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Measurement of rate of expansion in the perception of radial motion

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Abstract

Optic flow generated by rigid surface patches can be decomposed into a small number of elementary motion types. In these experiments, we show that the human visual system can evaluate expansion, one of these motion types, metrically. Moreover, we show that the discrimination of rates of expansion are spatially local. Because the estimation of the focus of expansion is somewhat imprecise, this locality sometimes produces predictable errors in the estimation of rate of expansion. One can make predictions like this with a model adapted from one previously developed for angular-velocity discrimination.
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1. Introduction

Ego-motion and motion in the world generate complex optical-flow fields on the retina. These fields can provide information on navigation, self-orientation, and the three-dimensional world (Gibson, 1950; Koenderink & van Doorn, 1976). To extract these types of information, the system must first quantify the flow field and extract its parameters. One can describe the optical-flow field information generated by rigid surface patches by four different motion components: translation, rotation, expansion, and deformation (Koenderink & van Doorn, 1976). Translation, rotation, and expansion are the motion components that have been the most vigorously researched (McKee, Silverman, & Nakayama, 1986; Regan & Vincent, 1995; Regan, 2000). Theoretically, it is possible to measure the parameters of each of these components from complex flow fields in a Bayesian manner (Yuille & Grzywacz, 1998). Among these parameters are the rates of motion, such as the speed of translation, the angular velocity, and the rate of expansion. Other essential parameters include the center of rotation and the focus of expansion.

The brain seems to be able to measure many of the parameters of optic flows metrically. In other words, it seems to measure or discriminate these parameters with high accuracy. For instance, it has been shown that the human brain can metrically discriminate differences in both direction (De Bruyn & Orban, 1988; Watamaniuk, Sekuler, & Williams, 1989) and speed (Bravo & Watamaniuk, 1995; Johnston, Benton, & Morgan, 1999; McKee, 1981; Welch & Bowne, 1990) of translations. Moreover, the visual system can metrically discriminate between angular velocities of rotational motions (Barraza & Grzywacz, 2002a, 2002b, 2003a, 2003b). Such

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metric motion sensitivity is consistent with results that indicate that there are specific mechanisms that analyze complex motions (Freeman & Harris, 1992; Morrone, Burr, & Vaina, 1995; Regan & Beverley, 1985). Cells sensitive to complex flow patterns exist in middle temporal and dorsal parietal sides of the middle superior temporal sulcus (MST—Duffy & Wurtz, 1991a; Graziano, Anderson, & Snowden, 1994; Tanaka & Satio, 1989).

However, the brain does not do a perfect job in estimating motion parameters. For instance, the visual system overestimates angular velocities for rotational motions when the centers of rotation are not on the fixation point (Barraza & Grzywacz, 2002b, 2003a). Interestingly, this overestimation of angular velocity is reduced when the region around the fixation point is masked. Experimental analysis of this phenomenon shows that errors made in estimating the center of rotation cause the overestimation.[1] Because the brain makes local estimates of angular velocity, they are sensitive to errors of position determination. A rotational-discrimination model that fits the data well computes the angular velocity in small patches and then integrates it to approximate its global value (Barraza & Grzywacz, 2002b).

In this paper, we test whether the brain estimates the parameters of expansion metrically and whether this estimation uses similar mechanisms as rotation. We thought that such similarity might be possible. This is because for moving planar-surface patches in the world, pure-expansion and pure-rotation components of optic flows only differ in that expansion velocities are perpendicular to rotation velocities (Footnote 1). This is not true for arbitrary surfaces. However, if the brain were to estimate optic-flow parameters locally, then, to a good approximation, each estimate would be for a small planar patch of a moving surface. We previously showed that the estimation of rotation parameters is local (Barraza & Grzywacz, 2003a). Consequently, if the same locality held for expansion, the brain might use similar strategies to deal with expansion and rotation. The following experiments are thus analogous to rotation experiments previously carried out by Barraza and Grzywacz (2002a, 2002b, 2003a, 2003b). Here, we focus on the rate of expansion and in particular, ask whether its estimation is local or global. Finally, we measure the stimulus duration needed to make a metric estimation of the rate of expansion.

2. Materials and method

2.1. General methods

All stimuli were created and displayed with Matlab PsychoToolbox (Brainard, 1997; Pelli, 1997). The background luminance for the stimuli was 19.9 cd m^{-2} and the stimuli had a luminance of 3.8 cd m^{-2}. We displayed the stimuli with a 48.3-cm CRT monitor, which had high-resolution (1024 × 768 pixels) and a frame rate of 75 Hz. The monitor was situated 50 cm away from the subject. Subjects for these experiments were one of the authors and two experienced-psychophysics subjects naïve to the purposes of the testing. They saw the stimuli in block intervals consisting of 120 trials per block. The duration of each trial was 275 ms unless otherwise specified. In four of the five experiments in this paper, subjects performed the tasks using the 2-AFC paradigm to judge which stimulus had the larger rate of expansion. In the different (fourth) experiment, subjects used a ruler to estimate the position of the focus of expansion. In the 2-AFC tasks, the reference and test expansion stimuli were separated by 100 ms.

There were two stimulus types in these experiments, expanding disks and random-dot fields. The former consisted of homogeneous-luminance disks that expanded with constant rates of expansion from randomly starting radii of 2°–3°. In turn, the latter were in a 13°-radius circular area and contained 250 circular dots that had 11 arcminutes radii. The dot density was homogeneous across the field. Dots had three-frame lifetimes to prevent subjects from tracking them and to facilitate fixation. In the first frame, each dot was randomly assigned a lifetime phase between the first and third frames, so that the dots would not be re-plotted all at the same time, thereby producing flicker.

3. Experimental design

We designed the stimuli in the first experiment to test whether humans estimate the rate of expansion metrically. The stimuli were disks of expanding radii, with the reference stimuli having random rates of expansion of $\rho = 1.5$–1.65 s^{-1} (see Footnote 1 for the definition of ρ). Test stimuli had randomly selected starting radii that were 0.4–1.6 times that of the reference and randomly selected rates of expansion that were 0.7–1.3 times that of the reference. The test and reference stimuli were randomly presented either first or second in each trial. Subjects were instructed to fixate at the focus of expansion (marked with a "+"), and to tell whether the first or second disk was expanding faster. Different radii were used so that test stimuli could have larger expanding speeds ($\dot{\theta}$, Footnote 1) while having smaller rates of expansion ($\rho = \dot{\theta}/\theta$), or vice versa. This allowed us to test whether

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[1] In a rigid rotation, the relationship between the angular velocity ($\vec{\Omega}$), the velocity of a point ($\vec{v}$), and its position relative to the center of rotation ($\vec{r}$) is $\vec{v} = \vec{\Omega} \times \vec{r}$. In turn, the corresponding definition for rate of expansion (ρ) in terms of these variables is $\vec{v} = \rho\vec{r}$. Taking absolute values gives $\rho = \dot{\theta}/\theta$, where $\theta = |\vec{r}|$ is the visual angle from the focus of expansion.

the brain measured rate of expansion or subjects performed the expansion-discrimination tasks based on local-speed signals.

