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A Novel Speed Illusion Involving Expansion and Rotation Patterns

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Using random dot stimuli well controlled for dot speed, we found that the moving features in expanding patterns appear to move faster than those in rotating patterns. The illusion is well correlated with the strength of the global motion signal. For example, in displays where the number of motion directions defining the patterns is reduced, the magnitude of the illusion decreases. Similarly, the strength of the effect diminishes as dot density is reduced. In patterns where only wedge-shaped segments of the stimuli are left exposed, the difference in perceived speed increases with the angular size of the wedge. Stimulus placement relative to the fixation point has little effect on the persistence of this phenomenon — expansion patterns appear to contain elements of greater speed, independent of stimulus eccentricity. These results argue against a local explanation for this perceptual illusion, suggesting that the global motion pattern of the stimulus, *per se*, is responsible. Copyright © 1996 Elsevier Science Ltd.

Motion perception Human Speed Optical illusions Psychophysics

INTRODUCTION

Visual motion perception has been studied extensively in primates (for a review see Nakayama, 1985). Much of this work has revolved around the detection, discrimination and representation of linear motion. Primate cortical area MT has been implicated in the perception of linear motion, based on neuron selectivity for homogeneous fields of translational motion (Maunsell & van Essen, 1983a, b; Albright, 1984).

More complex motion patterns, such as expansion, contraction and rotation, are thought also to be important in visual information processing. The medial superior temporal region (MSTd), a region of primate cortex with units specific for these motion patterns, has been identified (Graziano *et al.*, 1994; Sakata *et al.*, 1985, 1986; Saito *et al.*, 1986; Tanaka *et al.*, 1986, 1989; Tanaka & Saito, 1989). Such pattern selectivity may be important for the tasks of ego-motion representation and the analysis of object motion in the environment. However, the relationship between area MSTd and the perception of these patterns has yet to be established.

Whether the different types of complex motion are analyzed in separate neural processing channels has been subject to much debate. Unlike translational motion, these patterns do not "pop out" in displays containing distractors (Braddick & Holliday, 1991; Werkhoven & Koenderink, 1991), arguing against the parallel processing of these stimuli. Experiments looking at speed discrimination thresholds for complex motion have shown that the thresholds for looming, rotation and linear motion are all similar (Sekuler, 1992), further arguing against separate processing channels for these different motion types. Consistent with the theory that these patterns have a distributed representation at the level of local detectors, thresholds for complex motion patterns can be predicted based on the simple pooling of local, linear motion signals. Finally, superimposing a translational velocity field over an expansion pattern shifts the perceived focus of expansion in the direction of translation, arguing for a lack of separation between channels processing these motion types (Duffy & Wurtz, 1993).

On the other hand, data from adaptation experiments (Regan, 1986) suggests the presence of independent channels tuned to linear motion, expansion and rotation. Regan developed stimuli which selectively increased perception thresholds for one pattern type without affecting the others. Consistent with a "low-level" processing of complex motion pattern, studies in infants (Spitz *et al.*, 1993) have demonstrated that the capacity to integrate information contained within non-uniform velocity fields into coherent motion patterns develops as early as 7 months of age. Masking studies (Freeman & Harris, 1992) indicate that the detection of expansion in a

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stimulus is unaffected by the presence of rotation, suggesting independent channels for expansion and rotation.

In this study, we take a different approach to this problem and compare perceived dot speeds in expanding and rotating patterns. If there is a significant difference in perceived speed, this provides evidence for at least partial independence of the channels processing these motion types.

GENERAL METHODS

The following conditions were adhered to unless otherwise specified for a particular experiment. Stimuli were generated and data collected on a Macintosh computer with a 13 inch color Trinitron monitor. Subjects viewed the stimuli 24 inches (61 cm) away from the display in a moderately lit room. In many cases, the stimulus was a circle of diameter 200 pixels (7.63 deg of visual angle). The random dots for each stimulus were plotted into a virtual square with dimensions 200 × 200 pixels and a circular mask was used to limit those dots visible.

Each dot was a square pixel that extended over a visual angle of 0.038 deg. Each "on" pixel was a small black square against a white background. This arrangement eliminated persistence artifacts associated with bright moving features over a dark background. The fixation point was a filled circle of diameter 5 pixels (0.2 deg at the 24 inch viewing distance).

The refresh rate of the video card was 60.0 Hz, and each refresh cycle generated a software interrupt signal that caused the animated sequence of the stimulus, or "movie", to advance one frame. Accordingly, a 1 sec movie consisted of 60 consecutive image frames. To conserve memory, if the stimulus lasted longer than 1 sec, it was started over from the first frame. The life-time of the dots was limited to 12 frames (0.2 sec). Once a dot had persisted for this period of time, it was randomly assigned a new starting position with its trajectory and speed consistent with the global motion pattern of the stimulus (see below). For the first frame of a movie, a random age was assigned to each dot, ranging from zero to one frame short of being extinguished. This caused dots to "die" asynchronously and prevented a global blinking of the pattern. If a dot left the virtual square defining the stimulus boundary, it was given a new random location within the stimulus, whether or not it had completed its entire life cycle. This prevented any fluctuation in dot density across the pattern from frame to frame.

Except for Experiment 6, where dot density was specifically manipulated, 100 dots in the 200 × 200 virtual stimulus square were "on" at a time (one out of 400 pixels). Because various masks were used, not all of these pixels were visible. For example, when a 200 pixel diameter circular window was applied, 78.5% (31,416 out of a possible 40,000 pixels) were visible to the observer. Under this condition, an average of ~78 dots were visible each frame.

In most of the stimuli, the speed of each dot was proportional to the distance of its starting point from the center of the pattern. The motion of individual dots had no acceleration to their motion, i.e. velocity was constant. This restriction is inconsistent with the movement of features on real objects expanding and rotating. This constraint was necessary to allow matching of velocity vectors between stimuli with different motion patterns. For example, to convert a random dot display with local motion vectors organized into a global expansion (i.e. all velocity vectors pointed away from the center of the stimulus) into global rotation, all that needs to be done is to rotate each of these local vectors by 90 deg (Graziano *et al.*, 1994).

