**Boston University**

**OpenBU** **http://open.bu.edu**

Cognitive & Neural Systems CAS/CNS Technical Reports

1997-06-04

# Induced Motion and Visual Stability in an Optic Flow Illusion

https://hdl.handle.net/2144/2120

*Downloaded from DSpace Repository, DSpace Institution's institutional repository*

# Induced Motion and Visual Stability in an Optic Flow Illusion

Pack and Mingolla

**June 1997**

**Technical Report CAS/CNS-97-008**

Permission to copy without fee all or part of this material is granted provided that: 1. The copies are not made or distributed for direct commercial advantage; 2. the report title, author, document number, and release date appear, and notice is given that copying is by permission of the BOSTON UNIVERSITY CENTER FOR ADAPTIVE SYSTEMS AND DEPARTMENT OF COGNITIVE AND NEURAL SYSTEMS. To copy otherwise, or to republish, requires a fee and / or special permission.

Copyright © 1997

Boston University Center for Adaptive Systems and
Department of Cognitive and Neural Systems
677 Beacon Street
Boston, MA 02215

# Induced Motion and Visual Stability in an Optic Flow Illusion

Christopher Pack[*] Ennio Mingolla[*]
[*]Department of Cognitive and Neural Systems
and
Center for Adaptive Systems
Boston University
677 Beacon St.
Boston, MA 02215

**Key words: Optic flow, illusion, heading, area MST, pursuit**
**Running head: Optic Flow Illusion**

**June 4, 1997**
**Submitted to *Vision Research***

## Abstract

**When an expansion flow field of moving dots is overlapped by planar motion, observers perceive an illusory displacement of the focus of expansion (FOE) in the direction of the planar motion (Duffy & Wurtz, 1993. *Vision Research, 33,* 1481-1490). The illusion may be a consequence of induced motion, wherein an induced component of motion relative to planar dots is added to the motions of expansion dots to produce the FOE shift. Such a process could be mediated by local, "center-surround" receptive fields. Alternatively, the effect could be due to a higher level process which detects and subtracts large-field planar motion from the flow field. We probed the mechanisms underlying this illusion by adding varying amounts of rotation to the expansion stimulus, and by varying the speed and size of the planar motion field. The introduction of rotation into the stimulus produces an illusory shift in a direction perpendicular to the planar motion. Larger FOE shifts were perceived for greater speeds and sizes of planar motion fields, although the speed effect saturated at high speeds. While the illusion appears to share a common mechanism with center-surround induced motion, our results also point to involvement of a more global mechanism that subtracts coherent planar motion from the flow field. Such a process might serve as a means of maintaining visual stability during eye movements.**

## Introduction

Duffy and Wurtz (1993) describe a number of perceptual effects associated with the superposition of two sets of randomly distributed dots undergoing two different types of motion. One set of dots moves coherently within the frontoparallel plane (henceforth referred to as "planar motion"), while the other expands outwards from a single point, the focus of expansion (FOE). When the two types of motion are combined by vector addition into the trajectories of individual dots, observers accurately perceive the focus of expansion as being displaced in the direction opposite that of the planar motion. However, when the two types of dot motion are simply overlapped, with a given dot participating only in expansion or only in the translation, observers perceive the focus of expansion as being displaced in the direction of the planar motion (Figure 1a,b). This illusion has a number of implications for theories of computation of self-motion.

Gibson (1950) first pointed out that, for purely translational movement, the focus of expansion of an optic flow field indicates one's heading direction, and that this information could be useful for navigation. However, during rotation of the eye or head, the optic flow field[1] is combined

---

[1] Gibson (1966) drew a distinction between changes in the "optic array" caused by observer movement, and the "retinal flow" which describes the projection of the optic array onto the retina. We use the term "optic flow" to refer to the latter.

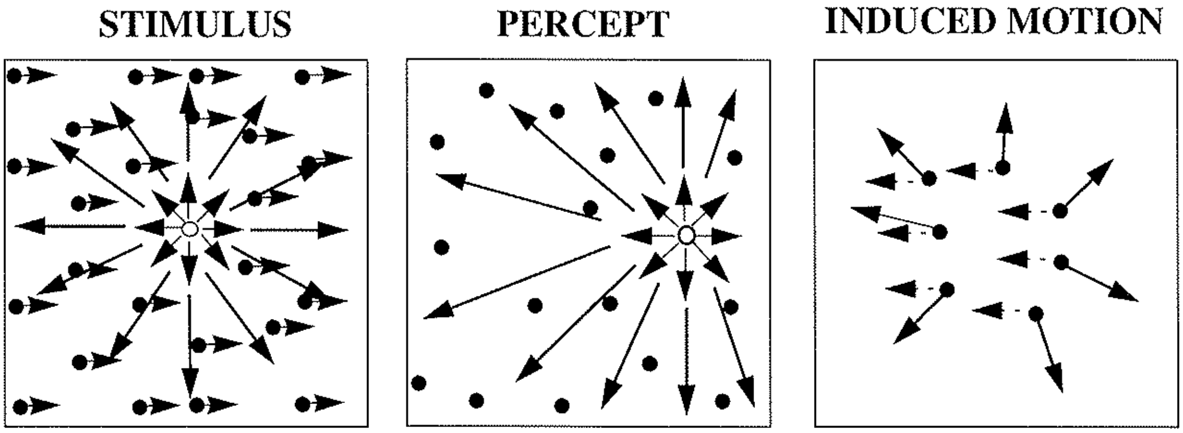

**Figure 1: Stimulus configuration used by Duffy and Wurtz (1993). Rightward planar motion is combined with expansion motion (a), creating an illusory displacement of the FOE in the direction of the planar motion (b). Components of induced motion added to the motions of expansion field dots may account for this effect (c). Parts (a) and (b) adapted with permission from Duffy and Wurtz (1993).**

with a constant rotational component, which displaces the FOE away from the direction of heading. In this case a new FOE is created around the fixation point. It has been suggested that the visual system may detect eye rotation, either by visual means (Van den Berg, 1996), or through an oculomotor efference copy (Royden *et al.*, 1994; Cameron *et al.*, 1997), and remove the visual consequences of the rotation from the internal representation of the flow field. In this case, the inferred FOE would once again accurately specify the direction of heading. Duffy and Wurtz (1993) suggested that their illusion may be related to a general strategy exploited by the visual system to compensate for the effects of eye movements. Specifically, they hypothesized that the visual system interprets full-field planar motion as a reafferent stimulus indicating an eye movement, and shifts the perceived FOE to compensate.

Duffy and Wurtz's (1993) suggestion does not address the mechanism by which the FOE shift might take place. Meese *et al.* (1995) suggested that the Duffy and Wurtz illusion could be explained by induced motion, which occurs when a stationary target appears to move in a direction opposite that of a surrounding object (Duncker, 1938). Since induced motion can combine additively with real motion (Post and Chaderjian, 1988), they hypothesized that the large-field planar motion in one direction induced motion in the opposite direction, which, when added to the expansion stimulus, produced the observed effect (see Figure 2).