The goal of the second experiment was to test whether humans measure rate of expansion locally or globally. The reference stimuli consisted of an expanding random-dot field, whose dots all had the same speed. Therefore, the dots closer to the center had a larger rate of expansion than the dots farther away, which in effect, made the expansion nonrigid (Fig. 1). Our goal in generating nonrigidity was to test whether the brain computed different rates of expansion for different parts of the display or a single global value. For this purpose, a 0.8°-thick ring to which the subject was to pay attention was demarcated within the nonrigid stimulus. The center radius (halfway between the outer radius and inner radius) of the ring was randomly set to be 3°–8° from the focus of expansion (also the fixation point). The test stimuli were random-dot fields that were rigidly expanding (constant ρ). These fields were in a circular area of 5° when the middles of the rings were 7° or 8° from the focus of expansion. In turn, when the rings were 3°–5° from the focus of expansion, the test fields where limited to appearing in annuli. However, the test annuli had inner and outer radii of 10° and 12° respectively. The distances from the fixation point to any of the dots in the reference stimuli were not the same as any of the dots in the test stimulus, so subjects could not perform the task by direct speed matching. The test stimuli had rates of expansion that were randomly 0.7–1.3 of the mean rate of expansion in the demarcated area of the reference stimuli. Subjects had to tell whether the rigidly expanding stimulus or the demarcated region of the nonrigid stimuli was expanding faster.

The third experiment tested whether humans overestimate the rate of expansion due to the locality of the measurement and to miscalculations of the focus of expansion. Stimuli used rigidly expanding random-dot fields, with the reference stimuli having random expansion rates of 3–3.3 s^{-1}. In the first part of this experiment, the test stimuli were random-dot fields whose foci of expansion were 0°–5° away from the fixation point at 45° diagonals in one of four quadrants (down-left, down-right, top-left, and top-right). In turn, the reference stimuli had foci of expansion that coincided with the fixation point and the geometric center of the stimuli. This protocol was repeated while masking the center of the stimulus with a circular aperture of background luminance. In the second part of the experiment, the fixation points of the test stimuli were away from the center, which coincided with the focus of expansion. Finally, both the focus of expansion and the fixation point were deviated together from the center of the stimulus, such that they coincided.

In the fourth experiment, we measured how much error humans make when estimating the focus of expansion. A random-dot field was created with a focus of expansion 0°–10° away from the fixation point, which was at the center of the stimulus (Fig. 2). After the stimulus presentation, a ruler appeared for 250 ms, having hash marks at 0°, 2°, 4°, 6°, 8°, and 10°. Subjects had to report using the ruler where they perceived the focus of expansion by pressing a 0, 1, 2, 3, 4, or 5 on the keyboard respectively.

Finally, the fifth experiment probed the time course of the measurement of the rate of expansion. The expanding stimuli appeared for random durations between 115 and 435 ms. Stimuli were expanding disks ($\rho = 1.5$–$1.65\ s^{-1}$) as in the first experiment, but the
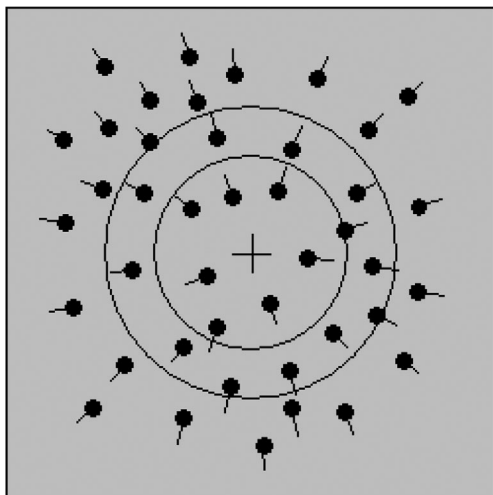

Fig. 1. Schematic of a random-dot pattern undergoing a nonrigid expansion, with a demarcated ring to which the subject is asked to attend. The lengths of the line segments are proportional to the speeds of the dots. Their directions of motion are indicated by the directions of the segments from the dots to the ends.
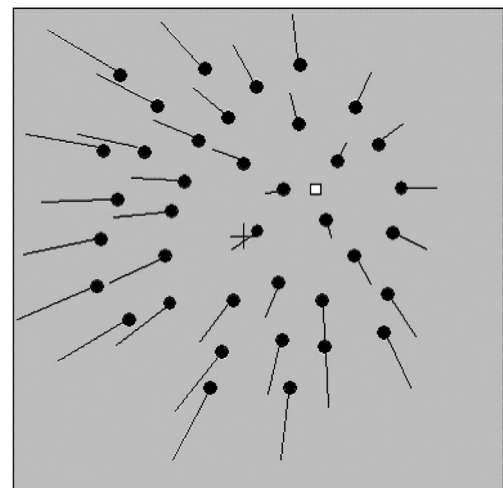

Fig. 2. Schematic of a random-dot pattern undergoing expansion, with the focus of expansion (white square) deviated from the center, which coincides with the fixation point (+).

difference between the intensities of the background and the disks fell with distance from the focus of expansion in a Gaussian manner (the standard deviation was 1/3 of the radius of the disk, i.e., the standard deviation increased during expansion). The luminance was 3.8 cd m^{-2} at the disk center as in other stimuli and then increased towards the background value (19.9 cd m^{-2}). The Gaussian luminance gradient was used, because otherwise, during trials with short durations, both the starting and ending sizes of the disk were perceivable at the same time, negating the experiment. There was still a perceivable border for the disk with the Gaussian window. However, this method was effective in preventing subjects from perceiving the size of the starting disk simultaneously with that of the ending disk.