If the paths of the individual dots in the rotation patterns were updated every frame according to a true rotation, their paths would be curved, and consequently their net displacement would be less than dots of the same speed in expansion patterns, where trajectories are straight. Although curvature was eliminated from the local motion of the individual dots to avoid this problem, global rotation is perceived because the visual system spatially integrates the signals. Because distortions would occur if the dots were allowed to travel too far before disappearing, life-times and speeds were kept well below the point where this effect became noticeable.

A two alternative forced choice (2-AFC) paradigm was used in all experiments. Subjects initiated each trial by pressing the space bar on a computer keyboard. They were told not to press this key until they were looking at the fixation point. Although subjects were instructed to look straight ahead at a fixation point for the duration of the trial, head and eye position were not monitored, as the perception seemed largely independent of how well the observer fixated. Although we insisted that the participants maintain a fixed viewing distance (24 inches), in pilot studies this variable had little effect on the data.

Following trial initiation, the first stimulus appeared at the center of the display, marked by the fixation point. The first movie was followed by a 1 sec gap, during which time only the fixation point remained on the screen. This gap was followed by the second stimulus, which was presented in the same manner as the first. After the presentation of the second stimulus, both fixation point and movie were extinguished. At this point, the subject had to decide which stimulus had dots moving at the greater average speed. Participants were urged to ignore all aspects of the stimulus except the average speed of the random dots, and they were discouraged from formulating their judgments based on the movement of individual dots. The subjects pressed "1" or "2" on the keyboard, depending on whether the first or second stimulus had dots with greater perceived speed.

For each trial, a "standard" expansion stimulus appeared as one of the two movies compared. The other movie in a trial was chosen from a set of "test" rotation patterns with dot speeds equal to 70, 80, 90, 100, 110, 120 and 130% of those present in the standard movie. The order of the standard and test movies was randomized, as

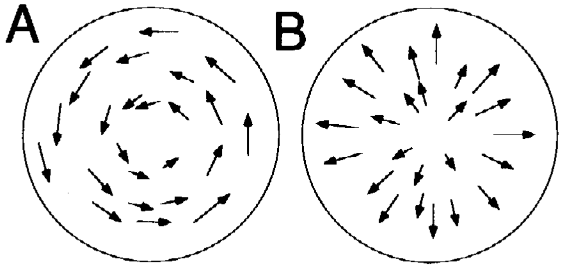

FIGURE 1. Stimuli used in Experiment 1. (A) shows an example of counter-clockwise rotation while (B) is an example of expansion. Each arrow is a motion vector that represents the direction and magnitude of individual dots making up these patterns. Note that the length of these vectors increases moving outward from the center of the stimuli. As explained in the text, transforming one pattern into the other simply involves rotating each local motion vector by 90 deg in the appropriate direction.

was the particular test pattern shown. The frequency at which subjects reported the rotation faster than the expansion pattern was plotted as a function of the actual rotation to expansion speed ratio. From these plots, perceptual equivalence points were recovered by fitting the data to a logit function and obtaining the 50% judgment point. For a subset of the experiments, the logit curves were refitted using the log of the speed ratio as the dependent variable, which would be the appropriate function if the data obeyed Weber's law. Because this change in axis had no effect on the perceptual equivalence points recovered, we report the data with a linear scale.

Because of the 2-AFC design of the experiment, exact 95% confidence intervals for the data points could not be established. It is not possible to produce a binomial confidence interval that will satisfy the strict definition of a confidence interval, namely one that will have the specified probability P of containing the unknown but fixed parameter p. This problem arises because the observed probabilities for each data point can only take on discrete values. Although probability estimates for binomial data do not follow a normal distribution, they approach this form for large N, and by using a "continuity correction", confidence intervals were estimated by the standard methods (Snedecor & Cochran, 1989).

The broken curves bracketing the solid regression lines in Figs 3, 5, 7 and 8 represent the 95% confidence bands for the data. They were obtained by fitting a logit function to the upper and lower bounds of the 95% confidence intervals. The dotted drop-lines extending downward from these curves bracket the equivalence point obtained from the data. This technique will be used to get an estimate of the uncertainty associated with measuring each equivalence point. An effect will be considered "significant" if this interval does not include the "no effect" condition.

Subjects were encouraged to take breaks from the task if they felt themselves becoming fatigued. Generally, a

