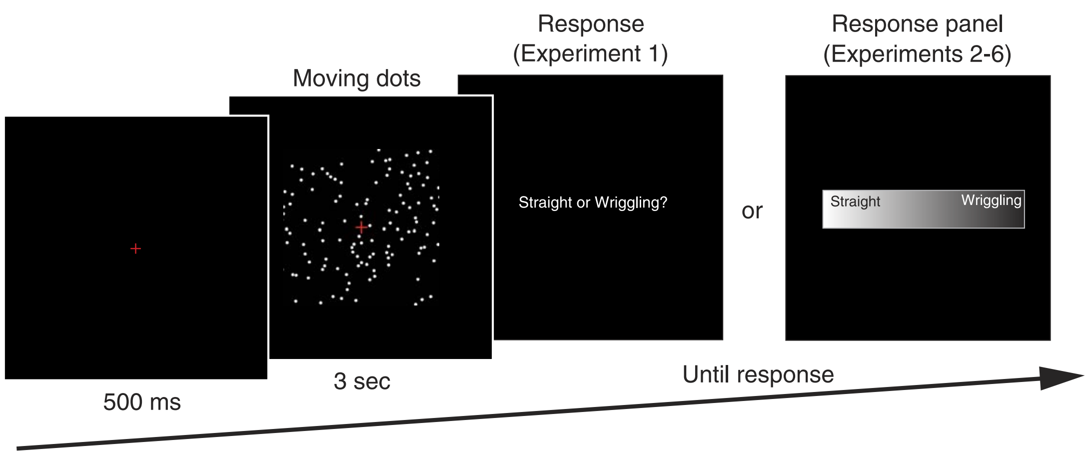


Figure 1. Stimulus presentation and response screens. The scales of the stimulus and the response screens have been modified for presentation purposes.

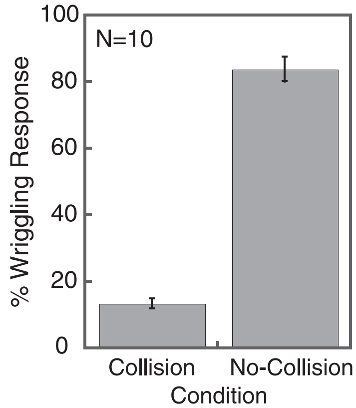


Figure 2. Experiment 1. The averaged percentage of the dot motion perceived as wriggling. Error bars represent ±standard error of the mean.

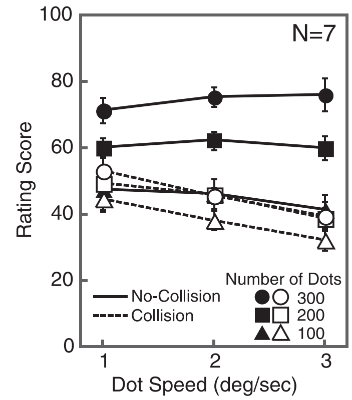


Figure 3. Experiment 2. The average rating score for each condition is plotted separately for the no-collision condition and for the collision condition. The *x*-axis represents the dot speed. The number of dots is represented by separate symbols: triangles for 100 dots, squares for 200 dots, and circles for 300 dots. The rating scores for the no-collision condition are plotted with filled symbols, and the rating scores for the collision condition are plotted with open symbols.

different conditions. In each trial, a red fixation cross subtending 1° was displayed against a black background for 500 ms followed by a movie of the moving dots for 3 sec. The red cross was displayed throughout the movie, and the subjects were asked to fix their eyes on it while observing the moving dots. After the presentation, a response panel, 4° in height and 23° in width, was displayed at the center of the screen. The word "Straight" was placed on the left side of the panel and the word "Wriggling" was placed on the right (Figure 1). The subjects were then asked to rate their perception of the dots' motions by clicking a position on the panel. For example, if they had perceived the motion of the dots as wriggling considerably, they were asked to click the rightmost section of the panel, and if they perceived the motion as very straight, they were asked to click the leftmost section of the panel. The subjects were urged to use the full width (range) of the response panel and were told that the location where the mouse click occurred corresponded to a rating score. The subjects first practiced the task in a session comprising 54 trials, in which each of the 18 conditions was repeated three times. In this practice session, they were instructed to create an internal criterion regarding which kind of perception they were to consider straight and which to consider wriggling. After the practice session, the subjects moved on to the main experiment. In the main experiment, the 18 experimental conditions were each presented 22 times, in random order. Subjects were allowed to take a break after every 36 trials.

Results and discussion

The subjects' rating scores were converted to a scale ranging from 0 to 100 in which a click on the leftmost section of the response panel (straight side) resulted in a rating of 0, while a click on the rightmost section of the response panel (wriggling side) resulted in a rating of 100. Thus, the rating score could be said to represent the extent of wriggling that they had perceived. The mean rating scores for each condition are plotted separately in Figure 3 for the collision and no-collision conditions.

The results revealed three key features of this phenomenon. First, the dots were perceived to be more wriggling when they were not allowed to collide. Second, the moving dots were perceived to be more wriggling when there were more moving dots present in the display. Third, when they were allowed to collide, faster moving dots were rated to be less wriggling than slower moving dots. A repeated-measure analysis of variance (ANOVA) with three factors (collision, dot speed, number of dots) confirmed significant effects of collision, $F(1, 6) = 21.0$, $p < 0.01$, and of number of dots, $F(2, 12) = 8.8$, $p < 0.01$. There were also significant interactions between collision and speed, $F(2, 12) = 15.9$, $p < 0.01$, and between collision and number of dots, $F(2, 12) = 13.7$, $p < 0.01$.