Induced motion is a general term assigned to a number of diverse effects (Reinhardt-Rutland, 1988). Therefore it is important to make the functional distinction between purely local induced motion, often referred to as *motion contrast* or *center-surround* induced motion, and a more global effect, which is related to perception of self-motion (c.f. Heckmann and Howard, 1991). The latter phenomenon is likely to be of interest for understanding perception of heading, while the former is more likely related to the perception of object motion. Global mechanisms have been invoked to explain psychophysical results on induced motion (Reinhardt-Rutland, 1988) and motion aftereffect (Cavanagh and Favreau, 1980; Hershenson, 1984). However, the demonstration by Nakayama and Tyler (1978) that motion can be induced simultaneously in two different directions strongly suggests the involvement of a local mechanism. One goal of the present work is to determine to what extent each of these mechanisms contributes to the illusion.

Our first experiment was designed to test whether the illusory percept can be explained by the addition of induced motion vectors with nearby optic flow vectors (Figure 1c). If this argument is valid, replacing the expansion stimulus with a circular one should induce a shift in a direction *perpendicular* to the planar motion (Figure 2). In four other experiments, we examine the validity of Duffy and Wurtz's assertion that the illusion is a consequence of a perceptual strategy for maintaining visual stability during eye movements. If this is the case, we would expect that the illusory effect would be facilitated by global stimulation more than by local stimulation, since eye movements affect the entire flow field. We address this issue by manipulating the size and speed of the planar motion field. In the Discussion section we relate our findings to neurophysiological data on primate visual area MST.

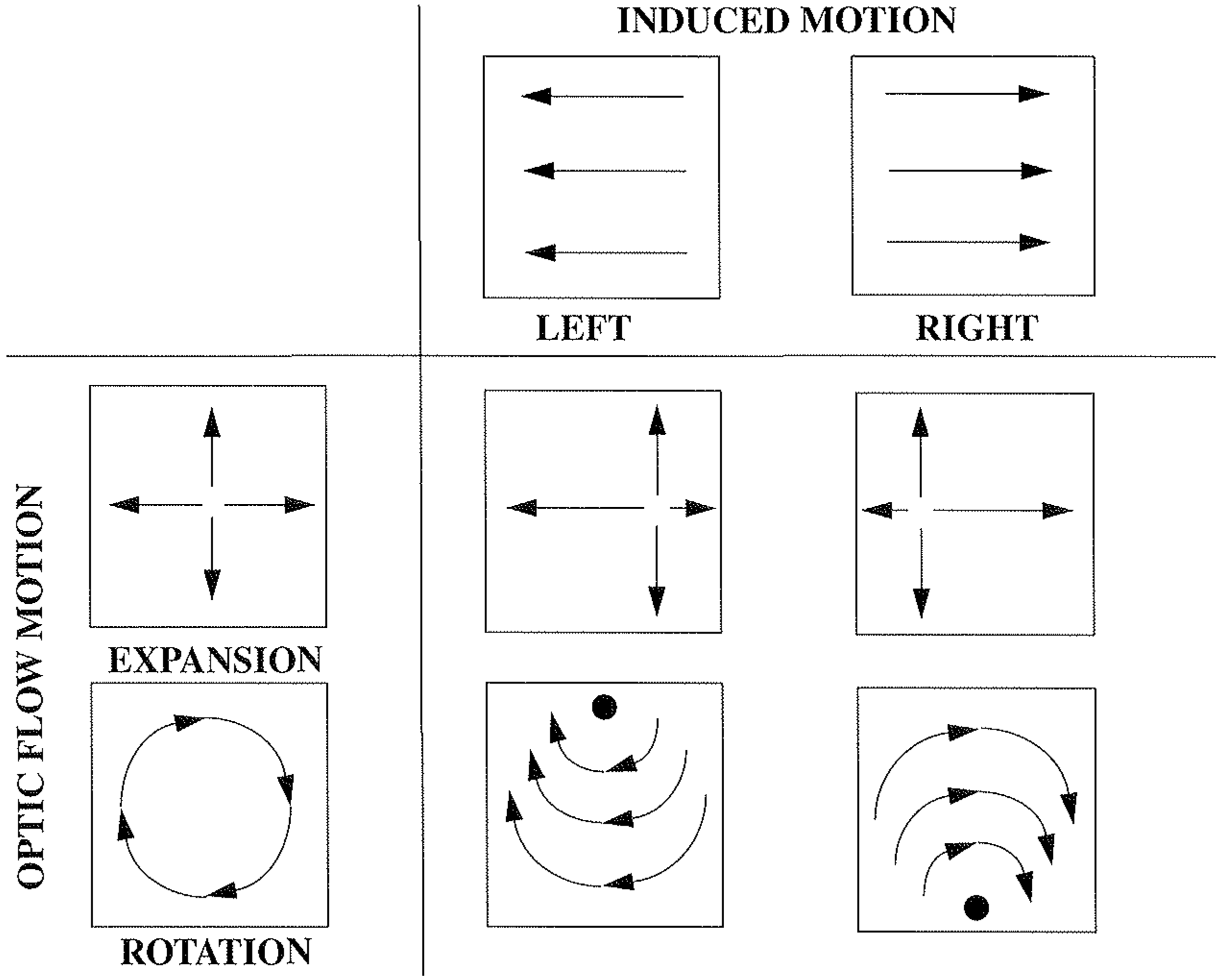

**Figure 2: Combination of induced planar motion and various types of optic flow motion. Note the vertical and horizontal shifts for rotation and expansion motion, respectively. Adapted with permission from Duffy and Wurtz (1995).**

## General Methods

Visual stimuli were generated on a Silicon Graphics Reality Engine$^2$ (model CMN-A011) at 66 frames per second. For Experiments 1 and 2, the display subtended a visual angle of $60^o$ at a viewing distance of 30 cm. The stimuli consisted of 200 white dots, with 100 undergoing expansion and 100 translation. Each dot subtended $0.6^o$ of visual angle in diameter against a black background. For every frame, each dot had a 5% chance of being removed, resulting in a mean dot lifetime of approximately 0.2 sec. Dots that exceeded their lifetime or reached the edge of the screen were assigned to a random location on the screen in the next frame. In Experiment 1 the speed of planar motion was fixed at $19^o$/sec. The direction of motion (leftward vs. rightward) was varied randomly across trials. The speed of expanding motion increased with distance from the focus of expansion, reaching a maximum speed of $16^o$/sec.

For Experiments 3-5, we used a larger monitor, which covered a visual angle of $85^o$ at a viewing distance of 35cm. This monitor seemed to have a slower rate of phosphor decay than the first, leading to visible traces of dot trajectories. We therefore reversed the contrast of display, using black dots on a white background. Planar dot speed was fixed at $22^o$/sec., and expansion speed reached $23^o$/sec. In Experiments 3 and 5, the number of planar dots was scaled to the size of the planar motion field, with a full planar motion field containing 120 dots. In Experiment 4, the number of planar dots was manipulated directly from a minimum of 50 to a maximum of 500.

Each trial began with a visual cue consisting of a single red dot at the center of a black screen, displayed for one second. The stimulus was then displayed for 3 seconds. A black cross then appeared against a gray background, and the subjects' task was to use the mouse to move the cross to the location of the perceived center of motion. In Experiments 2-5, the cross moved only along the horizontal meridian of the screen, since shifts along the y-axis were not being measured. Observers were given no instructions about fixation, and eye movements were not monitored. Adding a fixation point to the stimulus does not seem to affect the perception of this illusion (Duffy and Wurtz, 1993).