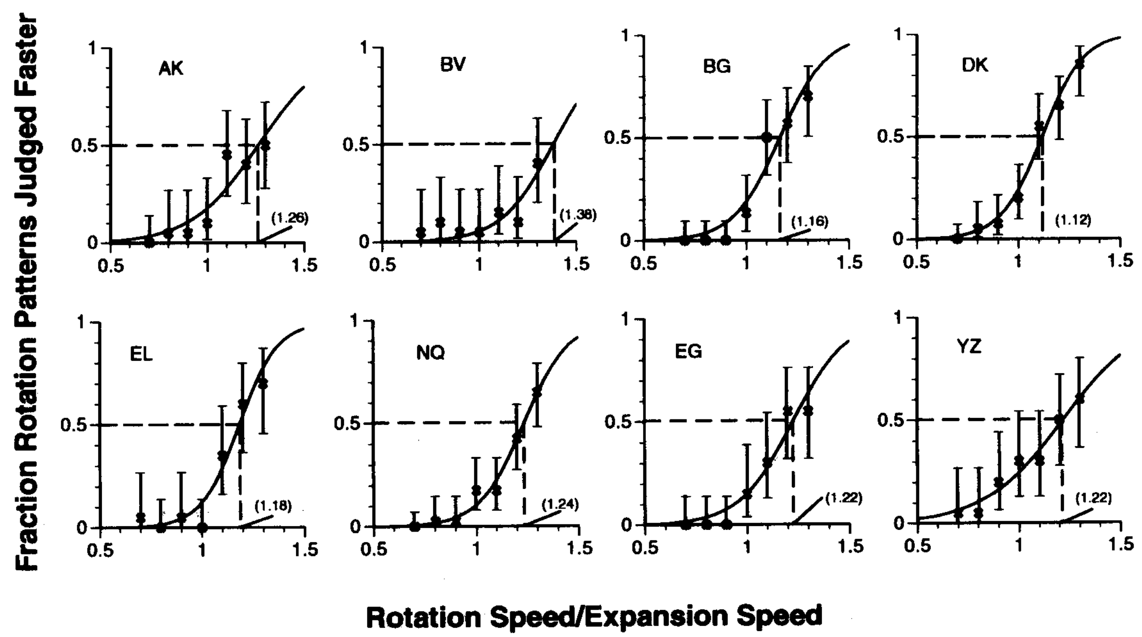

FIGURE 2. Individual subjects' data from Experiment 1. The x-axis represents the actual speed ratios of a set of test rotation patterns to a fixed standard expansion pattern. The y-axis represents the fraction of trials in which a test rotation pattern is judged moving faster than the standard expansion pattern. If the two types of motion pattern being compared appear to move equally fast when their actual speeds are the same, the point of inflection of the logit function would be at a speed ratio of unity. The abscissal location of this point for real data shifts to the left or right, depending on the subjective judgment of relative speed. The ordinal location of the inflection point is constrained by the general form of the logit function to be always at 0.5. The slope of the curve is inversely correlated with a particular subject's ability to consistently judge differences in speed. Each plot shows the psychophysical performance curve for a different observer. In each case, the point of perceptual equivalency is shifted to the right, indicating that each subject tended to judge dots in expansion patterns as moving more quickly. Error bars represent 95% confidence intervals.

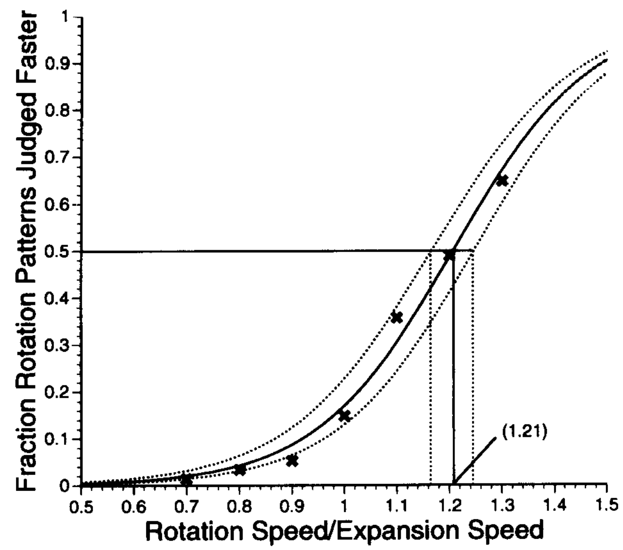

FIGURE 3. Performance curve obtained from pooling data from Experiment 1 across subjects. Broken curves are 95% confidence bands, as described in the text.

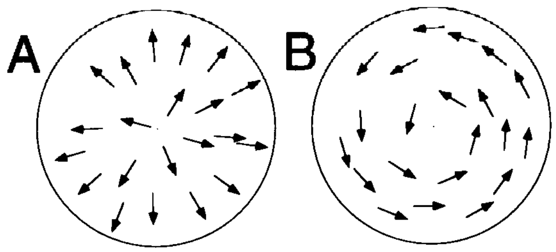

FIGURE 4. Stimuli compared in Experiment 2. These patterns are identical to those used in the previous paradigm, except that the radial speed gradient has been removed and speeds of all dots in a particular stimulus are identical.

few training trials were allowed prior to data collection. At no time was any feedback given to the subject about performance. For Experiments 2–6, two to three naive observers and the two authors served as subjects. For the first experiment, three additional naive subjects participated. None of the subjects reported experiencing vection while looking at the displays and generally found the task simple, although boring.

Experiment 1

Rationale/methods. Two basic stimulus patterns were used to demonstrate the basic finding of this investigation. The stimuli used are shown in Fig. 1. The speed for a particular dot in the standard stimulus was established according to the formula: speed = $k \times$ (distance from the origin in pixels). In all cases, k was fixed at 0.02/frame, which meant that the speed of a dot at the very edge of the stimulus window was 2 pixels/frame or 4.6 deg/sec. In the unlikely event that a dot happened to appear in exactly the center of the display, its velocity would be zero. This velocity field was chosen because it effectively simulates an approaching flat surface. However, because the velocity field and size of the stimulus did not change over time, the simulated distance of this object remained unchanged, i.e. the stimulus did not evolve. As discussed above in General Methods, by rotating each velocity vector defining the expansion by 90 deg to the left, a counter-clockwise rotating pattern was achieved. These rotation patterns had an angular speed of 68.7 deg/sec. Rotation stimuli of various average speeds, both slower and faster, also were created to complete the set of "test" patterns, as discussed above. It should be pointed out that when we refer to a distribution of velocity vectors as being "identical" we mean statistically identical and not literally so. Because every dot for each pattern is randomly assigned a location, we do not literally rotate the exact same set of vectors in transforming one stimulus pattern into another. However, because the number of these random events is large in constructing these stimuli, we were not concerned that stochastic fluctuations in average speed could have any effect on the results.

Results. Figure 2 shows the experimental results. The fraction of times the rotation stimulus was judged "faster" is plotted against the ratio of rotation speed to expansion speed. By following the horizontal line at the 50% judgment point over to the performance curve and then down to the abscissa, the point of perceptual equivalence can be recovered. For the "no effect" case, this is of course a speed ratio of 1. Each frame represents data collected from a single subject. In each graph, the perceptual equivalence point (shown in the lower right-hand corner of each frame) was greater than 1.0, indicating that all eight subjects perceived the dots in the expansion pattern moving faster than those in the rotation pattern. The bars drawn for each data point represent 95% confidence intervals. Figure 3 shows the data from the eight subjects used in Fig. 2 pooled into a single curve. From this last plot, it is seen that the equivalence point for the set of subjects as a whole was a speed ratio of 1.21. In other words, the dot speed for the rotation pattern needed to be increased 21% before the perceived speed was the same as for the expansion pattern. For reasons addressed in the Discussion, the magnitude of the illusion was potentially underestimated by our experimental design.

The experiment was repeated using a rotation pattern as the standard stimulus and expansion patterns as the comparison stimuli. The direction and magnitude of the illusion were unchanged (data not shown).