Because all dots traveled in straight lines in our stimuli, a higher rating score can thus be regarded as being the result of a wriggling illusion. The results of Experiment 2 indicated that the robust wriggling illusion occurs when multiple dots were moving in random directions without colliding. Therefore, whether the moving dots collided was evidently a determinant for the illusion. The number of moving dots also seemed to be an influential factor where a larger number of dots induced more wriggling percepts particularly in the case of the no-collision condition. Although there was a significant interaction between collision and speed, interpreting the effect of speed required extra caution as it was the collision condition that was affected by the dot speeds. While the rating scores for the no-collision conditions were similarly high for all speeds, the subjects gave higher wriggling scores for slower dots in the collision condition, which resulted in larger differences between the collision and no-collision conditions for the faster speed.

One of the possible reasons for the faster moving dots in the collision condition being perceived as being straighter than the slower moving dots might be due to the unequivalent number of collisions presented in the stimulus movies. Because the duration of the stimulus was constant in this experiment, the dot speed varied with the distance traveled, that is, the faster-moving dots traveled longer distances than the slower-moving dots. Further, when the distance traveled was longer, the stimulus movie in the collision condition contained more collisions. Thus, if the subjects rated their perception of wiggling based on the number of collisions in the stimulus movie, the scores for the collision condition would appear to be different for different speeds.

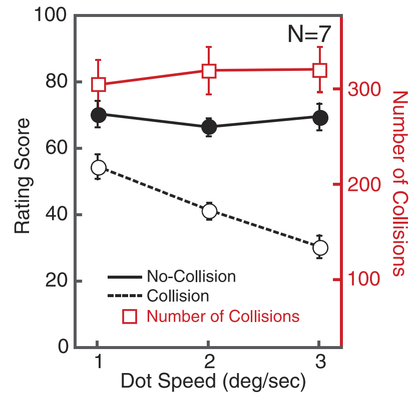


Figure 4. Experiment 3. The average rating score for each condition is plotted separately for the no-collision and collision conditions. The *x*-axis represents the dot speed. The number of dots and the moving distance were 300 and 3°, respectively, in all conditions. The rating scores for the no-collision condition are plotted with filled circles and solid lines, and the rating scores for the collision condition are plotted with open circles and dotted lines. The *y*-axis scale on the right reflects the average number of collisions in the collision condition, which is plotted with red squares.

Experiment 3: The role of speed and duration of the stimulus

In Experiment 3, we compared the effects of three speeds while keeping the distance traveled by the dots and the number of dot collisions constant. Evaluating the illusion under such conditions enabled us to narrow the factors contributing to this wriggling motion trajectory illusion.

Subjects

The seven subjects who had participated in Experiment 2 also participated in this experiment. Experiments 2 and 3 were conducted on different days.

Stimuli and procedure

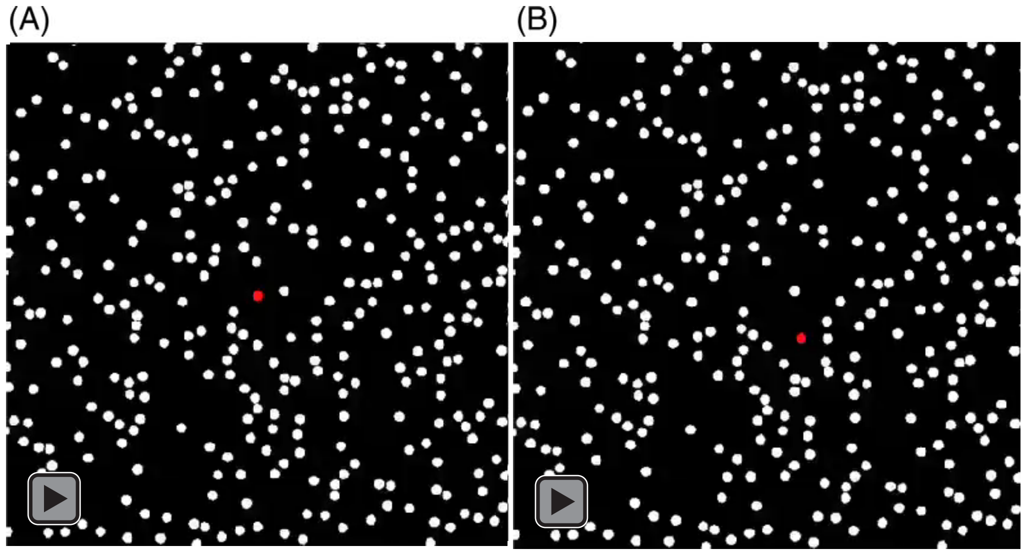
For the most part, this experiment was similar to Experiment 2 except for the following. The number of moving dots was fixed at 300. The combination of the dot speed (1°, 2°, and 3°/sec) and dot collision (collision, or no-collision) generated six conditions. The duration of dot motion was 3 sec for the 1°/sec condition, 1.5 sec for the 2°/sec condition, and 1 sec for the 3°/sec condition resulting in the distance covered being 3° for all conditions. Because the distance traveled was constant for all speeds, the average number of collisions in the collision condition was similar for all speeds.

The subjects were asked to rate their perception of the motion of the dots by clicking on the panel. They were instructed to use the full length of the response panel and were also told that the location of the mouse click corresponded to the rating score. The subjects first practiced the task in a session comprising 18 trials in which the six conditions were each repeated three times. In this practice session, they were instructed to create an internal criterion regarding which kind of perception they were to consider straight and which to consider wriggling. After the practice session, the subjects moved on to the main experiment. In the main experiment, the six experimental conditions were each presented 22 times in random order. Subjects were allowed to take a break after every 18 trials.