In each experiment the variable to be manipulated was assigned a value from a discrete set, in order to simplify plotting of the results. We chose to present 90 trials in each case, so that each value would be presented an average of 15 times, and each of the five experiments lasted approximately 10 minutes. We presented two or three experiments in a single session. Five observers participated in Experiments 1 and 2, and eight participated in Experiments 3-5. Author CP participated in all experiments, and author EM participated in Experiments 3-5. All other observers were naive as to the purpose of the experiment, and no feedback was given on any trial. Volunteer observers were paid $6 per session.

For each experiment a positive result was defined as a shift in a direction parallel to the planar motion. For Experiment 1 the direction of rotation was also taken into account, so that a positive vertical shift was defined as a perceived displacement in a direction consistent with induced motion. For example, an upward shift for the combination of leftward planar and clockwise rotation motion would be considered positive (see Figure 2). Since there was no discernible difference between the magnitude of perceived shifts for leftward and rightward planar motion, the two directions were combined in the presentation of experimental results.

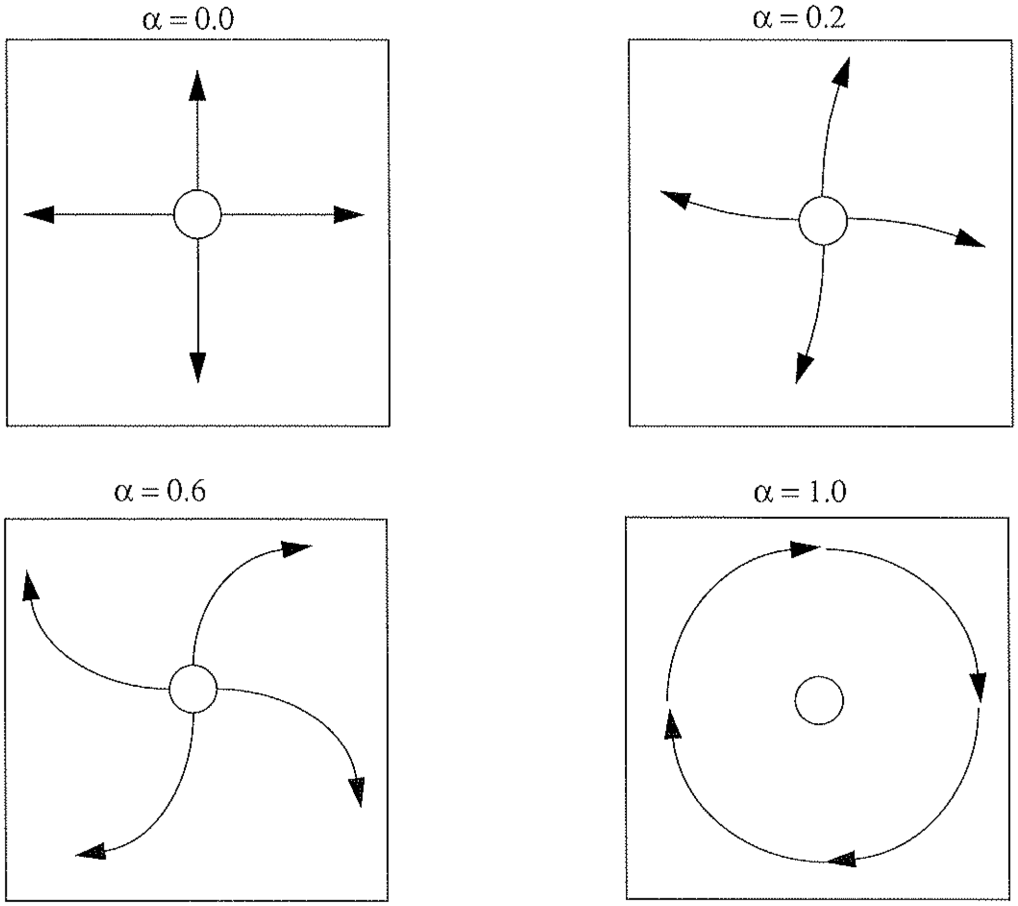

**Figure 3: Schematic of optic flow stimuli with varying amounts of rotation and expansion.**

## Experiment 1

The purpose of this experiment was to test the induced motion hypothesis. Planar motion was presented as described in the General Methods section, but the optic flow stimulus was chosen from a continuum of stimuli. The continuum ranged from pure expansion motion to circular motion, with a series of spiral stimuli in between. The spirals were generated by adding expansion and rotation motion such that each dot in the compound stimulus moved according to

$$V(x, y) = \alpha R(x, y) + (1 - \alpha) E(x, y)$$

where $E$ and $R$ define the rotation and expansion at a given point $(x,y)$ measured from the center of motion (see Appendix). The parameter $\alpha$ defines the ratio of expansion to rotation (Figure 3).

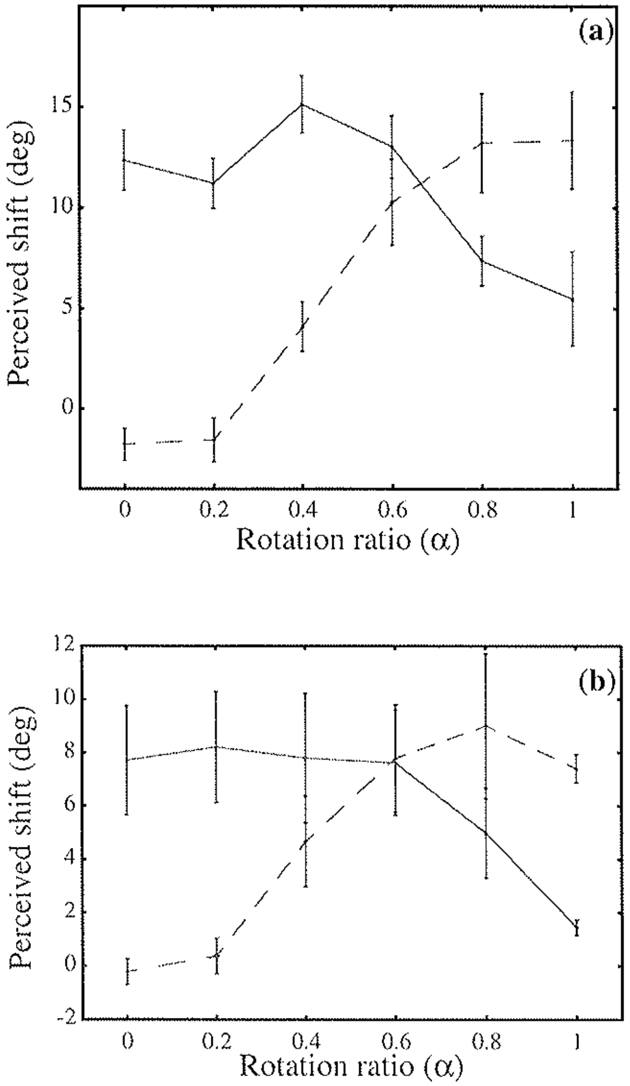

**Figure 4: Magnitude of perceived shift for optic flow stimuli overlapped with planar motion for one observer (a) and for the (N=5) group (b). The horizontal and vertical shifts are represented by solid and dotted lines, respectively. The abscissa shows the amount of rotation present in the combined stimuli. (See Methods section.) Vertical bars show standard error for (a), and show standard error of five observers' means from the means of observers' means in (b).**