Experiment 2

Rationale/methods. We decided to explore systematically which aspects of the stimuli were responsible for the speed illusion documented in the first experiment. There were at least two components to the global organization of the velocity vectors defining the previous patterns, i.e. the original stimuli had both a direction and speed gradient. In the previous movies, the speed of each dot was a linear function of its distance from the center of the display. In this second experiment, we eliminated this

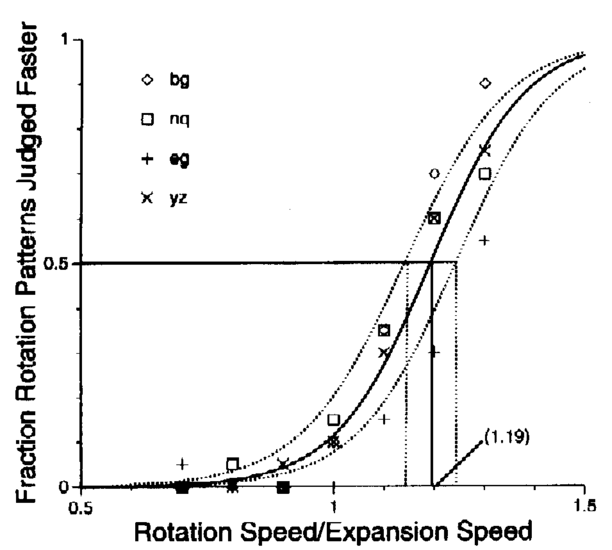

FIGURE 5. Data collected using stimuli lacking a speed gradient. The rightward shift of the equivalence point is comparable to that obtained with patterns containing a speed gradient. Data from each of the four observers is plotted. These data were pooled for the purpose of obtaining the solid regression line. Broken flanking curves represent 95% confidence bands, as described in the text.

aspect of the stimuli, giving all dots the same speed, regardless of location. Two representative velocity fields from these patterns are shown in Fig. 4. The speed of each dot was the same as a dot located 71 pixels away from the center of the display in the standard pattern from Experiment 1. In this way, the average speed of the dots in the two experiments was approximately the same, although this was a relatively unimportant detail since these different types of patterns were not directly compared. We call these new stimuli "direction fields" to distinguish them from the "velocity fields" explored previously.

Results. Figure 5 shows the data organized into the same plot format as the previous experiment. For brevity, although discrete data points from all four subjects are plotted, the curve from this figure was obtained by pooling data across all subjects. The speed ratio equivalence points for individual subjects were bg = 1.14, nq = 1.18, eg = 1.28, yz = 1.18. As seen from the plot of the pooled data, the overall equivalence point was a speed ratio of 1.19 and this effect was significant. Although the illusion was slightly less for the direction field compared to the velocity field in Experiment 1 (1.19 compared with 1.21, with overlapping confidence intervals), in each case the curves deviated significantly from veridical expectations. We concluded that the speed gradient contributed relatively little to the illusion.

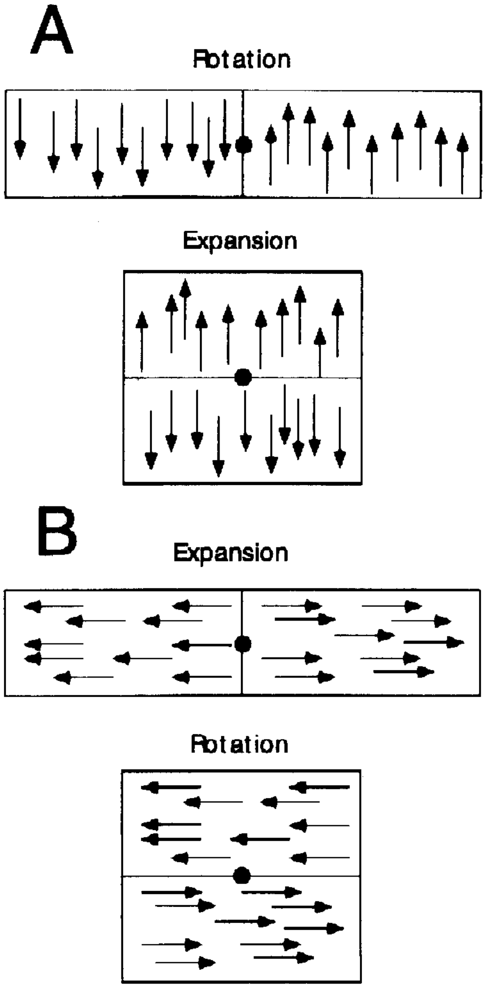

FIGURE 6. Stimuli used in Experiment 3. The patterns shown in (A) and (B) represent examples of axial rotation and expansion, with only two directions of motion defining these global motion patterns. For a particular stimulus, the speed of all the dots was identical. The solid dot in the center of each pattern represents the fixation point.

Experiment 3

Rationale/methods. In the previous experiment, the speed range of the individual dots was restricted. Next, the analogous experiment was performed with respect to the range of motion directions present. The "axial" patterns used are illustrated in Fig. 6. Within a stimulus, all dot speeds are equal and only two directions of motion are represented in each pattern. As in the other experiments, the expansion stimulus was used as the standard in the 2-AFC task. To transform the expansion pattern into a rotation pattern with identical velocity distributions, the expansion stimulus was effectively bisected orthogonal to its long axis. The left half of the stimulus was then placed on top of the right half, creating the axial rotation.

Because of the way these patterns were constructed, the expansion stimulus was 100 pixels wide and 100 pixels high while the rotation pattern was 200 pixels wide and 50 pixels high. Because the shape of the two pattern types was not identical and their motion borders differed in length, an unwanted variable was introduced that could potentially affect the perception. To control for this, we created axial expansion and rotation patterns like those in Fig. 6(B). In these stimuli, the expansion patterns were

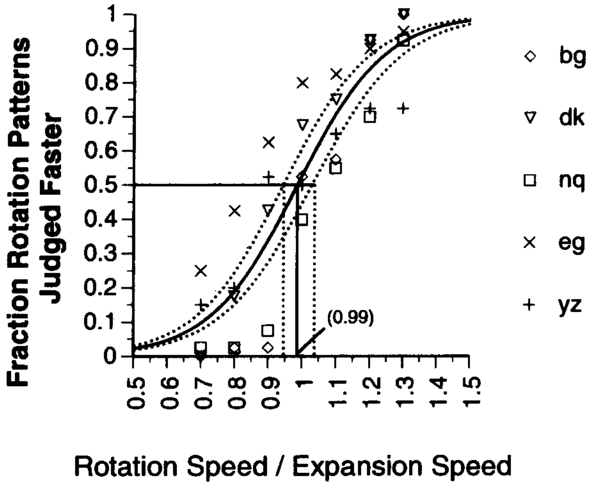

FIGURE 7. Comparison of axial expansion and rotation. The difference in perceived speed between expansion and rotation disappears when axial patterns are compared.

oriented horizontally and the rotation patterns were square. By pooling the data from these two stimulus sets, the confounding effect of stimulus dimension was eliminated (this assumes there is no interaction between the two possible effects).