Results and discussion

The subjects' rating scores were converted to a scale ranging from 0 to 100, and the mean rating scores for each condition are plotted separately in Figure 4 for the collision and no-collision conditions.

When the distance traveled was kept constant across all conditions, the wriggling rating scores were similar to those in Experiment 2. When dots did not collide, the rating scores were consistently higher regardless of the dot speed. However, when the dots were allowed to collide, the rating scores were lower than the non-colliding conditions, and the scores declined as the



Movie 2. Samples of the stimulus movies used in Experiment 4. (A) Fixated condition. (B) Pursuit condition.

speed increased. A repeated-measure ANOVA with two factors (collision and speed) revealed a significant effect of collision, $F(1, 6) = 17.5$, $p < 0.01$, and a significant interaction between collision and speed, $F(2, 12) = 13.5$, $p < 0.01$. We also calculated the number of collisions in the stimulus movies used for the collision condition and plotted the values along with the rating scores. The average number of collisions in a stimulus movie was constant regardless the dot speed and was confirmed by one-way ANOVA, $F(2, 65) = 2.5$, $p = 0.09$. Because the distance traveled and the number of collisions were set to be equivalent at all three speeds, the difference in the rating scores cannot be attributed to those characteristics of the moving dots. It was the moving speed itself that differentiated the rating scores in the collision condition.

It should be addressed that the averaged wriggling scores were above 20 even in the collision condition. This was likely due to the way we measured the rating scores. In the experiment, the subjects were asked to rate the wriggling perception, while presentations of the collision condition were intervened with the no-collision conditions. Thus, the rating scores were based on relative evaluations of how the dots looked less or more wriggling, and do not necessarily reflect how the straight moving dots are perceived when they are presented alone as a single condition. Also, note that the subjects were instructed to build an internal criterion using the first 18 trials, and the criterion was independent of that used in Experiment 2. Although all subjects participated in both experiments, these experiments were conducted on separate days, and they were encouraged to build a new criterion for Experiment 3. Therefore, we cannot quantitatively compare the results in Experiments 2 and 3. Nevertheless, the data suggest that it was the speed of the dots and not the distances traveled nor the number of collisions that affected the perception of wriggling motion in the collision condition.

Experiment 4: The role of eye movement

In both Experiments 2 and 3, the subjects observed the stimuli while fixating on a cross in the center of the frame. As the perception of trajectory could be influenced by eye movements in some cases (Festinger & Easton, 1974; Koga et al., 1996; Koga et al., 1998), in Experiment 4 we examined the wriggling motion illusion under two conditions, one with the eye fixated and the other with the eye pursing the movement.

Subjects

The seven subjects who had participated in Experiments 2 and 3 also participated in this experiment. The experiments were conducted on different days.

Stimuli and procedure

This experiment was similar to Experiment 2 except for the following. The number of moving dots was fixed at 300. A combination of dot speed (1°, 2°, and 3°/sec), dot collision (collision or no-collision), and eye movement (fixated or pursuing) generated 12 conditions. In the fixated condition, a red fixation dot was displayed at the center of the screen throughout the movie (Movie 2A). The red fixation dot was the same

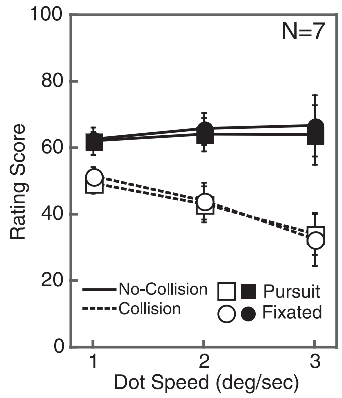


Figure 5. Experiment 4. The average rating score for each condition is plotted separately for the no-collision condition (filled symbols with solid lines) and for the collision condition (open symbols with dotted lines), the pursuit condition (squares), and the fixated condition (circles). The *x*-axis represents the dot speed. The number of dots was 300 for all conditions.

size as the other moving dots. In the pursuing condition, one of the moving dots was randomly selected and colored red (Movie 2B). The subjects were instructed to pursue the colored dot throughout the movie. At the beginning of each trial, the first frame of the movie was presented for 500 ms, followed by 3 sec of dot motion. The subjects were instructed to find and fixate on the red dot during the first 500 ms and fixate on or pursue the red dot in the subsequent movie. The subjects first practiced the task in a session comprising 36 trials, in which the 12 conditions were each repeated three times. In this practice session, they were instructed to create an internal criterion regarding which kind of perception they were to consider straight and which to consider wriggling. After the practice session, they moved on to the main experiment. In the main experiment, the 12 experimental conditions were each presented 22 times in random order. Subjects were allowed to take a break after every 24 trials.

Results and discussion

The subjects' rating scores were converted using a scale ranging from 0 to 100, and the mean rating scores for each condition are plotted separately in Figure 5 for the collision and no-collision conditions and for the fixation and the pursuit conditions.

The rating scores for the fixated and pursuit conditions were remarkably similar indicating that perception of the wriggling motion illusion is independent of eye movement. A repeated-measure ANOVA with three within factors (fixation, collision, and speed) showed a significant effect of collision, $F(1, 6) = 10.5$, $p = 0.02$, but no significance for fixation, $F(1, 6) = 0.05$, $p = 0.83$, nor for speed, $F(2,1\ 2) = 1.88$, $p = 0.20$. The subjects verbally reported that pursuit gave a strong impression that the red dot was moving in a straight line, but the motions of the other dots were still perceived as wriggling. The results of Experiment 4 confirmed the robustness of the wriggling motion illusion and the fact that it is independent of eye movement.

