Pergamon

PII: S0042-6989(97)00279-4

Vision Res., Vol. 38, No. 9, pp. 1223–1231, 1998

Printed in Great Britain
0042-6989/98 $19.00 + 0.00

The Effect of Complex Motion Pattern on Speed Perception

BARD J. GEESAMAN,*‡ NING QIAN†

Received 6 March 1997; in revised form 24 June 1997; in final form 11 August 1997

We recently reported a new motion illusion where dots in expanding random dot patterns appear to move faster than those in rotation patterns despite having the same physical speed distributions. In the current paper, we compared expansion and rotation motion to translational motion and found that the perceived dot speed in translation patterns was between that of expansion and rotation. We also explored contraction motion and found subjects perceived dots in contracting patterns as moving slightly faster than those in expanding patterns and much faster than those in rotating patterns. Finally, we found that stimulus presentation order in a trial plays an important role in determining the magnitude of the speed illusion—the effect is greater when the subjectively faster stimulus is viewed second (e.g., expansion after rotation). The dependence on stimulus order is greatest when comparing complex motion patterns with large subjective speed differences. This phenomenon is unlikely to be explained in terms of channel fatigue or adaptation. © 1998 Elsevier Science Ltd. All rights reserved.

Motion perception Speed illusion Expansion Rotation Translation

INTRODUCTION

We recently described a novel motion illusion involving rotating and expanding stimulus patterns (Geesaman & Qian, 1996). When expanding and rotating random dot patterns with identical dot speeds are compared, the dots in expanding patterns appear to move faster. It was shown that the global motion pattern, *per se*, was responsible for the motion illusion and the evidence argued against a local explanation of the illusion. Since then, preliminary data from another group (Metha, Bex & Wakous, 1997) have confirmed our results with Gabor stimuli.

An appealing explanation for the speed illusion attempts to link the effect to the population response characteristics of cortical cells tuned to complex motion patterns such as expansion and rotation (Geesaman & Qian, 1996). Cells tuned to such motion patterns have been identified in the medial superior temporal region (MSTd) of the macaque (Sakata, Shibutani, Kawano & Harrington, 1985; Sakata, Shibutani, Ito & Tsurugai, 1986; Saito, Yukie, Tanaka, Hikosaka, Fukuda & Iwai, 1986; Tanaka, Hikosaka, Saito, Yukie, Fukuda & Iwai, 1986; Tanaka, Fukuda & Saito, 1989; Tanaka & Saito, 1989; Graziano, Andersen & Snowden, 1994) and may be important for the tasks of ego-motion representation and the analysis of object motion in the environment (Geesaman & Andersen, 1996). Recent psychophysical data are beginning to associate the perception of expanding and rotating patterns to the response characteristics of cells in this region (Morrone, Burr & Vaina, 1995). In area MSTd there are more expansion- than rotation-tuned neurons (Duffy & Wurtz, 1991; Graziano *et al.*, 1994; Saito *et al.*, 1986; Tanaka & Saito, 1989) and this might be the physiological basis of the speed illusion. In our previous paper, we discussed how such differences might translate into differences in perceived speed, although we acknowledged that the link between cell number and perceived speed is tenuous. Since there are also many more expansion cells than contraction cells, and more contraction cells than clockwise or counter-clockwise rotation cells in area MSTd, in the current paper we test the "MST hypothesis" predictions that expansion should appear faster than contraction and contraction faster than rotation.

As an alternative explanation, although the trajectories of the individual dots in the rotating patterns we used were straight, spatial integration within these stimuli may have resulted in the perception of curved dot paths. Perceptually curved paths possibly could have resulted in the perception of decreased dot displacement and, therefore, decreased dot speed. To test the "curvature hypothesis", in the current study expansion and rotation patterns are compared against translational (straight) motion patterns well matched with respect to dot speed distribution. If the above hypothesis is correct, then

*Department of Medicine, Massachussetts General Hospital, Boston, MA 02139, U.S.A.

†Center for Neurobiology and Behavior, Columbia University, 722 W. 168th St., New York, NY 10032, U.S.A.

‡To whom all correspondence should be addressed at: Quincy House #517, 58 Plympton St, Cambridge, MA 02138, U.S.A. [*Tel*: 001 617 493 1754; *Email*: geesaman@husc.harvard.edu].

expansion and translational motion patterns should appear equally fast since there is no curvature in either pattern, and both should appear equally faster than rotation.

Finally, we show that the order of stimulus presentation affects the magnitude of the speed illusion. In the course of the previous study, we informally observed that the magnitude of the speed illusion is greater when the expansion stimulus is viewed after the rotation stimulus. In this paper, we document this phenomenon and further explore this effect with other pairs of patterns.

METHODS

Stimuli

Limited lifetime random dot stimuli were used in this study. Each stimulus was circular and had a radius of 200 pixels (7.63 deg of visual angle viewed at 50 cm). Each dot was a square subtending 0.076 deg (2×2 pixels). The dots were black against a white background (at nearly 100% luminance contrast) to minimize persistence artifacts. The fixation point was a larger square (5×5 pixels) extending 0.20 deg of visual angle.