Results. Unlike the first two experiments, no consistent effect of motion pattern on perceived average speed was evident. When stimuli like those of Fig. 6(A) were compared, the individual subjective equivalence points were bg = 1.09, dk = 1.01, nq = 1.12, eg = 0.84, yz = 1.12. The equivalence point obtained from pooling these data was 1.03, a much smaller effect than that reported above for the isotropic patterns. Furthermore, the range of equivalence points bracketed by the 95% confidence bands includes the "no effect" case. When stimuli like those of Fig. 6(B) were compared, the individual subjective equivalence points were bg = 0.98, dk = 0.89, nq = 1.04, eg = 0.84, yz = 0.89. The pooled equivalence point in this condition was 0.94 and again the effect was not significant. Figure 7 plots the result of pooling these two sets of data. The individual subjective equivalence points in this final case were bg = 1.04, dk = 0.95, nq = 1.08, eg = 0.84, yz = 1.00. The equivalence point obtained by averaging over all five subjects was 0.99, indicating that the speed illusion previously obtained for isotropic patterns was not present for axial patterns. We conclude that the presence of a wide range of directions in the original patterns used in Experiment 1 is required for the speed illusion. Note that this experiment also suggests that the centrifugal organization (away from the fixation point) of the motion vectors, *per se*, is not responsible for the phenomenon. Despite possessing more centrifugally oriented local motion signals in the axial expansion displays compared to rotation, the perceived dot speed was the same. We examine this issue further in the next experiment.

Experiment 4

Rationale/methods. Two competing hypotheses could explain the data obtained from the first two experiments. One possibility is that the illusion depends only on the global organization of the stimuli's component motion vectors. Alternatively, since in the previous paradigms the subject foveated the center of the stimuli, the illusion could also depend on the location of the motion pattern on the retina.

To distinguish between these two alternatives, we altered the experimental paradigm and presented the

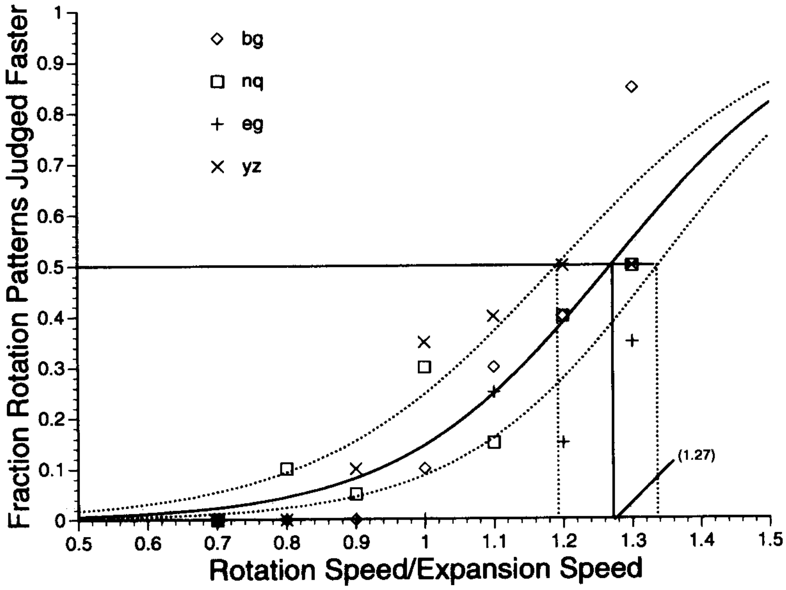

FIGURE 8. Effect of moving stimulus patterns away from the fovea. The rightward shift of the inflection point is again consistent with expansion appearing faster. The effect was slightly larger than when the patterns were viewed foveally.

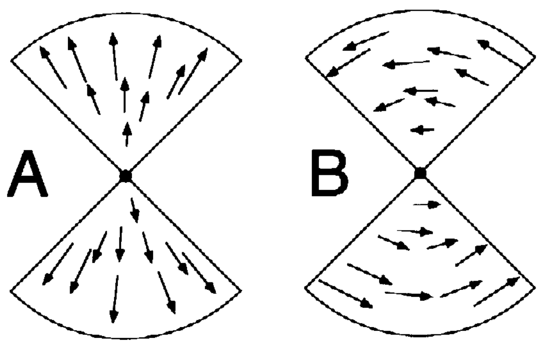

FIGURE 9. Stimuli used in Experiment 5. These patterns were created identically to those shown in Fig. 1 except that a double wedge-shaped mask was applied.

stimuli side by side, with an intervening gap of 48 pixels (1.83 deg). The fixation point was in the center of this gap. By placing the stimuli in the periphery, on average the two types of patterns had the same number of centrifugally oriented component motion vectors. Because this task was much more difficult, because of the eccentrically placed stimuli, the movies were shown for a full 3 sec. Subjects pressed "1" or "2" depending on whether the movie to the left or right of fixation, respectively, appeared to have faster moving dots.

Results

Figure 8 shows the results for this experiment, using data pooled over four subjects. The individual subjective equivalence points were bg = 1.20, nq = 1.30, eg = 1.39, yz = 1.23. The overall effect was somewhat larger than that observed in the first two studies, with the equivalence point from the pooled data established at 1.27, significantly above the "no effect" condition. This result suggests that it is the global motion pattern of the stimuli that is responsible for the illusion, since the effect did not rely on a particular arrangement of local motion signals on the retina.

Experiment 5

Rationale/methods. Based on the results of comparing axial patterns in Experiment 3, we predicted that the greater the range of local motion directions which defined the motion patterns, the stronger the speed illusion would be. To test this hypothesis, we constructed double "wedge" patterns as shown in Fig. 9. We used the same rules established for the stimuli in Experiment 1 for the movement of the random dots, but used two wedge-shaped masks instead of a circular one. This was repeated for wedges of angles 30, 60, 90, 120, 150 and 180 deg. A wedge pair of 180 deg is equivalent to two semi-circles and therefore was identical to the circular patterns of Experiment 1. For this data point, we used the previously collected data rather than repeat the identical study. Only wedges of the same size were compared with one another.