Experiment 5: The role of overlapping dots

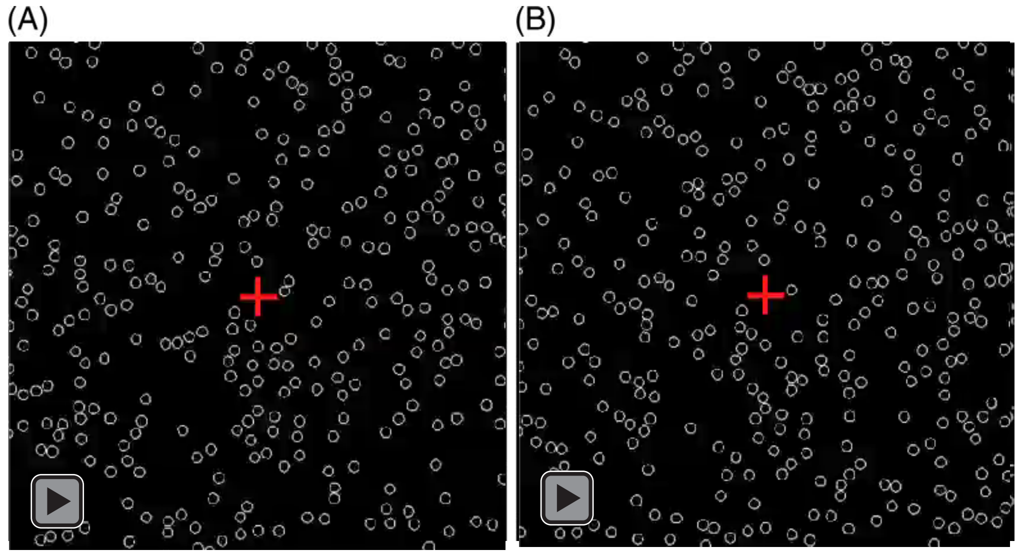
The wriggling motion illusion is represented by perceptual differences between the collision and the no-collision conditions. In the stimulus movies, whether the dots collide introduced some difference in the luminance distributions in each frame. When two dots collide, they partially or completely overlap generating a compound area, while the dots never changed their size or shape in the no-collision movies. As a result, there are fewer numbers of white objects and fewer numbers of white pixels in the collision condition compared to the no-collision condition. Because stimulus size sometimes affects motion perception (Tadin, Lappin, Gilroy, & Blake, 2003), the difference in the overall white area between these conditions could be a cause of the wriggling percepts. To examine the effect of luminance distributions in the illusion, we reduced changes in the luminance-defined area by making movies with open dots, and compared the effect between the open and the filled dots.

Subjects

Seven subjects with normal or corrected-to-normal vision participated in this experiment. Two subjects had also participated in Experiments 2, 3, and 4. The other five had never participated in previous experiments. Of the seven, five were male and two were female. The age range was 23–34 years, with a mean age of 26.7 years. All of these subjects were naïve to the purpose of the study. The subjects gave written informed consent for their participation in the experimental protocol, which was approved by the Institutional Review Board at the University of Tokyo.

Stimuli and procedure

Moving dots in a movie were all either filled or open (Movie 3A and B). The filled dots were same as in the previous experiments. The open dots were drawn as white circles. When two open dots overlapped, they created two intersections of their borders without



Movie 3. Samples of the stimulus movies used in the framed condition in Experiment 5. (A) Open collision condition. (B) Open no-collision condition.

occlusion. The experiment was similar to Experiment 2 except for the following. The number of moving dots was fixed at 300. A combination of dot speed (1°, 2°, and 3°/sec), dot collision (collision or no-collision), and dot type (filled or open) generated 12 conditions. A red fixation cross was displayed throughout the movie, and the subjects were asked to fix their eyes on it while observing the moving dots. The subjects first practiced the task in a session comprising 36 trials, in which 12 conditions were each repeated three times. In this practice session, they were instructed to create an internal criterion regarding which kind of perception they were to consider straight and which to consider wriggling. After the practice session, they moved on to the main experiment. In the main experiment, the 12 experimental conditions were each presented 22 times, in random order. Subjects were allowed to take a break after every 24 trials.

Results and discussion

The subjects' rating scores were converted using a scale ranging from 0 to 100, and the mean rating scores for each condition are separately plotted in Figure 6, for the collision and no-collision conditions and for the filled and open dots.

The rating scores for the filled dots and open dots were similar, indicating that perception of the wriggling motion illusion is independent of dot types. A repeated-measure ANOVA with three within factors (dot type, collision, and speed) showed a significant effect of collision, $F(1, 6) = 12.9$, $p = 0.011$, but no significance for dot type, $F(1, 6) = 0.59$, $p = 0.47$, nor for speed, $F(2, 12) = 5.12$, $p = 0.06$. The results of Experiment 5 confirmed that the wriggling motion trajectory illusion likely did not depend on changes in the luminance-defined areas, and that the perceptual difference between the collision and the no-collision conditions were *not* due to differences in size or shape of the moving dots.