The video card ran at 60.0 Hz and at each refresh cycle the stimuli were advanced one frame. Accordingly, a 1 sec stimulus movie consisted of 60 image frames. The lifetime of each dot was 12 frames (0.2 sec). After 12 frames, the dot disappeared and was assigned a new location. A new trajectory and speed was calculated for the dot based on the intended complex motion pattern of the stimulus (see Geesaman & Qian, 1996 for details). If a dot moved off the boundary of the stimulus, it was also immediately relocated. Each stimulus contained 100 dots and dot death and rebirth occurred asynchronously to prevent flickering of the stimulus every 12 frames.

The principal experimental stimuli contained a speed gradient, with the speed of each dot proportional to its distance from the pattern center. Patterns lacking this speed gradient (i.e., all dots in the pattern move at the same speed) are identified with a "NG" suffix (see right side of Fig. 1). The details behind the construction of these patterns were described previously (Geesaman & Qian, 1996). The motion direction of each dot was determined by the type of global motion of the stimulus (e.g., expansion, contraction, translational motion). During the 12-frame lifetime of a dot, the speed and direction were constant, which was necessary to allow matching velocity vectors between different motion patterns. With local acceleration absent, transforming one pattern into another simply involved rotating the trajectories of each dot by the appropriate amount, while preserving the speed distribution in the display. A more detailed justification of this approach is found elsewhere (Geesaman & Qian, 1996; Graziano *et al.*, 1994).

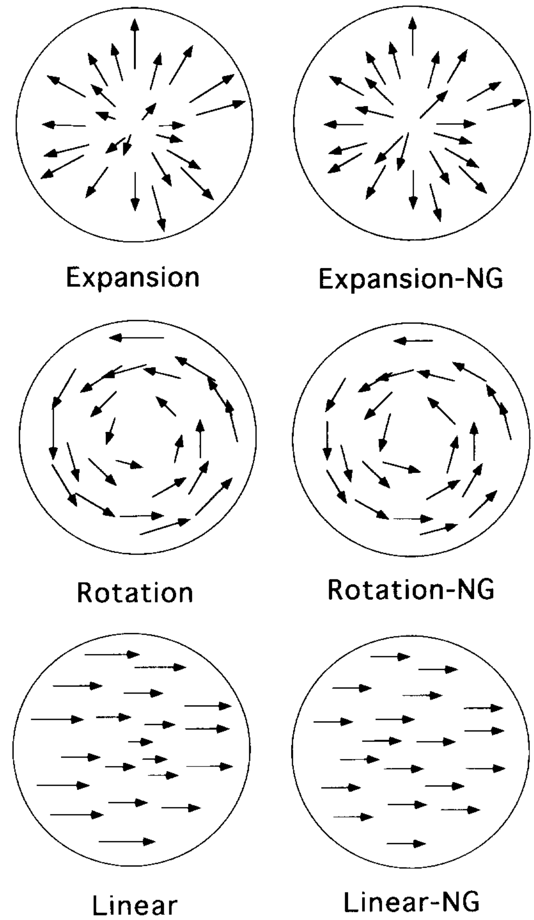
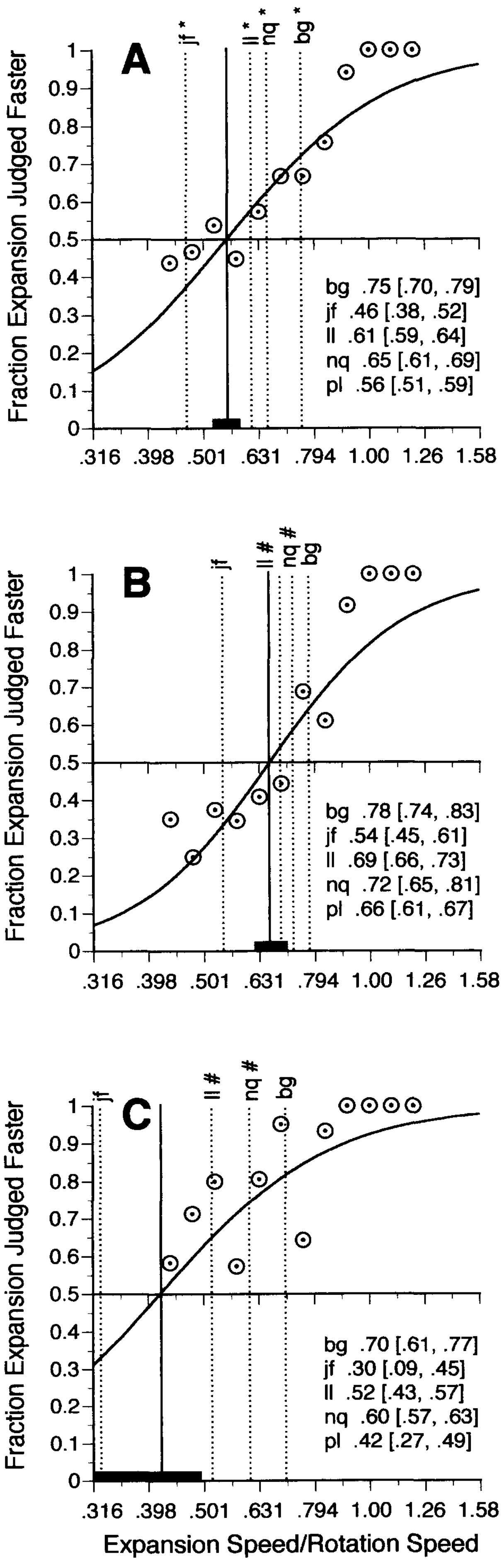


FIGURE 1. Selected experimental stimuli. Three types of complex motion patterns were used in this study: expansion, rotation, and contraction (not shown), as well as translational motion. Each arrow is a motion vector that represents the velocity of individual dots making up these patterns. The three stimuli on the left contain a speed gradient, as indicated by the increasing length of the motion vectors near the periphery of the patterns. The right-sided patterns are identical to their left-sided twins except that these patterns lack a speed gradient. In this study, all comparisons were made between stimuli on the same side, e.g., patterns with speed gradients were always compared against other patterns with speed gradients.