4. Results

Do humans estimate the rate of expansion metrically? The main difficulty in answering this question is that if a person has to tell which of two expansions is faster, then the reply could use local-speed signals. This is because two points equidistant to the focus of expansion in these motions would have different speeds. To control for this, one must make sure that such equidistant points are not presented. The first experiment performed this control (Section 2) and the results appear in Fig. 3.

The data in Fig. 3 indicate that humans can discriminate rates of expansion accurately. These data are not statistically significantly different from the veridical rate of expansion indicated by the dotted line. In contrast, they are different from the prediction made assuming the use of local speeds (solid line). Nevertheless, there is an apparent slight bias to pick large disks as having larger rates of expansion than small disks (experimental rates of expansion fall slightly with the ratio of radii in Fig. 3). Similar biases in rotation have been found by Werkhoven and Koenderink (1993) and Barraza and Grzywacz (2002a, 2002b). The latter authors provided evidence that local speeds were biasing estimations, that is, making the data approach the solid line slightly. A similar local-speed effect may exist for expansion.

Estimation of rate of expansion could be either local or global. If the estimation is global, then a single rate would apply for the entire display. Otherwise, the brain could assign individual rates of expansion to small parts of the image. One way to test this is to create possibly nonrigid expansion displays, such as illustrated in Fig. 1. When we generated these displays they looked nonrigid and prompted us to ask whether their individual portions were judged based on local speed or local rate of expansion. The second experiment answered this question (Fig. 4).

Fig. 4 shows that humans estimate the rate of expansion locally. Subjects could accurately match the rate of
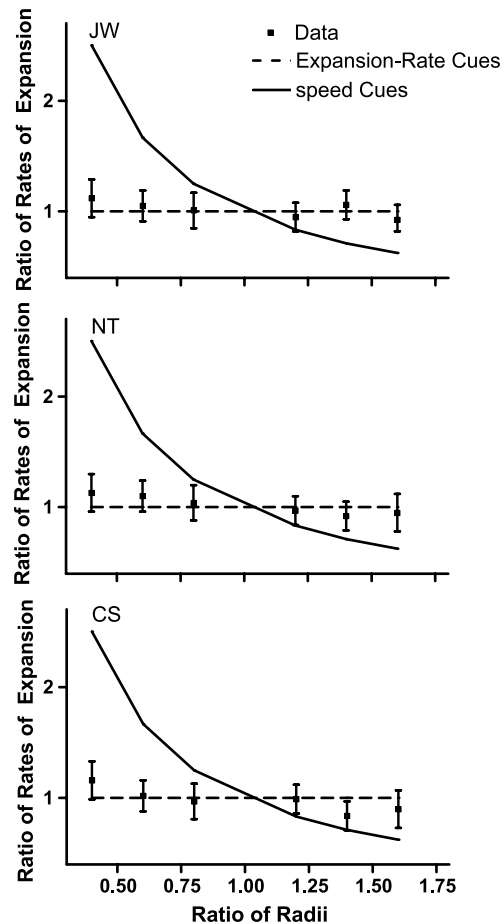

Fig. 3. Ratio between rates of expansion of matched-test and reference stimuli as a function of the ratio between their radii. To compute this ratio, we first found the test that appeared to be expanding as fast as the reference. Then, we computed the ratio between their veridical rates of expansion. Because the radii of reference and test were different, there was no a priori reason for them to be matched at the same veridical rates of expansion. In other words, there was no a priori reason for this ratio to be 1. However, as the data show, the ratio is close to 1, indicating that humans measure rate of expansion accurately. To emphasize this point further, perceptual data appear together with two different theoretical plots, namely, predictions based on local-speed cues (solid line) and on metrical measurements of rate of expansion (dashed line). All data in this paper (Figs. 3–8) are for three subjects (graphs stacked vertically). Data points in this and all other figures represent means and standard errors for 40 trials each and were computed using a probit analysis for the 2-AFC tasks (Foster & Bishof, 1991). In other words, we used probit to find when the test matched the reference along with error estimates.

expansion in the demarcated regions of the nonrigid display to that of the rigidly expanding dot field. In other words, the rate of expansion obeys $\vec{v} = \rho\vec{r}$ (Footnote 1) everywhere, even in nonrigid displays. Subjects did not perform this task by comparing $|\vec{v}|$ locally, since the ranges of $|\vec{r}|$ were different for the test and reference stimuli. The locality of the estimation of ρ allows the perception of nonrigid expansions. If subjects were not estimating ρ locally, but were performing some global
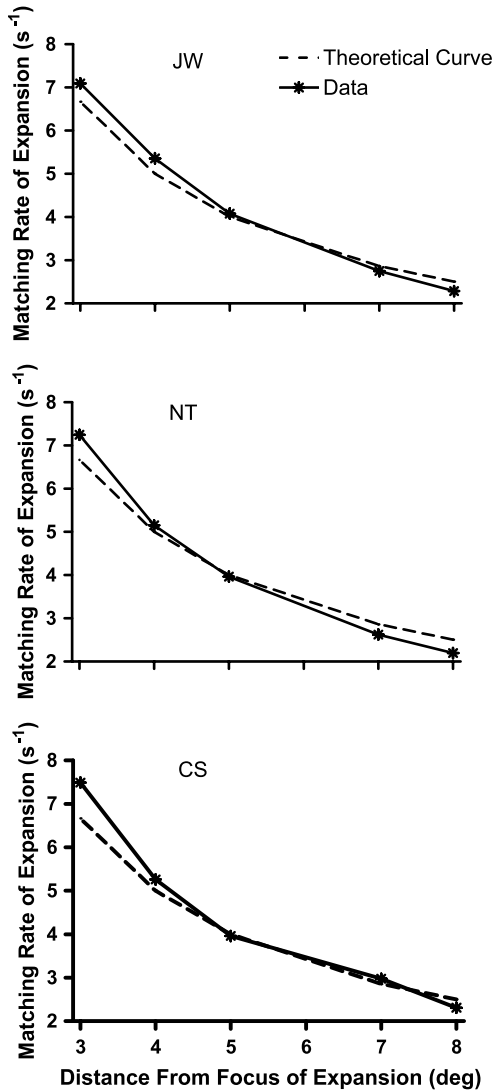
Fig. 4. Matching rate of expansion as a function of the distance from the fixation point. See caption of Fig. 3 for an explanation of how we obtain matching rates of expansion. Subjects did not perform this task by comparing local speeds, as distances from the focus of expansion were different in the test and reference stimuli (Methods). The theoretical curve is for local veridical estimation of the rate of expansion. The similarity of the theoretical and experimental curves show that humans estimate the rate of expansion locally.

between local speeds and these distances ($\rho = |\vec{v}|/|\vec{r}|$). Similar errors were noted for rotation, and the mean or median angular velocity was shown to overestimate its true global value (Barraza & Grzywacz, 2002b, 2003a). Because speeds (but not direction) are identical for pure rigid rotations and expansions, we predicted that errors in the localization of the focus of expansion would also cause overestimations of the rate of expansion. The third experiment used the paradigm in Fig. 2 to test this prediction and the results appear in Fig. 5.