Image statistics

The stimulus movies for the collision condition were generated by randomly plotting dots, and moving the dots in random directions. However, the stimulus movies for the no-collision condition had to be assigned to locations and directions that would not result in

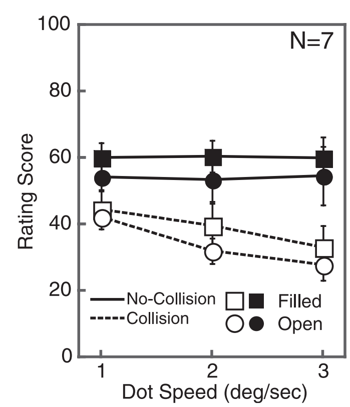


Figure 6. Experiment 5. The average rating score for each condition is plotted separately for the no-collision condition (filled symbols with solid lines) and for the collision condition (open symbols with dotted lines), the filled dots (squares), and open dots (circles). The *x*-axis represents the dot speed. The number of dots was 300 for all conditions.

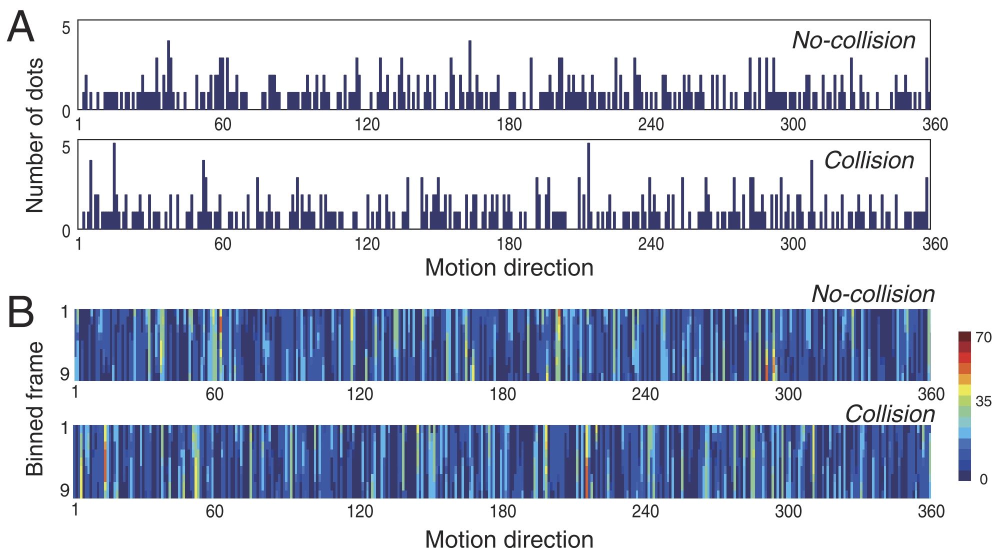


Figure 7. Histograms for direction calculated from the stimulus movies. (A) Histograms of directions from the 45th to the 46th frame for the no-collision condition (top) and for the collision condition (bottom). The *x*-axis indicates directions, 360° for upward, 180° for downward motion. (B) Binned histograms across 10 frames for the no-collision condition (top) and for the collision condition (bottom).

collisions. To find such dots' trajectories, the program randomly searched a position and a direction, computed its trajectory, and if a collision was predicted, then that position and direction was discarded, and the program searched the next location and motion direction. Such computations might have caused unequivalent directions presented in the collision and no-collision conditions, and the differences in the presented directions might have caused the illusion as an artifact.

To visualize equivalence of moving directions between the conditions, we computed the number of dots moving in each direction in the stimulus movies. First, among the stimulus movies used in Experiment 2, we selected ones with 300 dots moving at 3°/sec, and randomly selected a movie from the collision condition and a movie from the no-collision condition. Then, a histogram for the dots moving in each direction was generated for each of the 90 frames that comprised a 3-sec stimulus movie. Figure 7A shows histograms of the directions of the dots between the 45th frame (a frame presented 1.5 sec after the stimulus onset) and the 46th frame for the no-collision condition (upper panel) and for the collision conditions (lower panel). As shown in Figure 7A, the directions of the dots were widely distributed in the range of 1°–360°, and the apparent distributions are similar for the collision and the no-collision conditions.

To visualize temporal changes in directions, we applied further analysis to a movie with the collision condition and a movie with the no-collision condition both of which contained 300 dots moving at 3°/sec. First, we calculated histograms for the directions between each frame. As there were 90 frames presented in a movie, 89 histograms were generated for each condition. Then, the values in the histograms were summed across 10 successive frames creating eight bins and one bin for the last nine frames. Figure 7B visualizes as color maps how the distributions of the directions temporally changed across bins. Because all dots moved in straight lines in the stimulus movies, Figure 7B is mostly characterized by vertical profiles. Note that the vertical profiles fluctuated because the stimulus was presented in a square window, and many dots appeared/disappeared at the edges during the presentation. As shown in Figure 7B, the directions of the dots in the no-collision condition (upper panel) and in the collision condition (lower panel) appeared to be similar in their temporal characteristics. The visualizations of the image statistics suggested that the stimuli in the no-collision and collision conditions did not seem to differ in terms of their spatial and temporal distributions of directions, and the differences in the wriggling scores between these conditions are not to be attributed to such artifacts.