Experimental paradigm

A two-alternative forced-choice (2-AFC) paradigm was used in all experiments. After foveating the fixation point, subjects initiated each trial by pressing the space bar on a computer keyboard. At this point, the first 1 sec stimulus was shown, with the center of the stimulus centered on the fixation point. After a 1 sec gap when only the fixation point remained on the screen, the second stimulus was shown. The subjects pressed "1" or "2" on the keyboard, depending on whether the first or second stimulus had greater perceived average speed. Participants were urged to ignore all aspects of the stimuli except average dot speed and were discouraged from formulating judgments based on the movement or displacement of individual dots. Eye position was not monitored. Four subjects (two naïve) participated in the principal experiments.

In order to attain psychophysical curves, for each trial a "standard" stimulus (e.g., rotation) was compared with a family of "test" stimuli (e.g., expansion). The family of test stimuli was composed of movies that varied only with respect to dot speed; speeds bracketing that of the



standard stimuli were used. The order of the test and standard movies was randomized. For a particular experiment, the same standard movie always appeared; the test (i.e., comparison) movie was chosen based on a "2 step up, 2 step down" double-staircase method (Cornsweet, 1962). An experiment was terminated after 50 trials.

Data analysis

For each experiment, the frequency at which the subject chose the standard stimulus as appearing to move faster was plotted against the ratio of the test to standard stimulus speeds (Fig. 2). These data were then fitted to a logit function with slope and inflection point as the free parameters. Conveniently, the inflection point necessarily occurs at the 50% judgment point, i.e., the point where the perceived speed of the standard and test stimuli are the same. We will use the terms 50% judgment point, inflection point, and equivalence point interchangeably. The legend of Fig. 2 provides additional details of the analysis.

Monte Carlo simulations

To determine if a speed illusion was statistically significant required calculating confidence intervals around the 50% judgment point (Fig. 2). Monte Carlo simulations were run to avoid the non-trivial task of analytically estimating parameter confidence intervals for

FIGURE 2. Expansion vs rotation psychometric curves. All four subjects perceived the expanding dots moving faster than the rotating dots, as indicated by the 50% judgment point shifted to the left of 1.0. The x-axis represents the objective speed ratio between a set of test expansion patterns and a fixed standard rotation pattern on a logarithmic scale. The logarithmic scale was chosen with the presumption that Weber's law applied to the discrimination function. If the two types of motion pattern being compared appear to move equally fast when their objective speeds are the same, the inflection (50% point) of the logit function would be at a speed ratio of 1.0. The 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 logit function to be always at 0.5. The data points represent trials pooled from the four subjects (BG, JF, LL, NQ) and the curve is a best-fit of these data. The broken vertical lines extending the height of each graph indicate the 50% judgment point for the individual subjects, and the solid line marks the equivalence point for the pooled data. The short, thick horizontal line resting on the x-axis is the 95% confidence interval around the equivalence point for the pooled data, the bounds of which were established using Monte-Carlo simulations, as described in the text. Because the confidence interval does not overlap 1.0, the illusion for the pooled data was statistically significant. The "*" symbol after the subjects' initials in (A) indicates the illusion was statistically significant for each subject. (A) plots data from all trials, while (B) and (C) divide the data into trials where expansion appeared first (B), and rotation appeared first (C). For each subject, the illusion was greater when expansion followed rotation. The "#" symbol after a subject's initials indicates that the order of presentation was statistically significant for that subject. The confidence interval bars show that the order effect was statistically significant for the pooled data. The text in the lower right of each panel expresses the subjective equivalence points for each subject as speed ratios, with the 95% confidence intervals associated with this estimate in parentheses. "PL" provides this information for the data pooled across the four subjects. All following psychometric curves will adhere to these conventions.

a non-linear model. Based on the data for each experiment, 1000 experiments were simulated and fit to logit functions, resulting in 1000 stochastic parameter estimates from which 95% confidence intervals were calculated. The random data for each speed ratio were obtained by drawing frequencies from binomial distributions, where the number of simulated trials equated the number of experimental trials and the probability of the Bernoulli trials was assumed to be the curve-smoothed frequency of the observed data at that speed ratio. (See Press, Teukolsky, Vetterling & Flannery, 1992 for an excellent discussion of this approach to confidence interval estimation.)

RESULTS

Figure 2(A) replicates the basic result of our previous paper: random dots moving in expanding patterns appear to move significantly faster than dots of the same speed moving in rotating patterns (Geesaman & Qian, 1996). In the previous study, the method of constant stimuli was used to estimate perceptual equivalence. That approach has the potential shortcoming of underestimating the magnitude of the illusion because of a tendency for subjects to avoid repetitively choosing the same stimulus type (see discussion in Geesaman & Qian, 1996). Improving on this previous paradigm, the data from Fig. 2 were obtained using the double-staircase method (Cornsweet, 1962). The magnitude of the speed illusion was significantly greater, e.g., subject BG's equivalence point was 0.862 by constant stimulus and 0.748 by double-staircase. The equivalence point for the pooled data was 0.826 by constant stimulus and 0.555 by double-staircase (although the subjects tested were not the same in the two studies).