The data in Fig. 5 confirm the sensitivity of rate of expansion measurement on estimated focus of expansion. They show that subjects overestimate the rate of expansion for stimuli that have an off fixation-point expansion. As in the case of rotation (Barraza &
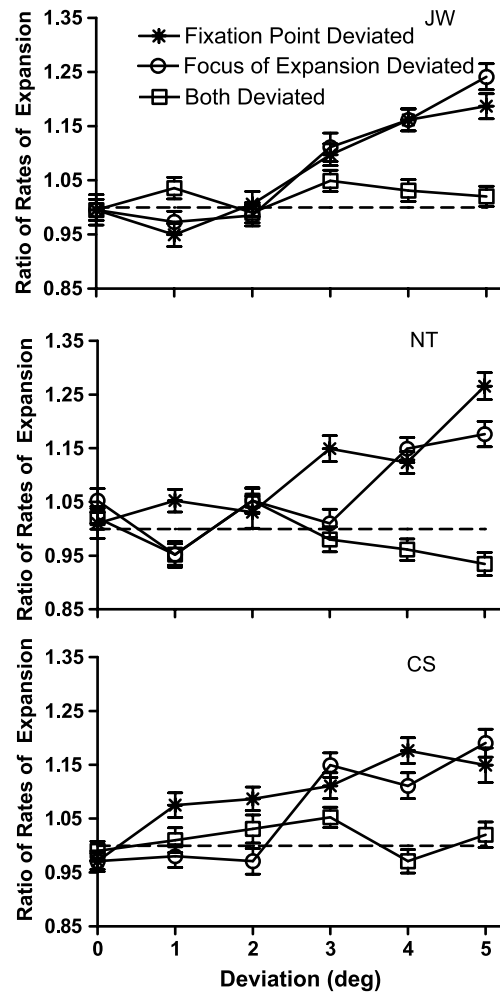

Fig. 5. Ratio between rates of expansion of matched-test and reference stimuli as a function of the separation of the focus of expansion and of the fixation point from the center of the display. See caption of Fig. 3 for an explanation of this ratio of rates of expansion. Circles are for focus-of-expansion-only deviations, asterisks are for fixation-point-only deviations, and squares are for both being deviated in the same direction by the same amount. Overestimation of the rate of expansion depends only on the separation between the fixation point and the focus of expansion.

estimate instead, then they might have perceived rigid expansions for displays as those in Fig. 1. Moreover, they might have chosen the same rate of expansion for all trials in our experiment, since its mean global rate of expansion was always the same. Hence, if subjects used a global mean rate of expansion, then Fig. 4 would follow a straight horizontal line.

Because rate-of-expansion estimation is local, it is sensitive to localization of the focus of expansion. If its position is wrong, then so are the distances from it to the expanding points. This induces errors in the estimation of rates of expansion, as they are the ratio

Grzywacz, 2002b, 2003a), this overestimation is lessened when an area around the fixation point is masked (Fig. 6). Moreover, as the size of the mask increases, the overestimation falls further. An explanation for this is that the brain may erroneously judge the focus of expansion to be close to the fixation point (Barraza & Grzywacz, 2002b, 2003a). Such a focus would provide more visual acuity. However, the speed signals near this wrongly estimated focus of expansion are not zero as they should be. Consequently, they erroneously represent high rates of expansion (finite speeds with very low distances to the estimated focus of expansion). If thus, one were to mask off these speed signals near the fixation point, then their contribution to the overestimation would disappear.

This explanation works fine, but it requires a systematic mis-location of the focus of expansion towards the fixation point. This turns out to be true for the center of rotation (Barraza & Grzywacz, 2002b, 2003a) and Fig. 7 shows that it is also true for the rate of expansion.

The data from the fourth experiment indicate that subjects underestimate the deviation of the focus of expansion from the fixation point (Fig. 7). In other words, the perceived focus of expansion was closer to the fixation point than to the true focus. Subjects almost never responded that the deviation was 8° or 10°, although this accounted for a third of the trials. Most of the time, subjects judged the deviation to be within only 2° of the focus of expansion. Systematic errors were more common for large deviations (>3°) than for short ones (<1°, Fig. 8). However, one observes large variation of responses for all deviations (Fig. 8). The
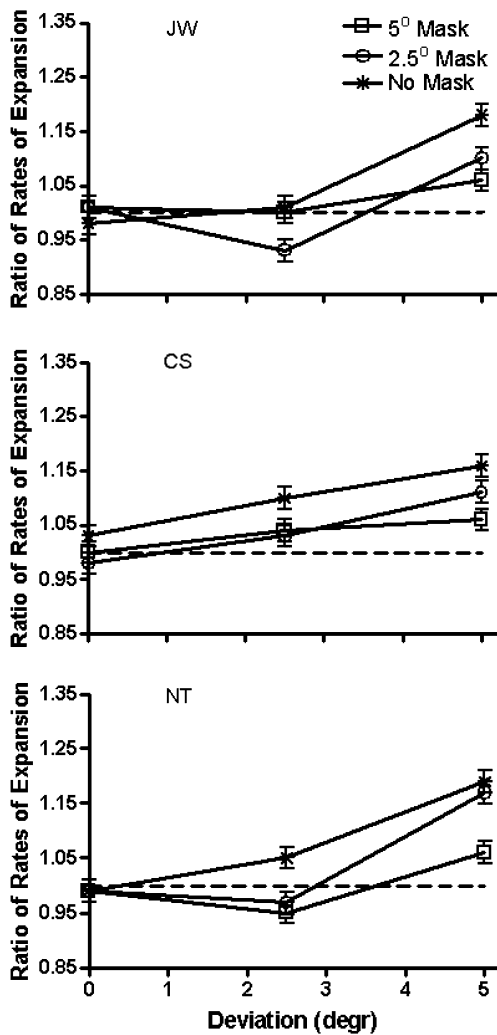