The analyses shown in Figure 7 indicated that there were no apparent differences in distributions of directions presented in the collision and the no-collision movies. However, these analyses do not give statistical evaluations, and do not necessarily mean the motion components were entirely equivalent between the conditions. Even though the spatially and temporally averaged moving directions did not show clear differences, there is still a chance that the dots motion differs in their local characteristics. Thus, in the next analysis, we computed local motion components in the stimulus movies, such as number of adjacent dots and similarities in directions among the adjacent dots, and

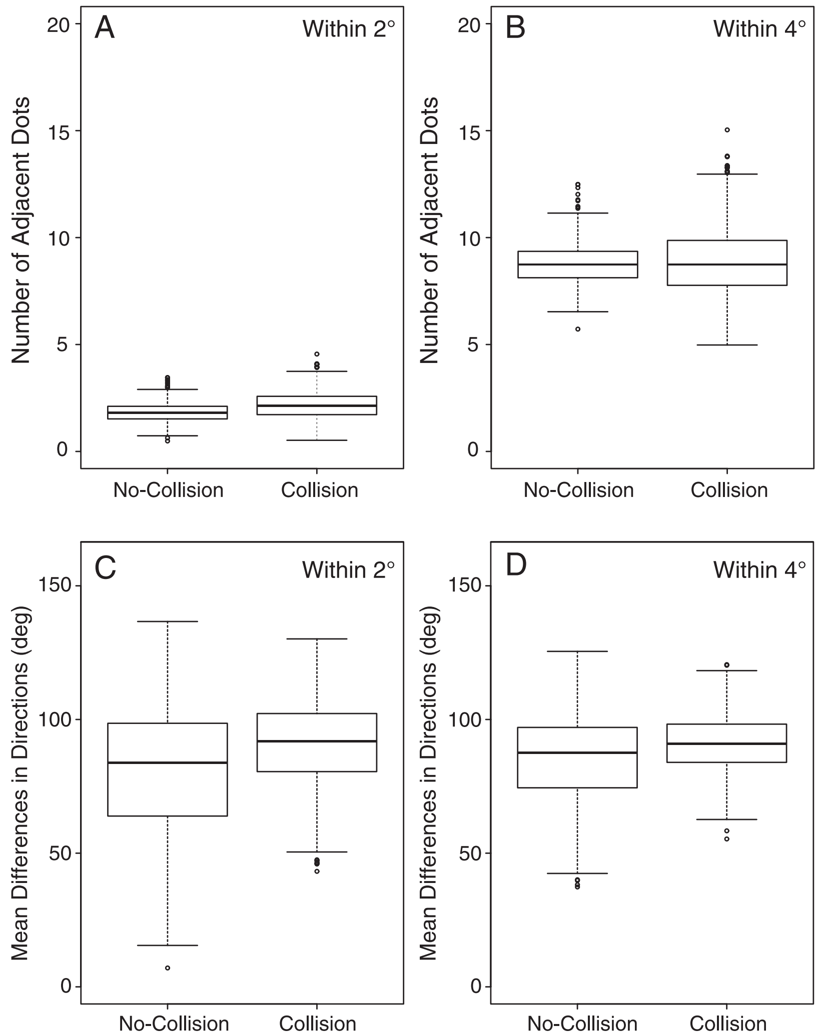


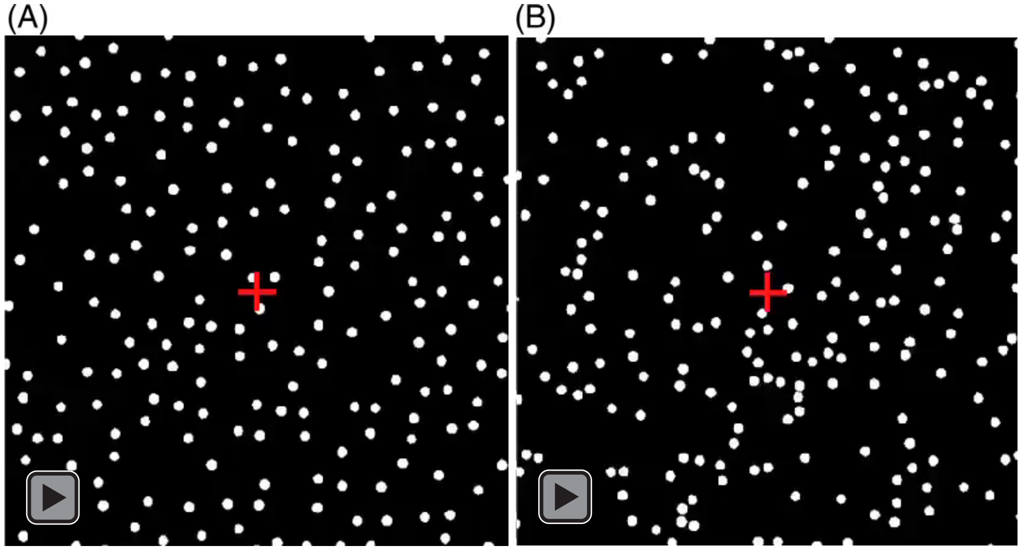
Figure 8. (A) Mean number of dots within 2° in radius of the selected moving dots. (B) Mean number of dots within 4° in radius of the selected moving dots. (C) Mean differences in directions between the selected dots and the adjacent dots within 2° in radius. (D) Mean differences in directions between the selected dots and the adjacent dots within 4° in radius.

compared them between the collision and no-collision conditions.

Among the stimulus movies with 300 dots moving at 3°/sec, we randomly selected 500 dots that did not exit the frame during the 3 sec of presentation (90 frames). Then, the number of adjacent dots within 2° or 4° in radius of the selected dot was counted for each frame and averaged across 90 frames. The mean numbers of adjacent dots across 90 frames were calculated for the selected 500 dots in the collision and in the no-collision conditions and plotted in Figure 8A and B. We also calculated the mean differences in directions between the selected dots and the adjacent dots. The mean directional differences across 90 frames were obtained separately for the 500 selected dots in the collision and no-collision conditions and plotted in Figure 8C and D. Note that the directions ranged from 1°–360°, thus the directional differences ranged from 1°–180°.