## Results

Figure 4 shows the magnitude of the perceived horizontal and vertical displacements for one observer (not an author) and for the group, as a function of the amount of rotation present in the optic flow stimulus. The amount of vertical shift covaries with the proportion of rotation, while

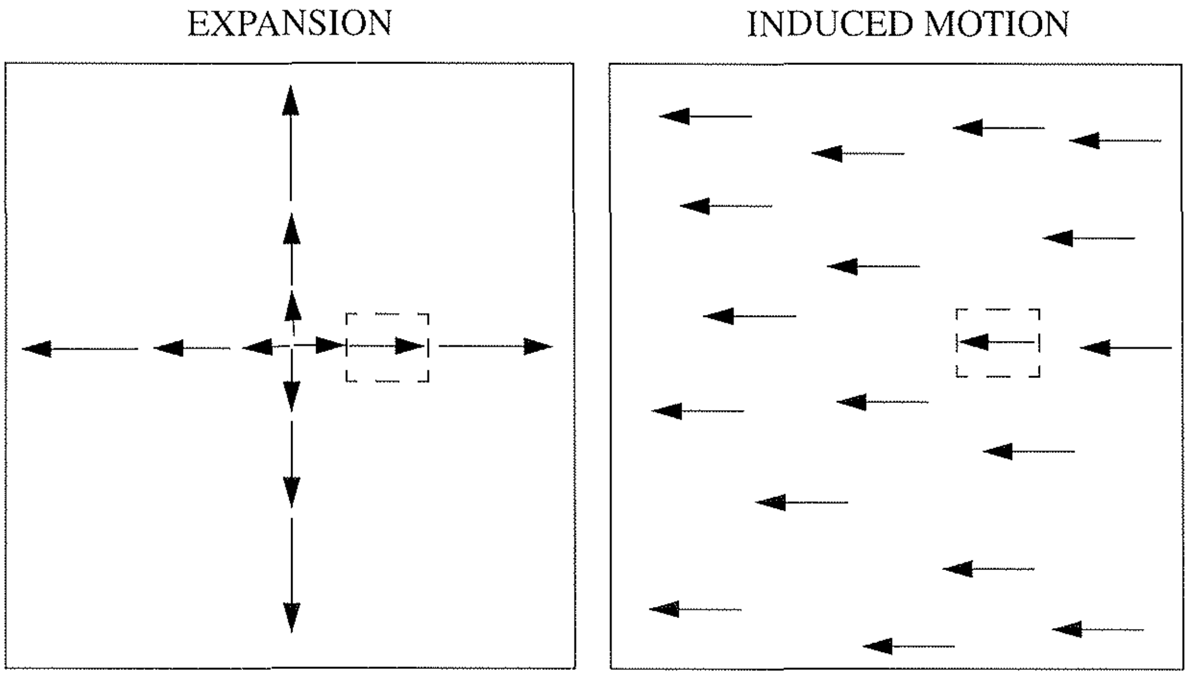

**Figure 5: Induced planar motion cancels expansion motion at a specific spatial locus.**

the amount of horizontal shift covaries with the proportion of expansion. The results of each observer manifested these trends, to varying degrees. This is consistent with the idea that the illusion is related to induced motion (see Figure 2), although it does not address the relative contributions of global and local mechanisms. There was a tendency for the perceived y-axis shift to decrease in the case of pure rotation ($\alpha = 1.0$), relative to its value for $\alpha = 0.8$. We attribute this to an aftereffect of the expansion component, which was present to some degree in all other stimulus configurations. In response to queries from the experimenter, conducted after data were gathered, some observers reported seeing the rotation stimulus contract about its center, which provided an additional cue as to the actual stimulus position.

## Experiment 2

Experiment 1 showed that the perceived displacement behaves as would be predicted by a process that sums induced motion vectors with the optic flow stimulus. Thus, we can think of the perceived FOE as the point where the induced motion exactly cancels some part of an expansion stimulus. Since the speed of expansion motion increases with distance from the FOE, we can use the magnitude of the FOE shift to calculate the speed of motion in the expansion field that is cancelled by planar motion (Figure 5). By studying the magnitude of the FOE shift for various speeds of planar motion, we can estimate the "gain" of the effect. This has direct relevance for the notion that this illusion is related to visual stability, since the effectiveness of such a strategy would depend on the ability to eliminate fully the effects of eye rotations, which would require a gain of 1.0. A smaller gain would indicate that the system could only partially compensate for the effects of eye movements without extraretinal information.

Measuring the effect of varying planar motion speed on the magnitude of the FOE shift is also useful as a probe of the mechanisms underlying the illusion. Levi and Schor (1984) and Wallach and Becklen (1983) found that increasing the speed of surrounding motion beyond an upper threshold decreases the perceived induced motion speed, for inducing speeds up to 31.7°/sec. These studies used relatively small stimuli (12° and 13° diameters, respectively), which are thought to be optimal for stimulating cells in visual cortical area MT which have inhibitory surrounds (Murakami and Shimojo, 1996). Consistent with these findings, Tanaka *et al.* (1986) found a population of MT cells that showed decreased inhibition when the speed of the surround motion was increased.

For full-field (optokinetic) stimulation, induced motion shows increases in perceived velocity for increasing inducing stimulus velocity, for speeds up to 180°/sec (Post, 1986). This type of stimulation would almost certainly be optimal for engaging a global mechanism. Thus, if the illusion is due entirely to a global effect, we would expect to see a monotonically increasing FOE shift for increasing speeds of planar motion. On the other hand, if the illusion is due entirely to a more local effect, we would expect a decreasing FOE shift. For Experiment 2, the speed was chosen from 10 values ranging from 0 to 67.5°/sec, while the rate of expansion was held constant. As in Experiment 1, subjects were instructed to indicate their judgment of the FOE position, but in this case, only expansion stimuli were used (no rotations or spirals), so only horizontal shifts in FOE position were measured.

## Results

The results indicate that the induced motion speed increased with planar motion speed up to a point, after which the effect began to level off, and even to decline slightly for some observers. While there was substantial variability across observers, in no case was there an monotonically increasing relationship between increased planar speed and perceived shift. This result indicates that neither local nor global induced motion is likely to be the sole cause of the illusion. Three of the five observers showed peaks at 20°/sec. Duffy and Wurtz (1993) found a monotonically increasing relation between planar motion speed and FOE shift, but the maximum speed used in their experiment (24°/sec) was lower than that for ours (67.5°/sec), so our results are not inconsistent with their findings. Figure 6 displays the speed of expansion motion that was cancelled by planar motion at various speeds for each observer, and for the group. The results were calculated by measuring the perceived location of the FOE, and computing the actual speed of the expansion motion at that point.