Fig. 6. Effect of masking around the fixation point on the overestimation observed in Fig. 5. Squares, circles, and asterisks represent 5°, 2.5°, and 0° circular masks respectively. The overestimation decreases as the size of the mask increases.
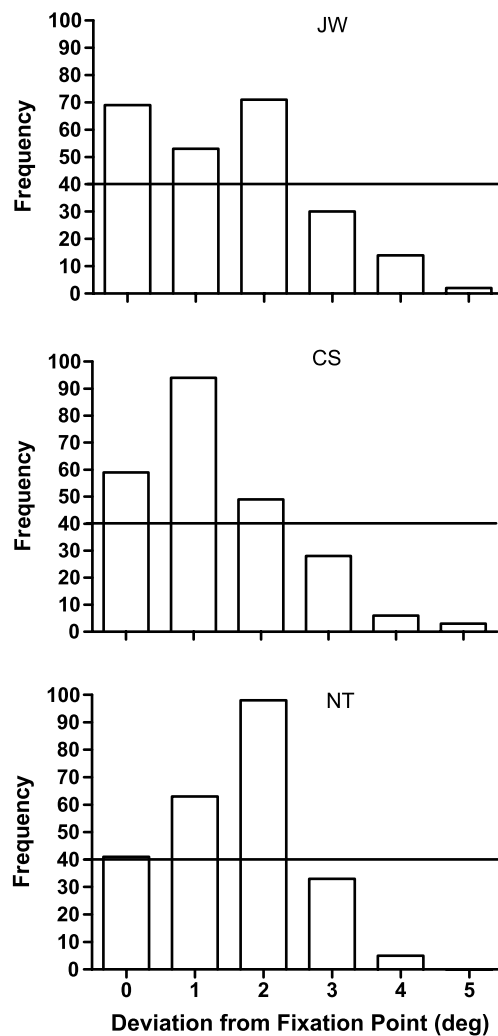

Fig. 7. Histogram of the perceived deviation of the focus of expansion from the fixation point. In other words, this histogram shows the number of times subjects judged the focus of expansion to be at a given distance from fixation. Judgments of focus-of-expansion deviations used a ruler (Section 2). The horizontal line represents the amount of times that each deviation was displayed (i.e., deviations were all displayed with equal frequency). Subjects tend to perceive the focus of expansion near the fixation point.
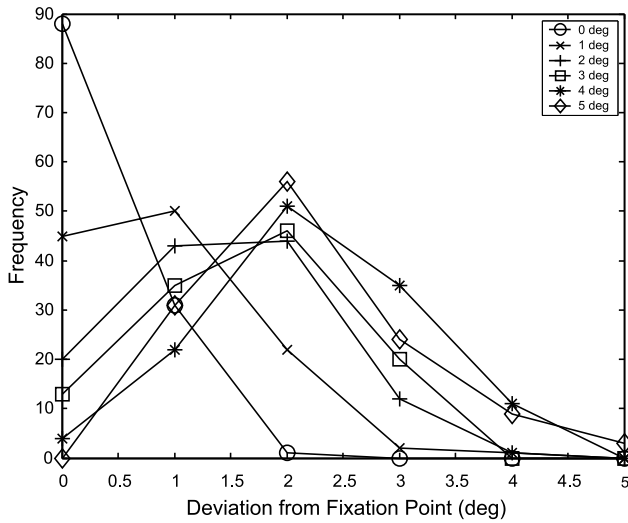
Fig. 8. Frequency of perceived deviation of the focus of expansion from the fixation point parametric on the actual deviation. Frequencies here are totals over all subjects in Fig. 7. When the deviation is small (<1°), subjects tend to report the correct deviation, but when the deviation is large (especially > 3°), subjects tend to underestimate it.
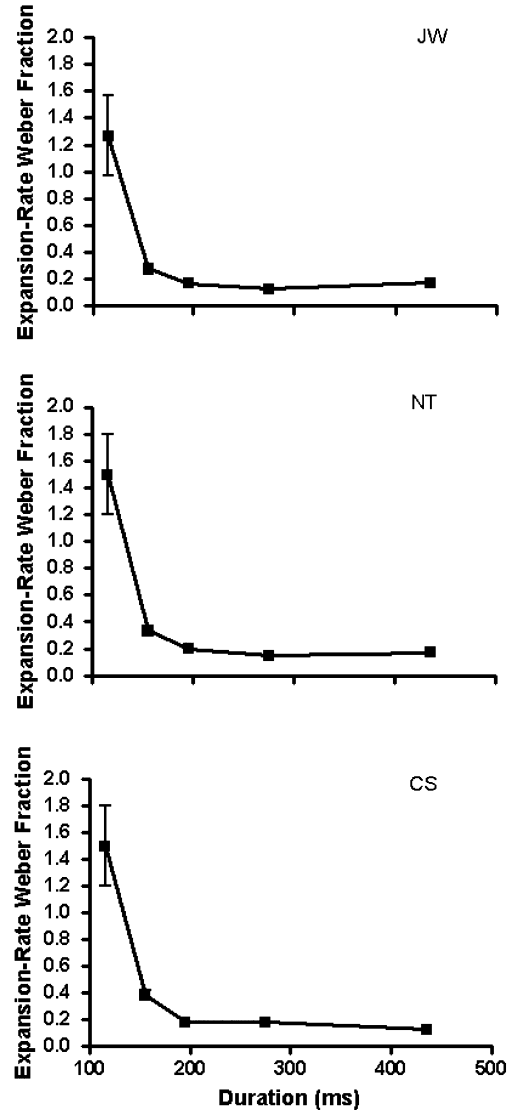

Fig. 9. Weber fraction with which subjects discriminate rates of expansion as a function of display duration. Weber fractions fall rapidly until 155 ms, indicating a relatively fast computation of rate of expansion.

underestimation in deviation from the fixation point may be the cause for the overestimation errors in the third experiment (Fig. 6).

Another way that may cause humans to misestimate the rate of expansion is if the presentation is too short. We expect incorrect estimations if the presentation is less than 100 ms, since humans cannot even measure local velocities for these durations. Because estimating rate of expansion involves integrating local velocities, we expect its necessary duration-of-presentation to be longer. However, it is hard to tell a priori how much longer. Because responses to expansions in MST are fast (Duffy & Wurtz, 1991b), the necessary duration could be short. On the other hand, other integration processes in the brain such as structure from motion (Hildreth, Grzywacz, Adelson, & Inada, 1990) or detection of long motion trajectories (Grzywacz, Watamaniuk, & McKee, 1995; Krekelberg & Lappe, 1999; Watamaniuk, McKee, & Grzywacz, 1995) can take hundreds of milliseconds. Fig. 9 shows the results on the integration time of rate of expansion.