Results. Figure 10(A) shows the pooled data from five subjects. The six curves represent data collected using each of the six wedge sizes. Rather than show the entire curve, a small portion of the x-axis has been expanded to show the shift in the equivalence point more clearly. Figure 10(B) shows these data organized into a different format. In this plot, subjective equivalence ratio is plotted as a function of stimulus wedge size. A clear trend is evident in both these graphs: the larger the area of the stimulus exposed, the more a subject's judgment of speed magnitude favored the expansion pattern. Two-way ANOVA showed a significant effect of wedge size on the equivalence point ($P < 0.05$).

For small wedge sizes, a reversal of the illusion was seen for some subjects — the rotation patterns were judged more frequently as possessing greater average speeds. We attribute this as arising from the phenomenon of "temporal capture" (Treue *et al.*, 1993). Dots in

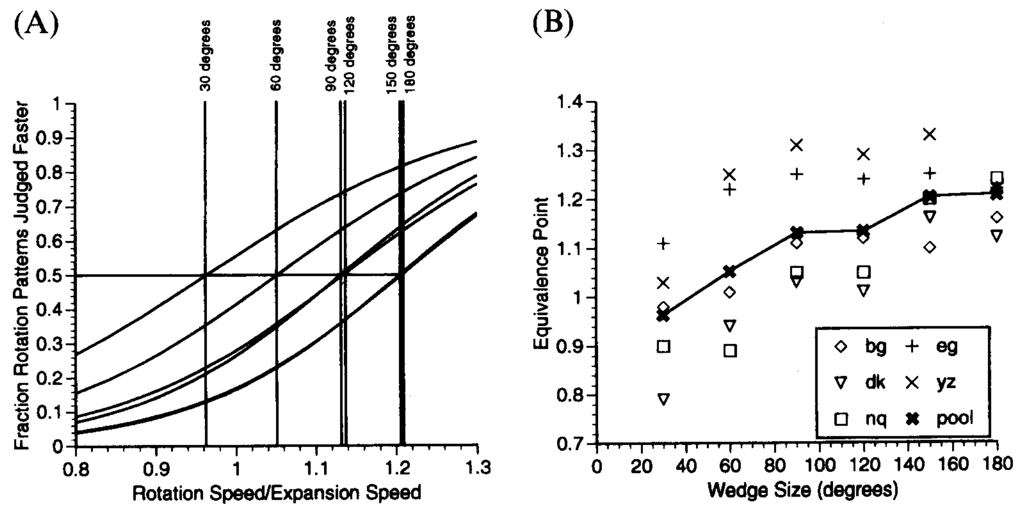

FIGURE 10. Effect of using patterns of different wedge size. Each curve in (A) was obtained by pooling data across the five subjects tested. The six curves correspond to the six wedge sizes used. The 180 deg double wedge was identical to the stimuli used in Experiment 1 (a full circle). (B) plots the subjective equivalence points for each subject as a function of wedge size. The solid line connects data points of the pooled data.

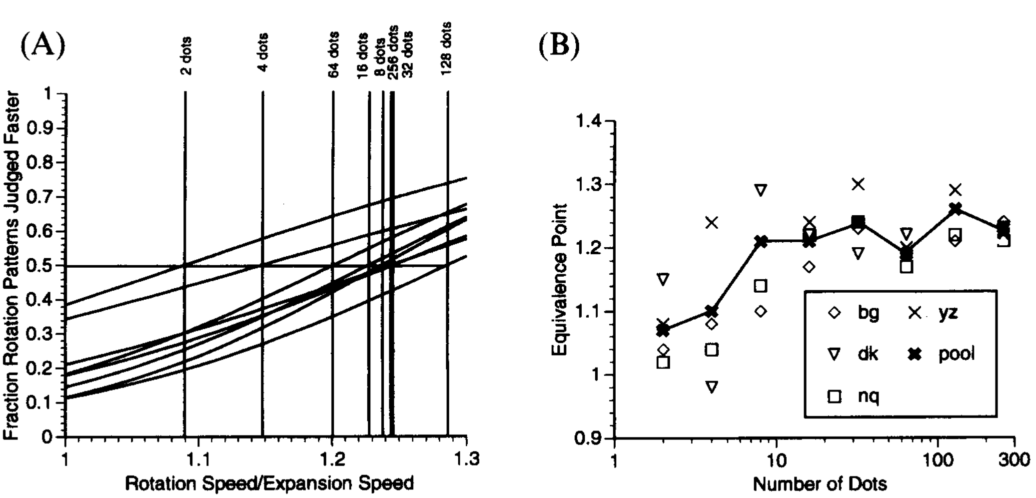

FIGURE 11. Effect of dot density on the location of the subjective equivalence point. Each curve in (A) was obtained by pooling data across the four subjects tested. The four curves correspond to the different dot life-times. (B) plots the subjective equivalence points for each subject as a function of dot number. The solid line connecting points of the pooled data set shows a generally upward slope. Beyond the four-dot case, this increase largely plateaus.

narrow wedge rotation patterns will have, on average, shorter life-times than those in expansion patterns because it is more likely that the dots will rotate off the two long sides of the wedge. This effect is reduced as wedge width increases, and the effect of motion pattern on perceived speed quickly dominates. Although the trend in the data reflects two competing effects, the results are consistent with an increasing effect of global motion pattern with an increase in the range of motion vectors that define these patterns.

Experiment 6

Rationale/methods. In order to test further the hypothesis that the magnitude of the illusion was related to the strength of the global motion signal, we systematically ran a series of experiments with different dot densities. 2, 4, 8, 16, 32, 64, 128 and 256 dots were used with patterns that were otherwise identical to those of Experiment 1. At low dot densities, problems associated with stochastic fluctuations in average speed potentially became an issue. To avoid this problem, the random number seed for the program generating the stimulus patterns was saved and reused before each movie was created. As a consequence, the initial spatial location of the random dots was identical for the patterns being compared.