In the previous study, we noticed that stimulus order had an effect on the magnitude of the speed illusion. The illusion was greater for trials where the perceptually faster stimulus pattern appeared after the perceptually slower stimulus. This effect is formally confirmed with this study. Figure 2(B) shows data from trials where the standard stimulus (in this case, rotation) appeared second; Fig. 2(C) shows data from trials where the test stimulus (expansion) appeared second. The illusion in Fig. 2(C) is significantly stronger than that in Fig. 2(B). Following this convention, for each of the experiments that follows, the "B" and "C" frames will show data from "forward" and "backward" trials and the "A" frame will combine these.

In the Introduction, we raised the possibility that the expansion vs rotation speed illusion could be the result of perceived curvature in the dot paths of rotation stimuli. This hypothesis predicts that expansion and translational motion should have the same perceived speed and that both should appear faster by the same amount than rotation. We first tested the second part of this prediction. Figure 3(A) compares translational motion (test stimulus) against rotation motion (standard stimulus). The perceptual equivalence point of the pooled data (i.e., pooled over the four subjects) was 0.874, indicating a modest

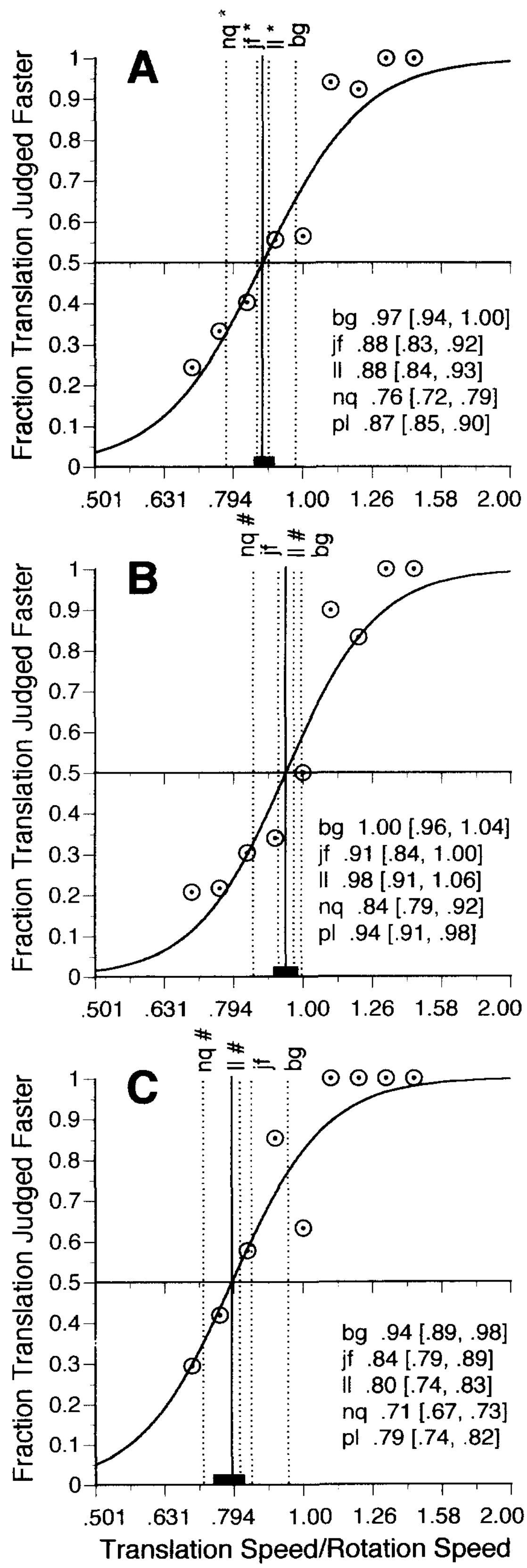


FIGURE 3. Translation vs rotation psychometric curves. All four subjects perceived the translation dots moving faster than the rotation dots, and this effect was statistically significant for three of the subjects and for the pooled data. For each subject, the illusion was greater when translation followed rotation [illusion in (C) greater than that in (B)] and the stimulus order was statistically significant for two of the subjects and the pooled data. See Fig. 2 legend for detailed explanation of plotting conventions.

tendency to perceive the translation dot patterns as moving faster. Note that this effect is not large enough to explain the magnitude of the expansion vs rotation illusion (Fig. 2) and argues in favor of complex motion pattern *per se* (i.e., global arrangement of motion vectors) being responsible for the illusion.

Figure 3(B) and (C) again show an effect of stimulus order. Trials where the perceptually faster translation patterns appeared in the second position [Fig. 3(C)] had a larger illusion than the reverse stimulus order. To see if the presence of the speed gradient present in these patterns contributed to the illusion, we repeated the study with these same motion patterns but eliminated the speed gradient (translation-NG vs rotation-NG). The pooled equivalence point for these data using the same four subjects was 0.851, which was not significantly different from the patterns with a gradient (see T-NG vs R-NG in Table 1).