The mean number of dots within 2° was 1.8 (SD = 0.46) and 2.2 (SD = 0.63), for the no-collision and collision conditions, respectively (Figure 8A). Further, the mean number of dots within 4° was 8.8 (SD = 0.99) and 8.9 (SD = 1.65), for the no-collision and collision conditions, respectively (Figure 8B). The analysis indicated that, regardless of whether the dots collided, the proximity among dots was kept constant, thus, the number of adjacent dots was not the cause of the illusion.

The analysis revealed that the collision and the no-collision conditions did not differ in their mean directional differences, either. The mean difference in directions between dots within 2° was 79.8° (SD = 23.7°) and 90.3° (SD = 16.4°), for the no-collision and collision conditions, respectively (Figure 8C). The mean difference in directions between dots within 4° was 85.7° (SD = 16.4°) and 91.2° (SD = 11.3°), for the no-collision and collision conditions, respectively (Figure 8D).



Movie 4. Samples of the stimulus movies used in Experiment 6. (A) no-collision-with-distance condition. (B) no-collision condition.

Experiment 6: Effects of dot proximity

The image statistics revealed no global or local differences between the collision and no-collision conditions in terms of the directions or dot proximity. To investigate the effect of dot proximity further, in Experiment 6 we manipulated the distances between moving dots in the no-collision condition and examined the resulting illusory perception.

Subjects

Seven subjects with normal or corrected-to-normal vision participated in this experiment. Four subjects had also participated in Experiment 5, and the other two had never participated in a previous experiment. Of the seven, five were male and two were female. The age range was 23–28 years, with a mean age of 24.7 years. All of these subjects were naïve to the purpose of the study. The subjects gave written informed consent for their participation in the experimental protocol, which was approved by the Institutional Review Board at the University of Tokyo.

Stimuli and procedure

The number of moving dots was about 200, and the dots moved at a speed of 1°/sec. The two conditions of no-collision and collision were identical to those in Experiment 2. An additional condition, called the "no-collision-with-distance" condition was introduced in this experiment (Movie 4A). In the no-collision-with-distance condition, the dot motion was constructed under the same rule as in the previously used no-collision condition (Movie 4B) except with an additional constraint under which dots must maintain at least 0.4° of separation at all times. As a result, while the number, density, and speed of dots were the same across all three conditions, the moving dots in the no-collision-with-distance condition were distributed more uniformly maintaining the distance from each other. It should be noted that we used the speed of 1°/sec because the new constraint necessitated a shorter moving distance.

The subjects were asked to rate their perception of the dots' motion by clicking on the panel. They were instructed to use the full length of the response panel and were also told that the location of the mouse click corresponded to the rating score. The subjects first practiced the task in a session comprising 18 trials, in which the three conditions were each repeated six times. In this practice session, they were instructed to create an internal criterion regarding which kind of perception they were to consider straight and which to consider wriggling. After the practice session, the subjects moved on to the main experiment. In the main experiment, the three experimental conditions were each presented 24 times, in random order. Subjects were allowed to take a break after every nine trials. The subjects were asked to fixate on a central red cross while observing the moving dots.

Results and discussion

First, we evaluated the dot proximity for each condition, by averaging the interdot distances in the stimulus movies. In the analysis, one stimulus movie

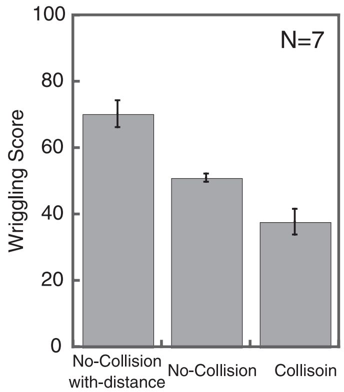


Figure 9. The average rating score for each condition in Experiment 6. Error bars represent ±standard error of the mean.

was chosen for each condition, and 50 dots were randomly selected in each frame of the movie. The distances from the selected dots to the nearest dots were calculated. The calculation was conducted for all 90 frames, and the resulting 450 interdot distances were averaged for each condition. The averaged interdot distance was 0.61°($SD = 0.18$), 0.39° ($SD = 0.32$), and 0.32° ($SD = 0.37$)for the no-collision-with-distance, the no-collision, and the collision conditions respectively. The analysis confirmed that the dots in no-collision-with-distance condition tended to stay further apart, and distributed more uniformly compared to other conditions.

The subjects' rating scores were converted to a scale ranging from 0 to 100, and the mean rating scores for each condition are plotted separately in Figure 9 for each condition.

The no-collision condition and collision conditions were the same as those in Experiment 2, in which the subjects perceived more wriggling in the no-collision condition. Similarly in this experiment, the no-collision condition produced higher wriggling scores than the collision condition, replicating the results of Experiment 2, $t(6) = 3.25$, $p = 0.03$, Bonferroni corrected. Additionally, in the no-collision-with-distance condition, where moving dots maintained a minimum distance from each other at all times, the dots motion was perceived to be more wriggling than in the no-collision condition, $t(6) = 4.23$, $p = 0.01$, Bonferroni corrected. These results indicated that maintaining a minimum distance between the dots enhances the wriggling motion trajectory illusion.