As Fig. 9 shows, subjects can accurately discriminate between rates of expansion for presentations as short as 155 ms. For presentations longer than that, the accuracy remains relatively constant but not perfect (Weber fraction better than 20%). In contrast, subjects cannot estimate rates of expansion accurately with durations shorter than 155 ms. The Weber fraction climbs to 150% even at 120 ms. Therefore, although fast, the visual system appears to require from 30 to 50 ms to compute rate of expansion after completing the computation of local velocities (McKee, 1981; Snowden & Braddick, 1991).

5. Model

We now develop a model for the computation of rate of expansion consistent with the data presented above. The starting point of the model is that the rotation and expansion data are similar. Furthermore, the characteristics of rotation and expansion are similar in that they only differ by rotating the direction of the local-velocity vectors by 90° (Section 1). Hence, adapting an existing model that accounts for the rotation data would seem like a good strategy for us. Barraza and Grzywacz (2002b) developed such a model. It computes the angular velocity in small patches of the image and then integrates their information to generate a more complex description of the rotational field. This model computes

a global value of angular velocity, while also being able to handle nonrigid rotations. The model follows a recently developed Bayesian framework (Yuille & Grzywacz, 1998) and uses an energy-minimization approach. We adapt that model here for the rate of expansion.[2]

The model estimate of the local rate of expansion is

$$\rho_l(\vec{r}_i) = \arg\min_{\rho^*}\left[\sum_{i=1}^{N}\left|\rho^*(\vec{r}_i)\vec{r}_i - \vec{v}_i\right|\right], \qquad (1)$$

where $\vec{v}$ is the local velocity[3] of a dot, $\vec{r}$ is the distance from the center of expansion, and N is the number of dots in the display. This equation says that ρ_l is the value of the independent variable ρ^* that minimizes the right-hand side sum. In words, Eq. (1) looks for the rate of expansion, whose corresponding velocity vectors are as close as possible to the measured ones across dots. Because the rate of expansion depends on positions, it can account for nonrigid expansions[4] (Fig. 1). Furthermore, the local rate of expansion is consistent with the local speed. Therefore, the rate of expansion is correct everywhere if the focus of expansion is correct. Hence, the model accounts for the data in Figs. 3 and 4.

To analyze the overestimation results of Figs. 5 and 6, one needs a global rate of expansion estimator to compare to rigid expansions. This was not necessary for Figs. 3 and 4, since all local estimations were identical in the former and subjects only performed local estimations in the latter. However, for Figs. 5 and 6, subjects had to perform global estimations from motions whose local estimations varied across space (see discussion before Fig. 7). The global estimator that we use for the rate of expansion is:

$$\rho = \arg\min_{\rho^*}\left[\sum_{i=1}^{N}\exp\left(-\frac{\varepsilon_i|\vec{r}_i|^2}{2\sigma^2}\right)|\rho^* - \rho_l(\vec{r}_i)|\right], \qquad (2)$$

where ε is a spatial variable that weighs each position according to eccentricity and σ parameterizes the weights. We use the eccentricity term, because positions near the fixation point have greater acuity and thus, pro-

vide more accurate data for the estimation ρ. This is especially relevant for expansions that have a focus of expansion not on the fixation point, such as the stimuli in the third experiment.

Elsewhere, it is shown that the median minimizes a sum of absolute values as in Eq. (2) (Hoagling, Mosteller, & Tukey, 1983), which thus yields a weighted median of local rates of expansion. We choose the median, since it is a robust statistical estimator (Hoagling et al., 1983), reducing the effects of outliers near a possibly incorrect focus of expansion. The advantage of representing the median as in Eq. (2) is that it becomes consistent with Bayesian approaches to vision (Yuille & Grzywacz, 1998). One can rewrite this equation such that it finds the most probable rate of expansion, assuming a rigidity-prior distribution. In addition, such a representation lends itself to weighing as in Eq. (2) (Hoagling et al., 1983), thus allowing the introduction of factors like eccentricity. In Eq. (2), the weight falls in a Gaussian manner with eccentricity and in our simulations, we chose $\sigma = 5.5°$ (Barraza & Grzywacz, 2002b).

Finally, our model made the same assumptions as that of Barraza and Grzywacz (2002b), regarding errors in the localization of the focus of expansion. They performed a series of experiments that were more complete than those in Fig. 7 for the center of rotation. Their
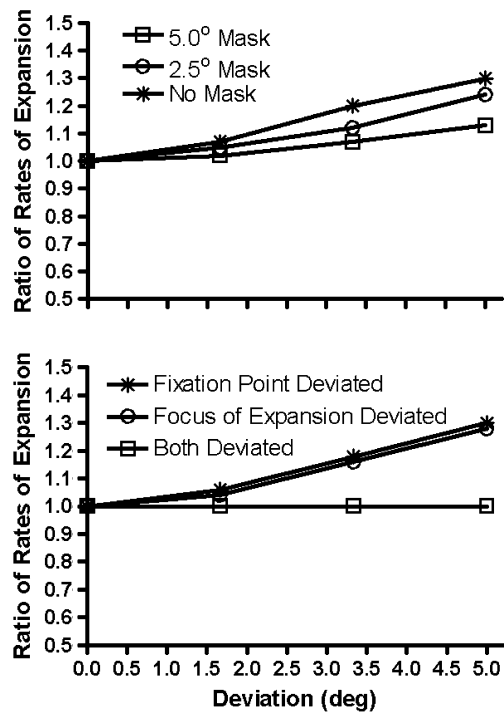

Fig. 10. Simulations of the off-fixation estimation of rate of expansion, using Eqs. (1) and (2) (see Figs. 5 and 6 for conventions). In the top panel, we show the simulations parametric on mask size. In the bottom panel, we show the simulations parametric on shifts of the fixation point and of the focus of expansion. The model accounts for all the experiments in which the effect of mis-locating the focus of expansion on perceived rate of expansion is studied (Figs. 5 and 6).

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[2] In this adaptation, we do not include the trust term of Barraza and Grzywacz, as it is not relevant here. For the same reasons we do not include their smoothing function.