Based on results from Experiment 5 which suggested a positive relationship between the range of local motion directions present in the patterns and the magnitude of the illusion, we predicted the difference in perceived speed would increase with the number of dots in the display. Because the dots were repositioned every 12 frames, the number of motion directions represented in the stimulus patterns over the duration of the movie was greater than the number of dots present at any one time on the screen. For example, in the two-dot condition approximately $2 \times (60\text{ frames})/(12\text{ frames})$, or 10 different motion directions were sampled over the course of a 1 sec movie.

Results. Figure 11 shows that the results were consistent with expectations. The magnitude of the illusion is considerably less for the two- and four-dot conditions than for the remaining cases. Figure 11(A) shows a series of eight curves, one for each dot density, for data pooled over four subjects. Figure 11(B) shows a clear positive correlation between dot density and the rightward shift in the perceptual equivalence point. Two-way ANOVA was performed, and a significant effect of dot density on the subjective equivalence point was established ($P < 0.05$). The results are consistent with the rest of the data collected in this study: the illusion is directly correlated with the strength of the global motion pattern present in the stimulus.

DISCUSSION

This study has documented a novel illusion involving the perceived speed of random dots in rotation and expansion motion patterns. When a given set of motion vectors is organized into an expanding global motion pattern, the average perceived speed of these features is greater than with a rotation pattern of the same vector composition. This finding supports the possibility that expansion and rotation motion are processed in separate perceptual channels.

The finding of Experiment 4, that the illusion was not dependent on a specific retinal stimulus location, supports the hypothesis that the phenomenon cannot be explained in terms of a local motion system and provides evidence for independent processing of expansion and rotation motion. This illusion may make sense from an evolutionary point of view: approaching objects are more relevant behaviorally than rotating ones and, by containing features which appear to move faster, are more likely to grab the observer's attention.

Magnitude of the speed illusion and experiment design

The 2-AFC paradigm used in this study potentially could have led to an underestimation of the illusion's magnitude. Because subjects more frequently chose the expanding pattern, they may have consciously or subconsciously tried to balance their responses by favoring rotation when the perception was ambiguous. Although they were instructed against such biases, it many have been difficult to avoid this tendency. Another experimental design, such as a staircase paradigm, would have avoided this potential problem. However, side by side comparison of expansion and rotation patterns, at the perceptual equivalence points recovered from our data, appear to move at the same speed, indicating that the 2-AFC design, although not ideal, gave reasonable results.

Another potential source of underestimation is related to the way the stimulus patterns were constructed. As discussed in the Methods section, individual dots moved with a constant velocity throughout their life-times. This was done to avoid problems such as path curvature which would prevent a balanced comparison of the two types of motion. If the motion of each dot was updated every frame (rather than just at the beginning of its trajectory), it would be impossible to rule out local motion differences, e.g. curved vs straight dot paths, contributing to the illusion. Unfortunately, because individual dots in the expanding patterns did not increase in speed as they moved outward, on average expanding dots moved slightly slower than rotating dots at the same distance from the pattern's center. When we compared expanding patterns with and without acceleration, the patterns with acceleration appeared slightly faster (data not shown). Fortunately, it is relatively easy to adjust for this discrepancy *post-hoc*. We calculated that the dots in the expanding patterns were all moving 13.0% too slowly and, therefore, the equivalence points in experiments 1, 4, 5 and 6 should be shifted further rightward by this amount. Taking this into account, the actual magnitude of the speed illusion reported in Experiment 1 is approximately 30%. This is not an issue for the patterns used in Experiments 2 and 3, where a speed gradient is absent.

Fortunately, both of these problems will produce an underestimation in the magnitude of the illusion and do not qualitatively jeopardize any of the findings. However, in order to experimentally recover a more accurate estimation of the illusion's magnitude, Experiment 1 was slightly modified and repeated, using the two authors as subjects. The trajectories of the dots in the expansion patterns were updated every frame, allowing individual dots to speed up as they moved outward. The rotation patterns were constructed as they were before, with a dot's trajectory updated only on the first frame of its 12-frame life-time. As discussed in the Methods section, updating the trajectories of rotating dots every frame would introduce local dot path curvature and reduce each dot's net displacement, inappropriately reducing the perceived dot speed. Although comparing "acceleration" expansion with "no-acceleration" rotation has the disadvantage of introducing a qualitative difference in the local motion of the dots, statistically the average speed of the dots in the patterns in now better matched. The expected increased shift in the subjective equivalence points would further confound the underestimation problem associated with the 2-AFC paradigm. To nullify this bias and anticipating the ~30% shift calculated above, we sampled evenly around a speed ratio of 1.3 rather than 1.0. As expected, expansion was judged faster than rotation approximately 50% of the time. The subjective equivalence point for BG was 1.27 (compared to 1.16 without expansion acceleration) and for NQ 1.35 (compared to 1.24 without expansion acceleration), in line with the 13% adjustment of the original data predicted on mathematical grounds.

We should emphasize that it is not clear whether the expansion pattern with or without acceleration is more appropriate for comparison with the rotation stimuli. As discussed above, both types of comparison have drawbacks. Fortunately, in both cases the illusion is in the same direction, and it is simple to adjust the subjective equivalence points by the addition of a constant.

Finally, it should be mentioned that because expanding dots born near the edges of the stimulus window can disappear off the edge of the display before living out their full life-times, expanding dots have slightly shorter life-times than rotating dots. It is well known that for dots of identical speed, the shorter the dot life-time, the greater the average perceived speed (Treue *et al.*, 1993). If this phenomenon were accounting for the illusion reported in this paper, we would expect that increasing the life-time of the dots in the stimulus patterns should increase the magnitude of the illusion. This is because with longer dot life-times, there is more opportunity for dots in expansion patterns to prematurely move out of the stimulus window. In a pilot experiment, we found that, if anything, the opposite effect was observed.

Other speed illusions and perceptual anisotropies

Although more attention has been paid to direction than to speed perception, the literature is scattered with reports of various speed illusions. Watamaniuk *et al.* (1993) noticed that increasing the dot density in translational motion fields increased the perceived dot speed. Along similar lines, Thompson (1982) reported that sine wave gratings appear to move faster when they contain higher contrast and found that the orientation of the grating affected perceived speed. Another study with drifting sinusoidal gratings found that these stimuli appear to move more slowly in the periphery than foveally (Johnston & Wright, 1986). Finally, Treue *et al.* (1993) reported that decreasing the dot life-times of stimulus features defining motion patterns increases perceived feature speed. This effect was evident even when non-moving flickering dots were added to moving random dot displays, a phenomenon which they call "temporal capture".