For all observers, the gain of the illusion never approached 1.0. One interpretation of these results is that, if the illusion is related to visual stability, the underlying mechanism can only partially compensate for the effects of eye movements. However, as we will argue in the Discussion section, it may be possible to alter the stimulus configuration used in these experiments to elicit a gain closer to 1.0.

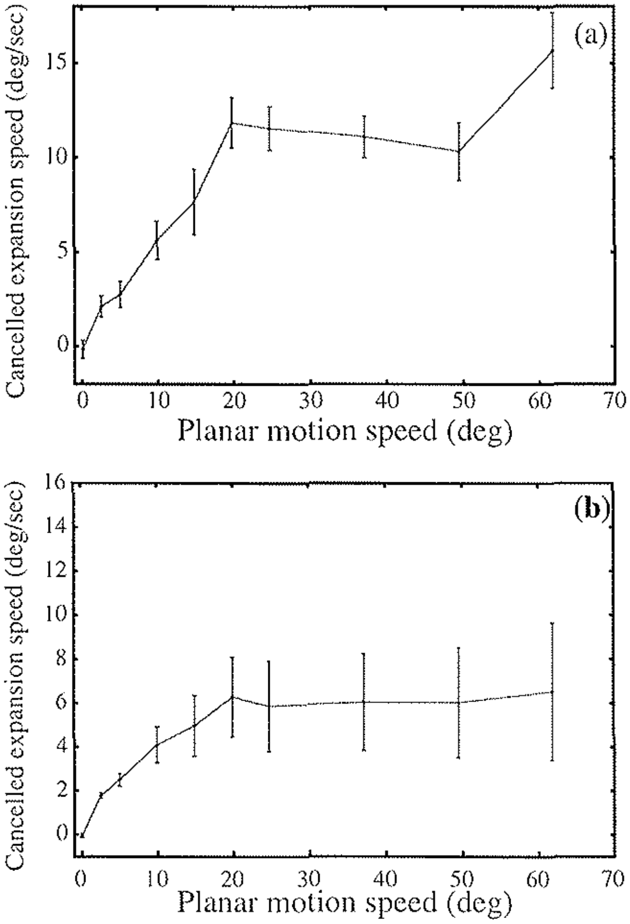

**Figure 6: Perceived FOE shift for varying speeds of planar motion for one observer (a) and for the (N=5) group (b). Vertical bars show standard error for (a), and show standard error of five observers from the means of means in (b).**

## Experiment 3

Experiment 2 raises an important question regarding the strength of this effect: if the visual system interprets large-field coherent motion as evidence of an eye movement, is a $60^0$ visual stimulus sufficient to engage the full force of this mechanism? The third experiment was designed in part to address this concern. We used a larger ($85^0$) monitor, and varied the area of the planar motion field, while holding constant the size of the expansion field (Figure 7). This is similar to the flow field generated by forward motion toward an object which is translating laterally, for which Royden and Hildreth (1996) reported an illusory displacement of the FOE. A model of cortical areas MT and MST suggested by Royden (1997) shows the same bias. In our experiment the "object", defined by the planar motion field, was transparent, while the object in Royden and

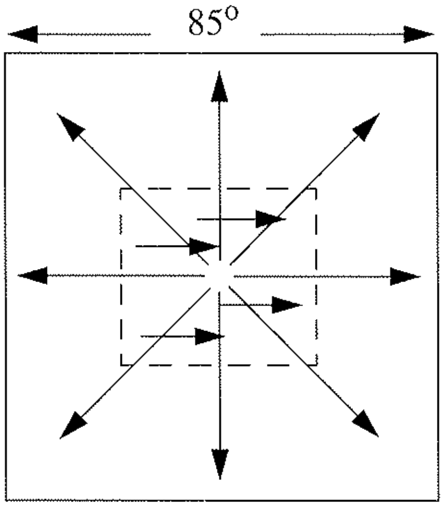

**Figure 7: Stimulus configuration for Experiment 3. The size of the planar motion field, indicated by the dotted line, varied across trials.**

Hildreth's (1996) Experiment 4 was opaque. Subjects once again indicated the perceived FOE based on the expanding motion.

## Results

There was a strong effect of the size of the planar motion field on the magnitude of the shift (Figure 8). This indicates that the low gain found in Experiment 2 may in part be due to the relatively small field of view. Furthermore, these results suggest that the visual system may integrate over the central visual field, using coherent motion as evidence for an eye movement. Alternatively, it could be that the increasing planar field size allows for more local interactions between the planar and expansion field, which in turn increases the amount of local motion contrast. We address these issues in the last two experiments.

## Experiment 4

In Experiment 3 observers perceived an increased FOE shift for increased planar field size. However, increasing the planar field size also increases the number of planar field dots. (See General Methods section.) The purpose of Experiment 4 was to determine if the increase in the perceived shift of the FOE was related to the number of dots in the planar field, rather than the size of the field. We used a full-screen planar field while varying the number of planar field dots between 50 and 500.

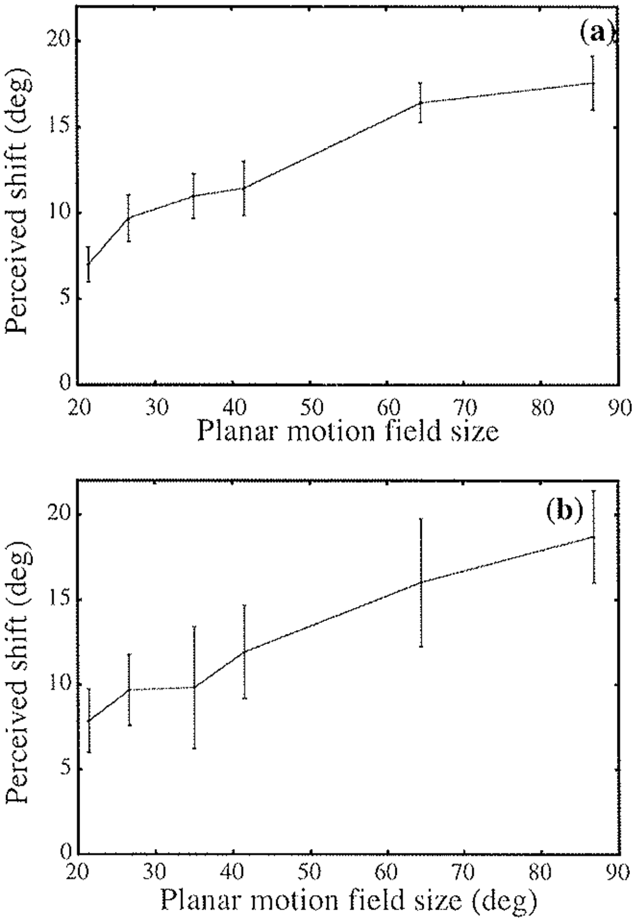

**Figure 8: Magnitude of the FOE shifts for varying planar field sizes for one observer (a) and the (N=8) group (b). Vertical bars show standard error for (a), and show standard error of five observers from the means of means in (b).**

## Results

There was little effect of increasing the number of planar field dots (Figure 9), suggesting that the increased shift in Experiment 3 was in fact due to the increasing *size* of the planar field.