[3] Several studies suggest mechanisms through which the brain may estimate local velocity. Section 1 already presented psychophysical evidence of the sensitivity to the direction and speed components of velocity. Physiologically, these measurements may be performed in MT (Perrone & Thiele, 2001), with population-code mechanisms suggested by several computational cortical models (Grzywacz & Yuille, 1990; Heeger, 1987; Perrone, 2004; Schrater, Knill, & Simoncelli, 2000; Simoncelli & Heeger, 1998).

[4] However, rigid expansions can also cause rates of expansion to depend on position. For example, if a slanted planar surface moves towards an observer, then the focus of expansion is spatially anisotropic and depends nonlinearly on the distance from the focus of expansion. We have evidence that humans are sensitive to this anisotropy, but it is outside the scope of this paper.

results showed that the perceived center of rotation is not at a fixed distance from the fixation point. Rather, the perceived center of rotation is at a fraction of the distance between the fixation point and the true center of rotation. The fraction is about a third. Although we do not have evidence that expansion exhibits a similar fraction, we assume it here for parsimony.

Fig. 10 shows the simulation results for our rate of expansion model in the case of an off-fixation expansion. As indicated by the results, the model produces a similar overestimation for off-fixation expansion as the subjects did, as well as a correct estimation for on-fixation expansion. The model also shows a reduction in the overestimation of the rate of expansion with masks and an increased reduction as the mask increases in size. Finally, the simulations of the model correctly show the overestimation whether the fixation point or the focus of expansion deviates from the center, but not when both deviate together.

6. Discussion

We conclude that the human visual system can discriminate between rates of expansion (Fig. 3). In other words, the system does not judge how fast an expansion is directly from the velocities in the optic flow. Rather, the visual system uses them to calculate rates of expansion, which are higher-order variables. This and the similar calculation of rotational angular velocities (Barraza & Grzywacz, 2002a, 2002b, 2003a, 2003b) suggest that the brain "fits" motion models to the optic flow (Yuille & Grzywacz, 1998). These models may be based on the decomposition suggested by Koenderink and van Doorn (Section 1). However, to show that such a decomposition occurs, one still has to prove that the brain measures the "deformation" motion parametrically (Koenderink & van Doorn, 1976; Koenderink, 1986). Moreover, one has to show that the brain can measure these variables when the motion is a mixture of the several components of Koenderink and van Doorn. (We recently obtained evidence that such a measurement may occur—Barraza & Grzywacz, in press.) Finally, one has to show that the Koenderink and van Doorn models are exclusive, an unlikely possibility.

We also found that the rate of expansion discrimination is performed locally (Fig. 4). This local-estimation mechanism gives evidence that the motion visual system has evolved to be more flexible than accurate. Local signals are sensitive to noise, but can encode nonrigid expansions or expansions from slanted surfaces (Footnote 3). The sensitivity to noise can cause the system to measure rate of expansion incorrectly. For instance, when the focus of expansion is not on the fixation point, there is a tendency for subjects to overestimate the rate of expansion (Figs. 5 and 6). Such overestimation is not altogether unlikely, as humans can misestimate the focus of expansion by 1° or more (Fig. 7). Cutting (1986) found that heading estimations need to be within 1° of the actual heading to perform multiple tasks. This number is on the lower end of what we found, however, we did not allow the subjects to subtend to the focus of expansion as they were to maintain a steady fixation. The goal of those experiments was not to show that we do make errors in heading as that has been shown, but that the subjects in our experiments were making errors in finding the focus of expansion and that these errors were the cause of the miscalculations of rate of expansion.

The overestimation may have practical relevance, since in ego motions, the focus of expansion is related to the heading direction (Hildreth, 1992; Warren, Morris, & Kalish, 1988). Previous experiments on perceived heading also showed that humans make significant errors in finding the proper heading direction (Beintema & van den Berg, 2001; Warren et al., 1988; Warren & Hannon, 1988, 1990). If these errors are like those for the focus of expansion, then they are systematic towards the fixation point. Such systematic errors make sense in that we tend to look towards where we are going. Therefore, the fixation point and the focus of expansion often coincide. Another reason for the visual system to assume these points to be close is that, as mentioned above, this could cause an overestimation of the rate of expansion (Fig. 9). Overestimation errors would cause a person to assume that an object is approaching faster and more head on than it is. This assumption is better from a survival standpoint than the opposite one.

Many models have been proposed for way finding and focus-of-expansion discrimination (Beintema & van den Berg, 1998; Hildreth, 1992; Lappe & Rauschecker, 1994; Royden, 1997; Royden, 2002). With previous findings that humans make a 1°–2° errors in focus-of-expansion discrimination (Beintema & van den Berg, 2001; Warren et al., 1988; Warren & Hannon, 1988, 1990) these models use this range as a target error rate and as a benchmark to show that they accurately account for the systems involved. Hence, our data falls in line with the data that are being modeled by these researchers. Some of these data show that misperceptions of focus-of-expansion seem to be invariant with a number of circumstances. Cutting, Springer, Braren, and Johnson (1992) showed about a 2° error when stimuli included the motion caused by bouncing created during the footfalls of a human's ego motion. In turn, Royden and Hildreth (1996) used stimuli with a moving object within a scene of ego motion. The moving object created only a slight bias in focus-of-expansion discrimination. However, if the object crossed the focus of expansion then errors increased.

Because rate of expansion is a variable of higher order than local velocity, we expected the computation

of the former to take longer. Its computation takes about 150 ms (Fig. 8), which is 30–50 ms longer than that for local velocity (Snowden & Braddick, 1991). This difference is longer than we expected, as it could reflect just the transition from one cortical (MT) area to another (MST—Schmolesky et al., 1998). However, perhaps the large difference can be explained by the complexity of the expansion computation, in which one or more foci of expansion must also be computed. Consequently, the computation may involve the "sluggish" convergence of a specialized neural network. This network's output would probably be limited by a multiplicative noise, since the performance converges to a constant Weber fraction (Bowne, Mckee, & Glasser, 1989). This is similar to the network computing local velocities (Gurney & Wright, 1992, 1996; Hirahara & Nagano, 1993; McKee, 1981; Turano & Pantle, 1989; Welch & Bowne, 1990). Similarly, this putative expansion network may be shared by the system estimating rotational angular velocities. This is because the results for the expansion experiments are similar to those in the analogous rotation ones. In rotation, subjects estimate angular velocity metrically, locally, and in a manner subject to foveal noise and center-of-rotation mis-location.