The only speed illusion we could find that involved rotating stimuli was in a report by Vicario and Bressan (1990) which examined the perception of rotating wheels on vehicles undergoing forward translation. They found that subjects consistently overestimate the angular velocity of the wheel relative to the forward velocity of the vehicle. This illusion creates the impression of the wheels partially "slipping" relative to the surfaces with which they are in contact. This is interesting because, given the results of this study, it might be expected that subjects underestimate the speed of rotating objects in general.

There are numerous reports of perceptual distortions in the human motion processing system. Thresholds for the detection of coherent motion in displays with low signal-to-noise ratios are generally higher along the vertical meridian, particularly for motion moving either upward or downward (van de Grind *et al.*, 1993). Another study (Raymond, 1994) reported that although foveal motion sensitivity was isotropic, a small but significant (about 0.1 log units) difference in sensitivity in favor of centripetal motion was observed at eccentricities between 5.0 and 12.5 deg out from the fovea. This was true for the entire horizontal meridian and the inferior half of the vertical meridian. Motion sensitivities for the superior portion of the vertical meridian were isotropic (i.e. identical for all motion directions.) Consistent with the previous study, motion thresholds were generally higher along the vertical axis.

The phenomenon reported in the current study cannot be explained by any combination of the above factors, because the effect was invariant with regard to retinal stimulus placement. This is important because it shows a dependence of perceived speed on the global organization of a stimulus" motion vectors.

Possible relation to cortical area MSTd

Cells in the dorsal part of the MSTd of the macaque monkey have been found that respond to motion stimuli containing elements of expansion, contraction and rotation (Graziano *et al.*, 1994; Sakata *et al.*, 1985; 1986; Saito *et al.*, 1986; Tanaka *et al.*, 1986, 1989; Tanaka & Saito, 1989).

MSTd is thought to be part of the motion-processing stream that courses dorsally in cortex from V1 to MT to area MST (Boussaoud *et al.*, 1990). Both V1 and MT contain units tuned to linear motion (Albright, 1984; Hubel & Wiesel, 1962; Livingstone & Hubel, 1988; Maunsell & van Essen, 1983a, b) and the selectivity of MSTd cells to more complex motion patterns is thought to be built up from these more simple inputs. It is likely that motion direction and speed discrimination are processed together in the same cortical pathway. Recent studies (Pasternak & Merigan, 1994) have showed that lesions to the fundus of the superior temporal sulcus (STS), known to affect both MT and MST areas, have raised both speed and motion direction detection thresholds for noisy stimuli.

The distribution of units in MSTd tuned to different motion patterns is biased in favor of expansion. Many more cells are tuned to stimuli containing expansion than either clockwise or counter-clockwise rotation, by a ratio of about 3:1 (Duffy & Wurtz, 1991; Graziano *et al.*, 1994; Saito *et al.*, 1986; Tanaka & Saito, 1989).

The results of the current study were well correlated with the response characteristics of MSTd neurons. Reducing the number of local motion directions defining expansion and rotation in Experiment 3 (down to two directions in the case of axial expansion/rotation) eliminated the illusion, consistent with the poor responses reported when these patterns were used to drive MSTd units (Tanaka & Saito, 1989). Removing the speed gradients from the patterns, thus reducing them to "direction fields", had little effect on either the speed illusion or responses in MSTd neurons (Tanaka & Saito, 1989). The centrifugal bias of MT direction selectivity reported by Albright (1989) cannot explain the illusion, as demonstrated in Experiment 4, where moving the patterns away from the fovea did not diminish the subjective speed difference between motion patterns.

Although it seems plausible that an anisotropy in MSTd response selectivity could affect the perceived speed of complex motion patterns, a real explanation of the illusion requires a computational model that relates MSTd cell activities to the perception of global pattern speeds. Unfortunately, such a model does not yet exist, although evidence from lesion experiments (Dursteler *et al.*, 1987) suggests some relation between neuron number and perceived speed. Many models for local translational velocity computation have been proposed in the past (Horn & Schunck, 1981; Hildreth, 1984; Heeger, 1987; Gryzwacz & Yuille, 1990). These models cannot predict adequately our speed illusion because, as we have demonstrated, the illusion is a global phenomenon depending on the overall arrangements of many different directions of motion and it disappears when the global patterns we used are viewed through narrow, wedge-shaped apertures. However, if we assume that the computation of global pattern speed involves similar steps as in some physiologically inspired local translational velocity models (Heeger, 1992, 1993), our speed illusion could be explained. A key element in these motion models is a normalization step at which the output of a specific translational motion mechanism is divided by the sum of outputs of all the translational motion mechanisms. We could generalize this procedure to the case of global pattern speed computation by assuming that the output of the expansion (or rotation) mechanism is normalized by the outputs of all global motion mechanisms present in MSTd. It is also reasonable to assume that the signal strength of a given global motion mechanism before normalization is proportional to the number of MSTd cells tuned to that global motion type. Because there are more MSTd cells tuned to expansion than rotation, the output of the expansion mechanism after normalization would remain stronger than the rotation mechanism. This could be the physiological basis of the speed illusion reported in this paper, although a more formal model is obviously needed.

In a pilot study using two naive subjects and the two authors, we repeated Experiment 1 with expansion and contraction dot patterns. The expansion patterns were prepared as described above in Experiment 1. The contraction patterns were created by showing the corresponding expansion pattern in reverse, allowing an exact matching of dot speeds, life-times and spatial distribution. In this case, dot speeds in the expansion pattern appeared faster than contraction, although the effect is small (5–10%). This is consistent with our suggestion that an MSTd anisotropy in response selectivity is responsible for the illusion, as expansion cells outnumber contraction cells in MSTd by a ratio of about 2:1 (Duffy & Wurtz, 1991; Graziano *et al.*, 1994; Saito *et al.*, 1986; Tanaka & Saito, 1989).

Alternatively, curved motion may appear slower than straight motion of the same speed. Since the rotation, but not the expansion, patterns contained globally curving motion, this could be the basis of the illusion we have reported. Although locally the motion of each dot is straight, the nervous system perceives the motion as curved in the rotation patterns because of spatial integration. More work needs to be done to pinpoint the exact stimulus attributes contributing to the speed illusion.

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