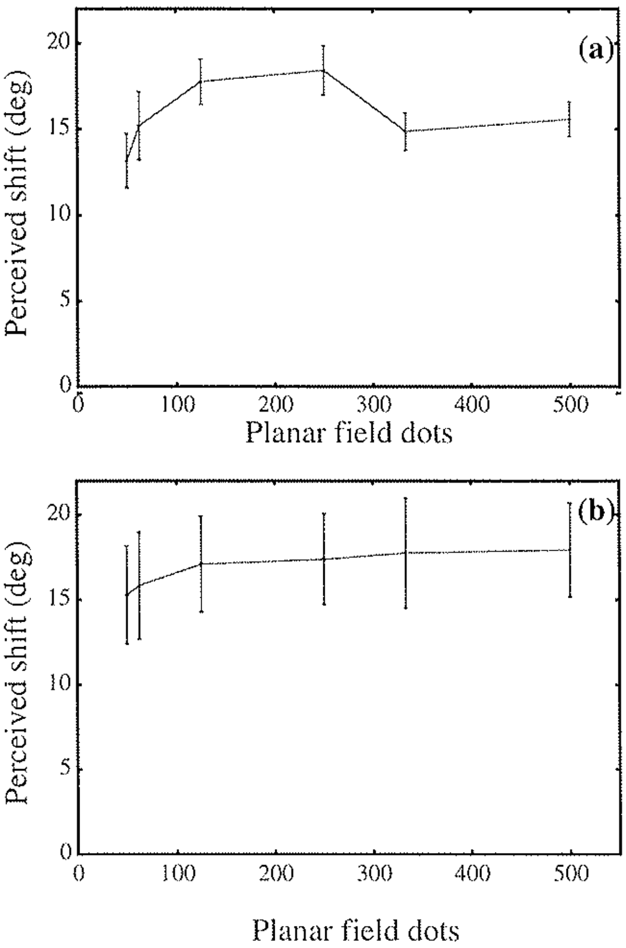

**Figure 9: Perceived FOE shift for increasing numbers of planar field dots for one observer (a) and for the (N=8) group (b). Vertical bars show standard error for (a), and show standard error of five observers from the means of means in (b).**

## Experiment 5

The results up to this point suggest that the illusory FOE shift is a manifestation of induced motion, and also of a mechanism that may serve to maintain visual stability during eye movements. To the extent that the illusion is a probe of underlying physiological mechanisms, it would be of interest to distinguish between a local center-surround mechanism (Murakami and Shimojo, 1993) and a global rotation-subtraction mechanism (Van den Berg, 1996). In order to explore this distinction, we repeated Experiment 3, with an expansion field covering $50^0$ of visual angle, rather than the $85^0$ used in the previous experiments. This resulted in a maximum expansion dot speed of $13^0$/sec. If the illusion is due only to a local center-surround effect, we would expect the magnitude of the perceived FOE shift to level off at or near the point where the planar field completely overlaps the expansion field (Murakami and Shimojo, 1996). However, if there is a more global mechanism which contributes to the illusion, we would expect the magnitude of

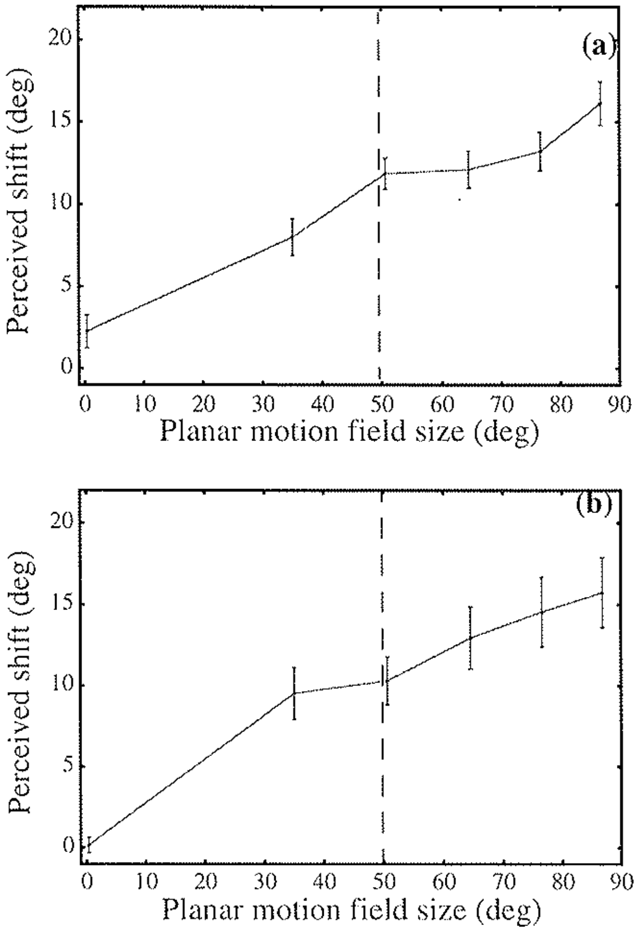

**Figure 10: Perceived FOE shift for increasing planar field size and expansion field size which is smaller than that of Experiment 3 for one subject (a), and for the (N=8) group (b). The dotted line indicates the point at which expansion and planar fields sizes are equal. Vertical bars show standard error for (a), and show standard error of five observers from the means of means in (b).**

the perceived FOE shift to continue to increase, even when the planar field is significantly larger than the expansion field.

## Results

The magnitude of the FOE shift continued to increase beyond the point where the two sets of stimuli overlap, as shown in Figure 10. This supports the hypothesis that there is a global component to the illusion which cannot be explained by a local center-surround mechanism, and which is likely to involve subtraction of planar motion, of the type which is typically generated during pursuit eye movements.

## Discussion

Our experiments show that large-field planar motion induces motion in the opposite direction, and that this induced motion is combined in an additive fashion with motion vectors in nearby parts of the visual field. The perceptual effect appears to be a *vector subtraction* of the planar motion. When the stimulus contains expanding motion, this results in a shift of the FOE in the direction of the planar motion. Experiment 1 showed that a shift in a direction perpendicular to that of the planar motion occurred when rotation was introduced into the stimulus. The magnitude of this shift is related to the speed of the planar motion, and the gain of the shift for different speeds of planar motion is dependent on the areal extent of the planar motion field. The effect of increasing planar field size continues beyond the point where the planar and expansion fields are equal in size, indicating that a global mechanism may underlie the illusory percept. The vector subtraction hypothesis, while closely related to induced motion, does not contradict Duffy and Wurtz's (1993) hypothesis concerning mechanisms of visual stability. In fact, the results of induced motion experiments are largely consistent with the idea of a global mechanism that maintains visual stability during self-motion (Post and Leibowitz, 1985).

Experiments 2 and 3 have direct consequences for the theory that this illusion is a consequence of a strategy for compensating for the visual effects of eye movements. It appears that the visual system integrates over the central visual field, and the amount of coherent motion present determines the gain of the vector subtraction. Experiment 3 showed an increasing relationship between the size of the planar motion field, and the magnitude of the shift, for planar field widths as small as $11^{\circ}$. It also appears that the correlation between increased planar speed and increased shift of the FOE saturates, on average, at approximately $20^{\circ}$/sec. This is close to the maximum speed reported ($30^{\circ}$/sec) for which humans can track objects smoothly using eye movements (Lisberger et al, 1987).