As mentioned above, the curvature hypothesis also predicts that expansion and translational motion should have the same perceived speed because individual dot trajectories are perceived as straight in both cases. To test this, translational motion (test stimulus) is compared with expansion motion [Fig. 4(A)]. All four subjects experienced the dots in expansion patterns as moving significantly faster, with a pooled equivalence point of 1.300. The effect of stimulus order was again important. Trials where expansion appeared second exaggerated the magnitude of the speed illusion. The experiment was repeated on the same subjects with stimuli lacking a speed gradient and the pooled equivalence point was 1.116, a significantly smaller effect than with the gradient patterns. Because dot paths in translation and expansion patterns are both perceptually and physically straight, the curvature hypothesis cannot explain their difference in perceived speed.

An alternative explanation for the speed illusion between expansion and rotation was the "MST hypothesis" raised in the Introduction. We also know that there are more expansion- than contraction-tuned cells and more contraction-tuned cells than cells tuned to either direction of rotation in MSTd (Graziano *et al.*, 1994; Geesaman & Andersen, 1996), which gives rise to two additional predictions. Figure 5(A) tests the first prediction that expansion should appear faster than contraction. Contrary to expectations, all four subjects experienced the dots in the contraction patterns as moving faster, although the effect was quite small (equivalence point = 0.921). There was also a small, but statistically significant effect of stimulus order. Patterns without a speed gradient showed similar results (equivalence point = 0.932), although in this case the effect of stimulus order was not significant (see C-NG vs E-NG in Table 1).

The MST hypothesis also predicts that contraction should appear faster than rotation. In the interest of space, the remaining experiments are summarized in Table 1, along with the equivalence points and confidence intervals for the previous experiments. As expected, when contraction (test stimulus) was paired against rotation (standard), all four subjects experienced the dots in the contraction pattern as moving faster (pooled equivalence point = 0.580; see C vs R in Table 1). This is similar in magnitude to the expansion vs rotation comparison. The effect of stimulus order is small, but statistically significant for the pooled data. Experiments comparing these same motion patterns without speed gradients gave similar results (equivalence point = 0.638; see C-NG vs R-NG in Table 1).

TABLE 1. Summary of equivalence points

	Pooled data		Pooled data
	0.56 [0.51, 0.59]		0.58 [0.56, 0.60]
E vs R	0.66 [0.61, 0.67]	C vs R.	62 [0.59, 0.65]
	0.42 [0.27, 0.49]		0.55 [0.52, 0.58]
	0.87 [0.85, 0.90]		0.64 [0.61, 0.66]
T vs R	0.94 [0.91, 0.98]	C-NG vs R-NG	0.69 [0.66, 0.72]
	0.79 [0.74, 0.82]		0.57 [0.50, 0.61]
	0.85 [0.82, 0.88]		1.41 [1.35, 1.47]
T-NG vs R-NG	0.97 [0.91, 1.04]	T vs C	1.62 [1.49, 1.94]
	0.77 [0.74, 0.80]		1.25 [1.19, 1.30]
	1.30 [1.25, 1.36]		0.98 [0.96, 1.01]
T vs E	1.41 [1.34, 1.49]	CCW vs CW	0.99 [0.95, 1.02]
	1.16 [1.08, 1.24]		0.98 [0.96, 1.01]
	1.12 [1.11, 1.21]		1.00 [0.98, 1.02]
T-NG vs E-NG	1.27 [1.23, 1.34]	CCW vs CCW	1.00 [0.98, 1.02]
	1.02 [0.90, 1.06]		1.00 [0.97, 1.03]
	0.92 [0.90, 0.94]		1.00 [0.97, 1.03]
C vs E	0.97 [0.94, 1.02]	E vs E	1.01 [0.97, 1.05]
	0.87 [0.85, 0.90]		0.99 [0.96, 1.03]
	0.93 [0.90, 0.96]		
C-NG vs E-NG	0.96 [0.90, 1.03]		
	0.92 [0.88, 0.96]		

The motion patterns compared are arranged into rows. Each box contains three sets of equivalence points with 95% confidence intervals, in the same format as in Fig. 2Fig. 3Fig. 4Fig. 5. The top set of numbers reflects both forward and backward trials; the middle set of numbers reflects forward trials; the bottom set of numbers reflects backward trials. E, expansion; R, rotation; T, translation; C, contraction; CCW, counter-clockwise; CW, clockwise. The "NG" suffix indicates that these stimuli lacked a speed gradient (see Fig. 1 legend). Table entries less than 1.0 indicate that the first pattern (e.g. expansion with "E vs R") appeared faster.

Based on the above results and the assumption of transitivity between the different speed illusions, we predicted that contraction should appear faster than translation. We compared translation (test stimulus) against contraction (standard) and confirmed this prediction (T vs C in Table 1). All four subjects experienced the dots in contraction patterns as moving significantly faster, with a pooled equivalence point of 1.405. There was a significant effect with stimulus order (1.62 vs 1.25).