General discussion

When hundreds of dots move in straight lines in random directions without colliding, their trajectories are perceived as wriggling rather than straight. This wriggling motion illusion illustrates the susceptible nature of trajectory perception and how perception sometimes deviates from the physical nature of the stimuli. The wriggling motion illusion was strongest when there were a large number of dots present in the display. It was also shown that the illusion did not result from artifacts such as the global and local distributions of the motion directions, number of adjacent dots, and the extent and shape of the luminance defined areas. When different dot speeds were compared, the wriggling scores for the no-collision condition were independent of the speed. It was only the ratings in the collision condition that scored lower (or perceived more straight) with faster moving dots. Because the moving dots tend to be perceived as moving straighter at faster speeds in the collision condition, using that as a baseline, the wriggling motion trajectory may be said to be speed-dependent.

As noted in the Introduction, several studies have shown discrepancies between the perceptual and the actual physical trajectory of a moving stimulus; these discrepancies were attributed to smooth pursuit eye movements (Festinger & Easton, 1974; Koga et al., 1996; Koga et al., 1998). In our study, however, we found that the wriggling motion illusion was observed regardless whether the subjects fixated on a point or made a smooth pursuit. Because our stimuli consisted of hundreds of moving dots, and because it is impossible to pursue all of the dots, it is unlikely that the wriggling motion illusion resulted from delays in smooth pursuit eye movements.

Misperceived direction has also been reported with motion transparency. When two sets of random dots move in different directions, the perceived angle between the two directions is misperceived, the so-called motion repulsion effect (Hiris & Blake, 1996; Marshak & Sekuler, 1979). Motion repulsion has been interpreted as evidence for inhibition between two direction-tuned channels in the visual system (Blakemore, Carpenter, & Georgeson, 1970). The moving dots in our stimuli differed critically from those in the motion repulsion studies. In the motion repulsion studies, random dots were assigned to either one of two directions, and therefore caused interactions between the two motion direction channels. In our study, however, the direction of the moving dots was randomly distributed in the range of 1°–360° with no specific direction channels being more active than others. Therefore, the wriggling motion trajectory illusion cannot be explained by motion repulsion.

Another kind of susceptibility to motion direction/trajectory perception has been demonstrated by bi-stable motion stimulus (Metzger, 1934; Michotte, 1954). Sekuler, Sekuler, and Lau (1997) reported that when two identical objects move towards each other, collide, and then move apart, introducing a sound indicating collision promoted the perception of bouncing rather than streaming. Their study showed the extent of the influence of auditory input on motion perception. However, the factors influencing the bouncing/streaming perception are not limited to coinciding auditory information. Tactile stimulations (Shimojo et al., 2001) as well as visually presented distracters (Watanabe & Shimojo, 1998) also reportedly alter the bouncing/streaming perception. In our study, the collision condition allowed multiple dots overlapping in their trajectories; however, as demonstrated in Movie 1A, the multiple moving dots were always perceived as streaming. While the collision condition in our study produced a streaming perception, there is a possibility that bistable perception may have affected the perception in the no-collision condition. Caplovitz, Shapiro, and Stroud (2011) demonstrated that when two objects move toward each other without physically overlapping, those objects appear to bounce off instead of streaming, and such a bouncing percept is so robust that it sometimes overrides the consistency of the object's features. The random dots presented in the no-collision condition in our study were never allowed to overlap; however, the dots that sometimes came very close to each other might have induced an ambiguity in the dots' identities. That is, when the moving dots passed by each other, the identities of the dots might be confused making the perceived trajectory of a dot swap with that of the other dot resulting in a bouncing percept. While the robustness of bouncing percepts affects motion perception under some circumstances, our results suggested that this was not the cause of the wriggling motion trajectory illusion. As shown in Experiment 6, the wriggling motion trajectory illusion appeared more prominent when moving dots maintained distances from each other. Because the dots were farther apart, and it was less likely for the dot's identity to be confused in this condition, the cause of the wriggling perception needs to be explained otherwise.

What causes the wriggling motion trajectory illusion? Is the illusory perception based on the global processing of the moving dots as a whole or on the local processing of the moving dots? Is the illusion caused by bottom-up visual processing of the moving components or by a top-down visual processing such as attention? Although we found no difference in the number of adjacent dots or in the local distribution of directions between the collision and no-collision conditions, we cannot exclude the possibility of interactions between local components being a key to this illusion. Larger distances between moving dots enhanced the illusion; therefore, if the illusory perception is based on local motion interactions, such interactions need to occur across a relatively large area. One possible interaction that might contribute to the wriggling perception is perceptual grouping of the noncolliding dots. If locally adjacent multiple dots are perceptually grouped, the virtual outer boundary of the group changes its shape as the dots move, and when the dots never collide, the virtual boundary might sometimes imply rotation and lead to the wriggling perception. If this is the case, it needs to be assumed that such grouping does not occur with colliding dots, and that the grouping occurs even with uniformly distributed dots as those in Experiment 6. Furthermore, the wriggling motion trajectory illusion was salient regardless the subjects' knowledge of the actual dot trajectories. When the subjects were asked to pursue one of the moving dots in our experiment, they verbally reported that they could not help perceiving other dots wriggling. This indicates that the perception of this illusion is rather an automatic process, which does not require the subjects' effort or knowledge. With our results, the mechanisms underlying the wriggling motion trajectory illusion are not yet concluded. More study will be needed to understand fully the underlying mechanisms of this illusion.

Conclusions

The wriggling motion trajectory illusion is a novel and robust visual motion illusion. When hundreds of dots move in straight lines in random directions without colliding, their trajectories are perceived to be wriggling. The illusion is more pronounced when there are a large number of moving dots; it is independent of eye movement; and it might be explained by some midrange local interactions between the moving dots.

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