Center-surround induced motion is usually attributed physiologically to cells in visual cortical area MT which have inhibitory surrounds. These cells exhibit response selectivity for a particular motion direction in their receptive field centers, but the responses are suppressed when the preferred motion direction is presented outside the receptive field center (Allman *et al.*, 1985a). The receptive field centers average $2.5^{\circ}$ in diameter (Albright and Desimone, 1987), with surrounds that with surrounds that may measure 50-100 times the size of the center (Allman *et al.*, 1985b). The center-surround receptive field organization makes these cells well-suited to detect motion contrast, and motion contrast almost certainly plays a role in generating the effects described in this paper.

MT cells are also well-suited to detect global context, based on the long-range interactions observed in their inhibitory surrounds . This long-range inhibition could result from descending connections from higher cortical areas, which have been shown to influence receptive field surrounds (Marrocco *et al.*, 1982). Descending cortical input has been demonstrated to be useful in computational models of motion perception (Chey *et al.*, 1997). Such a descending pathway would provide a neural substrate for the global effects observed in this paper, particularly in Experiment 5, and would be quite useful for eliminating the effects of eye movements at a local level.

There is substantial neurophysiological support for the idea of high-level vector subtraction. Cells in MSTd respond preferentially to expansion stimuli in a specific location of the visual field (Duffy and Wurtz, 1995), and are selective for speed (Orban et. al., 1995). Thier and Erickson

(1991) found that cells in this area compensate for the results of eye rotation, concluding, "such signals are not uniformly transmitted through the visual system, but are selectively removed from the 'motion pathway' at the level of MST." (p.612) Recently, Duffy and Wurtz (1994) and Bradley *et. al.* (1996) have shown that some expansion-selective cells in MST shift their preferred locus for the FOE in order to compensate for eye movements. Bradley *et al.* (1996) also found that rotation-selective cells shift their preferred center of rotation in a direction orthogonal to that of eye movements. These results provide support for rotation-subtraction, but they only address the extraretinal contribution to this mechanism, not the visual contribution.

Combining extraretinal and visual information may be necessary to compensate for the less-than-unity gain of the extraretinal signal (Honda, 1990), which has been estimated psychophysically to be approximately 0.8 (Hansen, 1979; Mack and Herman, 1978). Conversely, the low gain of the illusory FOE shift found in Experiment 2 may be necessary to prevent overestimation of the rate of eye rotation (Wertheim, 1987). A similar additive mechanism has been suggested (Wertheim, 1994) to account for the cancellation of perceived background motion during eye movements (the Filehne illusion), and the gain of this mechanism appears to be highly dependent on the stimulus size and speed. An alternative model by Van den Berg and Beintema (1997) suggests that retinal and extraretinal information combine multiplicatively.

Komatsu and Wurtz (1988) found that smooth pursuit cells (i.e. those cells activated by slow eye movement in a particular direction) in MST could be driven equally well by full-field visual stimulation, and that the preferred direction of stimulus motion was opposite that of the preferred eye movement direction in the majority of the cells tested. Similarly, Wurtz *et al.* (1990) describe an MST cell that responded to stimuli that have the perceptual effect of inducing motion in the cell's preferred direction of smooth pursuit. These results suggest that MST cells combine extraretinal and retinal eye movement information additively. Consistent with our experiments 3 and 4, Komatsu and Wurtz (1988) also found that the size of the planar motion field strongly affected the response of the cells, and that the number of dots used in the stimulus was not a factor in the cell response. Furthermore, their cells showed a saturation in response for pursuit speeds greater than 20°/sec, as did our observers in Experiment 3. Thus, it may be that MST cells combine extraretinal and visual information at an early stage, and that these cells initiate the vector subtraction which drives the illusory FOE shift.

It remains to be seen, then, if the gain of the FOE shift can be significantly improved by means other than increasing the field of view. One possibility is that the addition of depth information would yield a more realistic stimulus for the global mechanism. During self-motion, more distant objects appear to move more slowly relative to the observer than do nearer objects. As a result, the addition of a constant vector caused by eye rotations is more easily detected at greater depths beyond the fixation point. Intuitively, one can imagine that points near the horizon have no relative motion caused by self-motion, hence any perceived motion at far depths is due solely to eye rotation. There is some evidence that the visual system exploits this property, interpreting the motion of distant points as due to eye movements. Van den Berg and Brenner (1994a,b) showed that decreasing the available range of depth information negatively affects subjects' ability to decompose flow fields consisting of translation and rotation. Van den Berg (1992) demonstrated that the motion of points at the horizon was necessary for accurate heading perception. Similarly, Heckmann and Howard (1991) and Previc and Donnelly (1993) have found that some types of induced motion perception are strongly increased by motion beyond the plane of fixation. Telford *et al.* (1992) showed that kinetic depth cues indicating motion beyond the fixation point, in the central visual field, were most effective in inducing vection. These results strongly suggest that depth information, specifically motion beyond the fixation point, is used by the visual system to calculate self-motion. If this is the case, it follows that the addition of depth information would facilitate the perceived shift of the FOE in the Duffy and Wurtz paradigm. We are currently implementing experiments to test this hypothesis.

## References

Allman, J., Miezin, F., & McGuinness, E. (1985a). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience*, *8*, 407-430.

Allman, J., Miezin, F., & McGuinness, E. (1985b). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception*, *14*, 105-126.

Bradley, D. C., Maxwell, M., Andersen, R. A., Banks, M. S., & Shenoy, K. V. (1996). Mechanisms of heading perception in primate visual cortex. *Science*, *273*, 1544-1547.

Cameron, S., Grossberg, S., and Guenther, F. (1997) A self-organizing neural network architecture for navigation using optic flow. *Neural Computation*, in press.

Cavanagh, P. and Favreau, O. (1980) Motion aftereffect: a global mechanism for the perception of rotation. *Perception, 9,* 175-182.

Chey, J., Grossberg, S., and Mingolla, E. (1997) Neural dynamics of motion grouping: from aperture ambiguity to object speed and direction. *Journal of the Optical Society of America A,* in press.

Duffy, C. J. & Wurtz, R. H. (1993). An illusory transformation of optic flow fields. *Vision Research*, *33*, 1481-1490.

Duffy, C. J. & Wurtz, R. H. (1994). Optic flow responses of MST neurons during pursuit eye movements. *Society for Neuroscience*, *20*, 1279.

Duffy, C. J. & Wurtz, R. H. (1995). Response of monkey MST neurons to optic flow stimuli with shifted centers of motion. *Journal of Neuroscience*, *15*, 5192-5208.

Dunker, D. (1929). Induced motion. In Ellis, W. D. (Ed.), *A sourcebook of Gestalt psychology*, (pp. 161-172). London: Routledge and Kegan Paul, Ltd.

Gibson, J. J. (1950). *The perception of the visual world.* Boston, Mass.: Houghton Mifflin.

Gibson, J.J. (1966) *The senses considered as perceptual systems.* Boston, Mass.: Houghton Mifflin.

Hansen, R. (1979) Spatial localization during pursuit eye movements. *Vision Research, 19*, 1213-1221.