Several experiments were conducted to further explore the effect of stimulus order. One possible explanation of the order effect is channel fatigue or adaptation: if inhibitory connections exist between channels tuned to different types of motion, fatiguing a channel's inhibitory inputs should increase the activity of that channel, leading to such phenomena as the motion after-effect (Lovegrove, Over & Broerse, 1972; Vautlin & Berkley, 1977; Harris, Morgan & Still, 1981; Nishida & Sato, 1992; Hiris & Blake, 1992; Blake & Hiris, 1993;

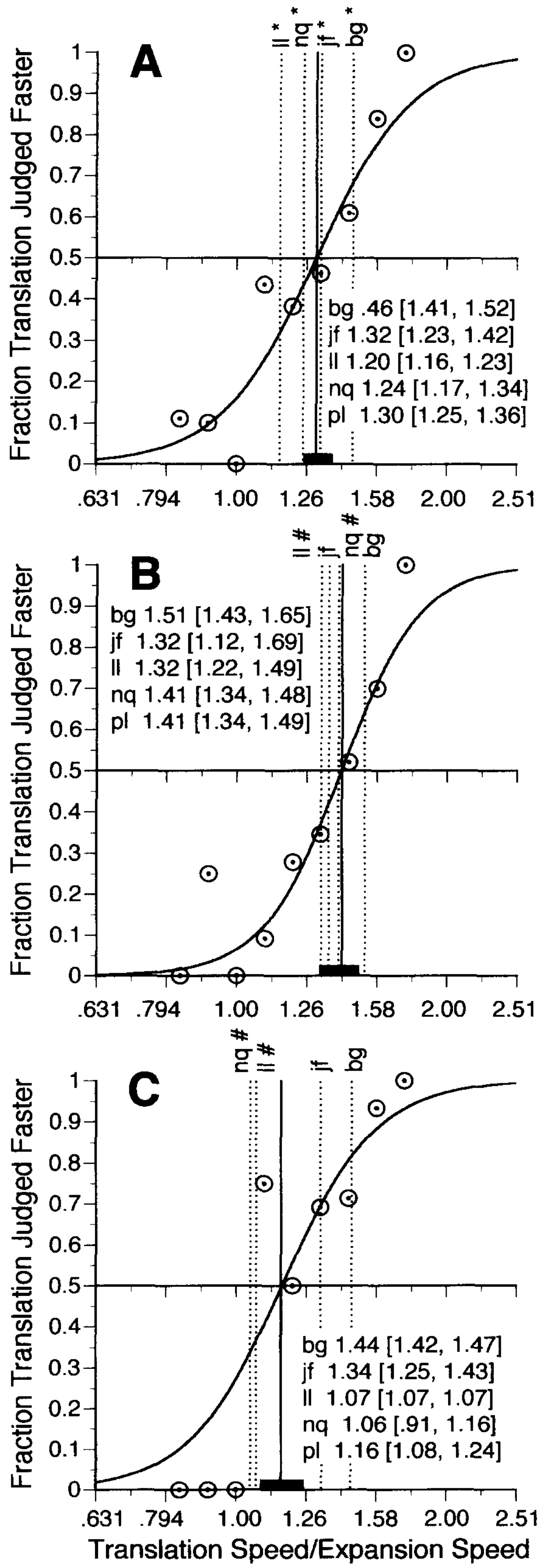


FIGURE 4. Translation vs expansion psychometric curves. All four subjects perceived the expansion dots moving faster than the translation dots, and this effect was statistically significant for all four subjects and for the pooled data. For each subject, the illusion was greater when expansion followed translation [illusion in (B) greater than illusion in (C)], and the stimulus order was statistically significant for two of the subjects and the pooled data. See Fig. 2 legend for detailed explanation of plotting conventions.