Heckmann, T. & Howard, I. (1991). Induced motion: Isolation and dissociation of egocentric and vection-entrained components. *Perception*, *20*, 285-305.

Hershenson, M. (1984) Phantom spiral aftereffect: Evidence for global mechanisms in perception. *Bulletin of the Psychonomic Society,* 22, 535-537.

Honda, H. (1990). The extraretinal signal from the pursuit-eye-movement system: Its role in the perceptual and the egocentric localization systems. *Perception and Psychophysics*, *48*, 509-515.

Komatsu, H. & Wurtz, R. H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. III. Interaction with full field visual stimulation. *Journal of Neurophysiology*, *60*, 621-644.

Levi, D. & Schor, C. (1984) Spatial and velocity tuning of processes underlying induced motion. *Vision Research*, *24*, 1189-1196.

Lisberger, S. G., Morris, E., & Tychsen, L. (1987). Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annual Reviews of Neuroscience*, *10*, 97-129.

Mack, A. & Herman, E. (1978). The loss of position constancy during pursuit eye movements. *Vision Research*, *18*, 55-62.

Marrocco, R. T., McClurkin, J.W., and Young, R. A. (1982) Modulation of lateral geniculate nucleus cell responsiveness by visual activation of the corticogeniculate pathway. *Journal of Neuroscience, 2,* 256-263.

Meese, T., Smith, V., & Harris, G. (1995). Induced motion may account for the illusory transformation of optic flow fields found by Duffy and Wurtz. *Vision Research*, *35*, 981-984.

Murakami, I. & Shimojo, S. (1993). Motion capture changes to induced motion at higher luminance contrasts, smaller eccentricities, and larger inducer sizes. *Vision Research, 33*, 2091-2107.

Murakami, I. & Shimojo, S. (1996). Assimilation-type and contrast-type bias of motion induced by the surround in a random display: evidence for center-surround antagonism. *Vision Research*, *36*, 3629-3639.

Orban, G., Lagae, L., Raiguel, S., Xiao, D., & Maes, H. (1995). The speed tuning of medial superior temporal (MST) cell responses to optic-flow components. *Perception, 24*, 269-285.

Pack, C. & Mingolla, E. (1997). Visual stability and induced motion in an optic flow illusion. *Investigative Ophthalmology and Visual Science*, *38*, 397.

Post, R. (1986). Induced motion considered as a visually induced oculogyral illusion. *Perception*, *15*, 131-138.

Post, R. & Chaderjian, M. (1988). The sum of induced and real motion is not a straight path. *Perception and Psychophysics*, *43*, 121-124.

Post, R. & Leibowitz, H. (1985). A revised analysis of the role of efference in motion perception. *Perception*, *14*, 631-643.

Previc, F. & Donnelly, M. (1993). The effects of visual depth and eccentricity on manual bias, induced motion, and vection. *Perception*, *22*, 929-945.

Reinhardt-Rutland, A. (1988) Induced movement in the visual modality: An overview. *Psychological Bulletin*, *103*, 57-71.

Royden, C., Crowell, J., & Banks, M. (1994). Estimating heading during eye movements. *Vision Research*, *34*, 3197-3214.

Royden, C. & Hildreth, E. (1996). Human heading judgments in the presence of moving objects. *Perception and Psychophysics*, *58*, 836-856.

Royden, C. (1997) A model using motion differences to compute curved path observer motion accounts for biases in perceived heading in the presence of moving objects. *Investigative Ophthalmology and Visual Science, 38,* 2223.

Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., & Iwai, E. (1986) Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *Journal of Neuroscience, 6*, 134-144.

Telford, L., Spratley, J., & Frost, B. (1992). Linear vection in the central visual field facilitated by kinetic depth cues. *Perception*, *21*, 337-349.

Telford, L. & Frost, B. (1993). Factors affecting the onset and magnitude of linear vection. *Perception and Psychophysics*, *53*, 682-690.

Thier, P. & Erickson, R. (1991). A neuronal correlate of spatial stability during periods of self-induced visual motion. *Experimental Brain Research*, *86*, 608-616.

Van den Berg, A. (1992). Robustness of perception of heading from optic flow. *Vision Research*, *32*, 1285-1296.

Van den Berg, A. & Brenner, E. (1994a). Why two eyes are better than one for judgements of heading. *Nature*, *371*, 700-702.

Van den Berg, A. & Brenner, E. (1994b). Humans combine the optic flow with static depth cues for robust perception of heading. *Vision Research*, *34*, 2153-2167.

Van den Berg, A. (1996). Judgements of heading. *Vision Research*, *36*, 2337-2350.

Van den Berg, A. & Beintema, J. (1997) Motion templates with eye velocity gain fields for transformation of retinal to head centric flow. *Neuroreport, 8,* 835-840.

Wallach, H. & Becklen, R. (1983) An effect of speed on induced motion. *Perception and Psychophysics, 34,* 237-242.

Wertheim, A. (1987). Retinal and extraretinal information in movement perception: How to invert the Filehne illusion. *Perception*, *16*, 299-308.

Wertheim, A. (1994). Motion perception during self-motion: The direct versus inferential controversy revisited. *Behavioral and Brain Sciences*, *17*, 293-355.

Wurtz, R., Komatsu, H., Dürsteler, M., & Yamasaki, D. (1990) Motion to movement: Cerebral cortical visual processing for pursuit eye movements. In: Edelman, G. and Cowen, W.M. (Eds.), *Signal and Sense: Local and global order in perceptual maps,* (pp. 233-260). New York: John Wiley.

*Acknowledgements* - We thank Dr. Constance Royden for helpful comments on an earlier version of this manuscript. Christopher Pack was supported by a grant from the Office of Naval Research (ONR N00014-94-1-0597, ONR N00014-95-1-0409, ONR N00014-95-1-0657). Ennio Mingolla was supported by Office of Naval Research grants ONR N00014-94-1-0597, ONR 00014-95-1-0409. A preliminary report has appeared previously (Pack and Mingolla, 1997).

## Appendix

The compound stimuli used in Experiment 1 can be decomposed for each dot into linear combinations of rotation and expansion motion, according to

$$V(x, y) = \alpha R(x, y) + (1 - \alpha)E(x, y)$$

where $\alpha$ indicates the proportion of rotation. For all experiments, the displacement of a point $(x,y)$ was defined in the case of expansion by

$$E(x, y) = \varepsilon\sqrt{(x - x_0)^2 + (y - y_0)^2}$$

where $\varepsilon$ was set to 0.008 pixels for each 1280x1040 pixel screen, refreshing at 66Hz. The values of $x_0$ and $y_0$ represented the offset of the FOE, and were constrained according to:

$$|x_0| < 128,\ |y_0| < 104$$

so that the actual shift of the FOE was less than 10% of the screen width in each direction. Similarly, the displacement for rotation was defined for each dot by

$$R(x, y) = \varepsilon \operatorname{atan}\left(\frac{y - y_0}{x - x_0}\right)$$

The value of $\varepsilon$ was set to 0.008 for clockwise rotations, and -0.008 for counter-clockwise rotations. In all cases, dots that moved off the screen were reassigned a random position in the next frame.