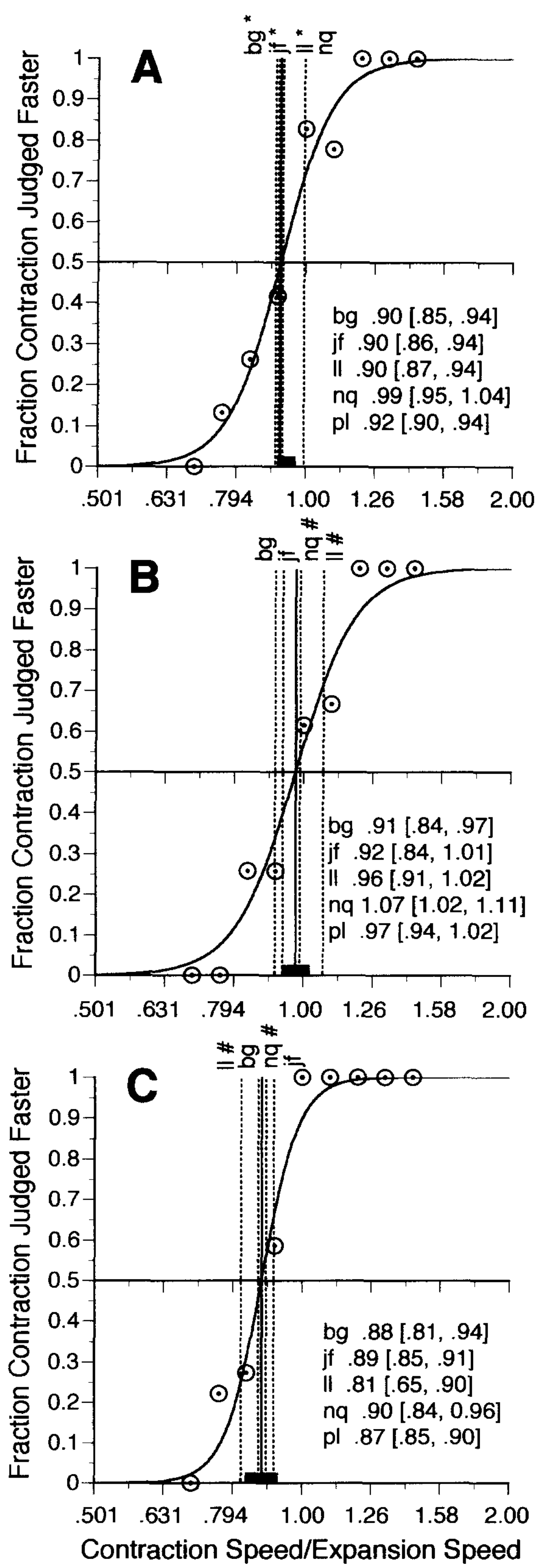


FIGURE 5. Contraction vs expansion psychometric curves. All four subjects perceived the contraction dots moving faster than the expansion dots, and this effect was statistically significant for three of the subjects and for the pooled data. In all cases, the magnitude of this illusion was quite small. For each subject, the illusion was greater when contraction followed expansion and the effect of stimulus order was statistically significant for two of the subjects and the pooled data. See Fig. 2 legend for detailed explanation of plotting conventions.

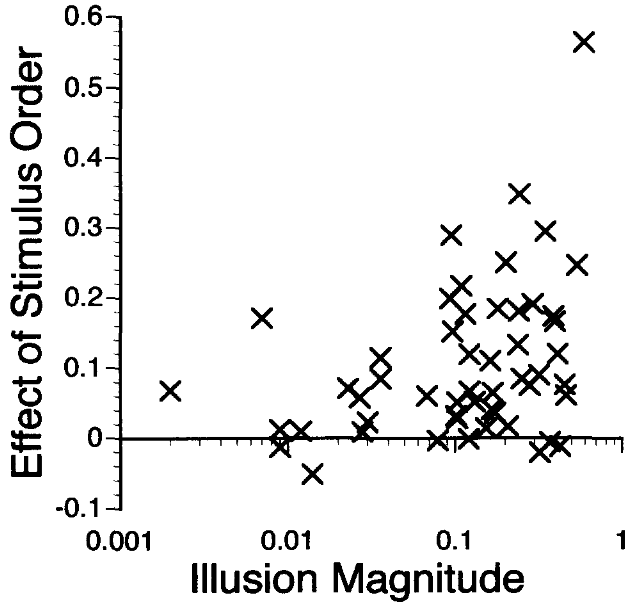


FIGURE 6. Illusion magnitude and effect of stimulus order. The illusion magnitude was the distance between the perceptual equivalence point and the physical equivalence point (speed ratio 1.0). The effect of stimulus order was calculated by subtracting the 50% equivalence point calculated from "forward" trials from "backward" trials. The definition of "forward" and "backward" trials is discussed in the text. Note that the abscissa is plotted on a log scale.

Grunewald & Lankheet, 1996), and possibly increasing the perceived speed of moving stimuli. For cells tuned to translational motion, the inhibitory connections are strongest for opposite directions of motion (Snowden, Treue, Erickson & Andersen, 1991; Qian & Andersen, 1994). For complex motion, opposite directions of motion are expansion/contraction and clockwise/counter-clockwise rotation (see discussion in Graziano *et al.*, 1994). When we compared expansion and contraction (C vs E in Table 1), there was a smaller order effect than between expansion and rotation (Fig. 2; E vs R in Table 1), arguing against the fatigue hypothesis. To further test this hypothesis, we compared counter-clockwise and clockwise rotation and, as expected, no speed illusion or order effect was observed (CCW vs CW in Table 1). Up vs down translation-NG motion and up vs left translation-NG were also compared, demonstrating no speed illusion or effect of stimulus order (data not shown). All these results are inconsistent with the adaptation or fatigue hypothesis.

Except for rotation vs contraction, in general the greater the magnitude of a speed illusion, the greater the effect of stimulus order. Figure 6 is a scatterplot showing this relationship for each experiment and each subject. The positive correlation between illusion magnitude (e.g., difference in perceived speed between two stimulus types) and order effect (e.g., effect of stimulus presentation order on perceived relative speed) was significant ($P < 0.05$) by one-way ANOVA. In general, very little order effect was observed if the perceptual equivalence point was between 0.9 and 1.1.

DISCUSSION

There are three main findings of this study. First, for stimuli having the same dot speed distribution, the perceived speed of translational (straight) motion patterns lies somewhere between the perceived speed of expansion and rotation patterns. The perceived speed of the translation patterns is closer to that of the rotation than the expansion stimuli. These results were true whether or not the stimuli compared contained a speed gradient. The spatial integration/curvature hypothesis discussed in the Introduction may explain part of the illusion. However, because patterns with perceptually straight paths (e.g., expansion vs translation) have different perceived speeds, we conclude that complex motion pattern *per se* is largely responsible for the illusion.

The second finding is that the link between MSTd physiology and the speed illusion proposed in the previous paper is, in part, supported and, in part, contradicted by the current results. The relative number of cells in MST follows the order expansion>contraction>rotation (Duffy & Wurtz, 1991; Graziano *et al.*, 1994; Saito *et al.*, 1986; Tanaka & Saito, 1989). Good quantitative data comparing numbers of complex motion and translational motion-tuned cells in MSTd have not been published. While expansion and contraction were judged faster than rotation, contraction appeared slightly faster than expansion, the opposite of what would be predicted from the disproportionate number of expansion-tuned cells in macaque MSTd (although relative numbers of cell-tuning types may be different in humans). The hypothesis that the speed illusion is a consequence of MSTd physiology remains appealing but relatively weak without human data, and a formal model linking cell number and perceived speed.

Alternatively, certain characteristics of the stimuli compared, unrelated to global motion, may contribute to the speed illusions. For example, expansion motion contains local motion signals in all directions whereas translational motion has only one. The relative motion between opposing vectors in the expansion stimuli may contribute to the enhanced perceptual speed. Although this asymmetry with respect to local motion vector content may contribute to the expansion vs translation illusion, it cannot explain the expansion vs rotation illusion (Geesaman & Qian, 1996).

A second possible criticism is that expansion, rotation, and translation potentially induce different eye movements which may affect the perceived speed of these patterns. For example, rotating stimuli might produce torsional nystagmus, while expansion patterns provide their own reference frame. Although we did not monitor eye movement, in a previous study (Geesaman & Qian, 1996) and in new pilot studies we performed the experiments with the stimuli simultaneously placed to the left and right of the fixation, rather than sequentially on top of the fixation point. Although a more difficult task, eye movement was less of a concern because the stimuli were removed from the direction of gaze. Similar results were obtained (data not shown).

Our third finding is that stimulus presentation order affects the magnitude of the speed illusion. Specifically, we found that the speed illusion is stronger when the perceptually faster pattern (e.g., an expansion pattern) is presented after the perceptually slower pattern (e.g., a rotation pattern) in a given trial. The simplest explanation of the order effect is to assume that expansion and rotation channels in the brain mutually inhibit each other. Adaptation or fatigue of the rotation channel by a rotating stimulus will weaken its inhibition to the expansion channel and therefore increase the perceived speed of the subsequently presented expansion pattern. This explanation is problematic, however, for the following reason. There is a large body of experimental evidence documenting mutual inhibition between opposite directions of motion (Snowden *et al.*, 1991; Hiris & Blake, 1992; Blake & Hiris, 1993; Qian & Andersen, 1994). If the above explanation were correct, one would predict a strong order effect for the leftward and rightward motion patterns, for the expansion and contraction patterns, and for the clockwise and counter-clockwise rotation patterns. As we have mentioned, these predicted order effects were not observed. For this hypothesis to apply, one has to assume that in the cortical area responsible for the order effect, there are inhibitory connections between expansion and rotation channels, etc., but not between expansion and contraction channels, etc. We conclude that adaptation does not seem to provide a natural explanation for the order effect we observed.

Figure 6 shows that the order effect is correlated with the magnitude of the speed illusion: for a pair of patterns such as expansion and rotation that yield a strong speed illusion, the order effect is also strong, and for pairs (such as expansion and contraction) without the speed illusion, the order effect is negligible. This observation suggests that the order effect and the speed illusion are likely to be generated by the same neural machinery in the brain.

The finding that perceived average dot speed in random dot displays depends on the organization of the motion vectors argues in favor of separate neural processing channels for different types of complex motion. Whether channels specific to complex motion patterns such as expansion, rotation, and contraction exist continues to be a subject of debate (Werkhoven & Koenderink, 1991; Sekuler, 1992; Regan, 1986; for a brief review see Geesaman & Qian, 1996). Our laboratory's finding that perceived speed depends on global motion pattern argues for separate processing of these patterns, at least with respect to speed estimation. Similar perceived speeds between expansion/contraction and between the two directions of rotation suggest one neural system of analyzing expansion/contraction motion and one for processing rotational motion. However, other investigators have found perceptual asymmetries with respect to expansion and contraction. Reinhardt-Rutland (1994) reported centrifugal (away from center of fixation) motion after-effect exceeding centripetal (towards center of fixation) motion after-effect (MAE) for rotating, spirals and Kelly (1989) also found asymmetries between centrifugal and centripetal MAEs. Furthermore, Edwards and Badcock (1993) found that human observers were more sensitive to centripetal than either centrifugal or frontoparallel motion, although other groups have reported opposite results (Ball & Sekuler, 1980; Fahle & Wehrhahn, 1991).

Stimuli with high biological significance should be highly perceptually salient. Expansion and contraction flow fields have particular biological significance and may therefore be particularly salient stimuli (Regan & Beverley, 1978; Beverley & Regan, 1980). Objects on a collision course with an observer need to be dealt with quickly (Ball, Ballot & Dibble, 1983; Cavallo & Laurent, 1988; Sun, Carey & Goodale, 1992), and receding objects also may be important to detect—from the point of view of a predator, they may represent dinner. The detection of rotational motion lacks the same urgency. Other reported illusions suggest a connection between saliency and perceived speed. Sine-wave gratings appear to move faster when they contain higher contrast and this may be related to the greater saliency of high contrast patterns (Thompson, 1982; Stone & Thompson, 1992; Thompson, Stone & Swash, 1996). Along similar lines, Watamaniuk, Grzywacz, and Yuille (1993) reported that dot speed increases in translation patterns with increasing dot density.

In summary, we have further documented the speed illusion we reported previously and explored possible explanations. While the perceived curvature in the rotation patterns may partially contribute to their low perceived speed, the illusion is mainly caused by differences in global motion pattern.

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Acknowledgements—The authors would like to thank Jon Fullerton, Louisa Lund, and Jay Rideout for participating as subjects in this study. We would also like to thank Dr Lothar Spillmann for his helpful discussions and comments. This work was supported in part by NIH grant #MH54125 and a Sloan Research Fellowship, both awarded to Ning Qian.