As explained after Eq. (2), our model is Bayesian. This model accurately predicts the rate-of-expansion performance of humans and the errors that will be made when the focus of expansion is not correctly identified. How does this model compare with template models proposed for self-motion estimation (Beintema & van den Berg, 1998; Hatsopoulos & Warren, 1991; Perrone, 1992; Perrone & Stone, 1994)? On one hand, one may say that Bayesian models are template models. This is because, like template models, the Bayesian framework tries to see how much optic flows match a particular kind of motion, e.g., expansion. On the other hand, one often thinks of template models as deterministic, whereas the Bayesian framework is explicitly probabilistic to account for the noisiness in the brain. One may say that the Bayesian framework expresses the probability of various templates being applicable. But for a sharp probability distribution, the Bayesian model converges to the conventional template model. Consequently, the Bayesian framework provides a generalization of template models. One of the criticisms of template models is that a person would need an infinite amount of them to be able to handle all the possible motion fields. However, even some of the template models try to address this by limiting the number of templates by finding the ones most often needed by humans (Perrone & Stone, 1998). Such approach is the root of the Bayesian generalization for template models.

What is the importance of measuring rate of expansion? We already mentioned that it may be one of the parameters of the models that the brain may try to fit to optic flows. Furthermore, the rate of expansion may

be important, since it is the reciprocal of the time-to-collision (Hoyle, 1957). Time-to-collision experiments have shown that time to collision is a metric property of motion that can be discriminated (Gray & Regan, 1998; Kim, Turvey, & Carello, 1993; Regan & Hamstra, 1993). Different from those experiments, our experiments kept the rate of expansion constant, which corresponded to objects that decreased in velocity as they approached the observer. In contrast, in time-to-collision studies, experiments used an increasing rate of expansion (decreasing time-to-collision). Consequently, in those experiments, objects would have motions that would result in a collision. This was important so that subjects could respond as to when they thought the object would collide with them. Another difference between our experiments and those performed previously is that the older experiments had durations from 0.5 s to 5.0 s. Those times are typically much longer than those used here. Perhaps as a result of these differences, the earlier experiments showed a tendency for humans to underestimate times of collision. On the other hand, our data are consistent with veridical estimations of rates of expansion (Fig. 3). We propose that the visual system estimates the rate of expansion and then temporally integrates it to average out noise. This average would tend to underestimate the time to collision in the presence of an object approaching with a constant velocity. Fortunately, it is better to underestimate the time-to-collision than the other way around, so one can plan conservative braking protocols. Hence, although time-to-collision and rate of expansion are mathematical reciprocals (meaning that if you know one you know the other), cognitively, we estimate them differently. They may contribute to different tasks and thus, have different requirements.

That humans can discriminate rate of expansion raises a puzzling question. Expansions are rarely observed alone in optic flows, but are mixed with other optic-flow components, such as a rotation and translation. One can conceive of uses for rate-of-expansion discrimination in instances when a pure or semi-pure expansion is occurring in the world. However, this will not be the case often. Therefore, the ability to discriminate rate of expansion would be more useful if humans could decompose optic flows into separate motion types. Can humans decompose optic flows in this manner? There is evidence that MST neurons do not carry out the necessary decomposition (Orban et al., 1992; Perrone & Stone, 1998). However, these experiments can only account for a small number of cells in MST, and while these particular cells by themselves may not carry out decomposition, it is still possible that it happens in the brain. In support of this possibility, psychophysical testing has suggested that humans may decompose spiral motions into their radial and rotational components (Barraza & Grzywacz, 2003b, in press). It was postulated that this decomposition is carried out not with single

cells but through a population code. Barraza and Grzywacz proposed a model for how this code would work.

Acknowledgments

References

Barraza, J. B., & Grzywacz, N. M. (2002a). Measurement of angular velocity in the perception of rotation. *Vision Research, 42*, 2457–2462.

Barraza, J. B., & Grzywacz, N. M. (2002b). Temporal coherence in visual rotation. *Vision Research, 42*, 2463–2469.

Barraza, J. B., & Grzywacz, N. M. (2003a). Local Computation of angular velocity in rotational visual motion. *Journal of the Optical Society of America A—Optics Image Science and Vision, 20*, 1382–1390.

Barraza, J. B., & Grzywacz, N. M. (2003b). Parametric measurements of optic flow in humans. In L. Vaina, S. Beardsley, & S. Rushston (Eds.), *Optic flow and beyond* (pp. 249–271). Amsterdam: Kluwer Academic Publishers.

Barraza, J. F., & Grzywacz, N. M. (in press). Parametric decomposition of optic flow by humans, *Vision Research*.

Beintema, J. A., & van den Berg, A. V. (1998). Heading detection using motion templates and eye velocity gain fields. *Vision Research, 38*, 2155–2179.

Beintema, J. A., & van den Berg, A. V. (2001). Pursuit affects precision of perceived heading for small viewing apertures. *Vision Research, 41*, 2375–2391.

Bowne, S. F., Mckee, S. P., & Glasser, D. A. (1989). Motion interference in speed discrimination. *Journal of the Optical Society of America A, 6*(7), 1112–1121.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*, 433–436.

Bravo, M., & Watamaniuk, S. (1995). Evidence for two speed signals: a coarse local signal for segregation and a precise global signal for discrimination. *Vision Research, 35*, 1691–1697.

Cutting, J. E. (1986). *Perception with an eye towards motion*. Cambridge, MA: MIT Press.

Cutting, J. E., Springer, K., Braren, P. A., & Johnson, S. H. (1992). Wayfinding on foot from information in retinal, not optical, flow. *Journal of Experimental Psychology: General, 121*, 41–72.

De Bruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research, 28*, 1323–1335.

Duffy, C. J., & Wurtz, R. H. (1991a). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology, 65*, 1329–1345.

Duffy, C. J., & Wurtz, R. H. (1991b). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology, 65*, 1346–1359.

Foster, D. H., & Bishof, W. F. (1991). Thresholds from psychometric functions: superiority of bootstrap to incremental and probit variance estimators. *Psychological Bulletin, 109*, 152–159.

Freeman, T. A. C., & Harris, M. G. (1992). Human sensitivity to expanding and rotating motion: effects of complementary masking and directional structure. *Vision Research, 32*, 81–87.

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

Gray, R., & Regan, D. (1998). Accuracy of estimating time to collision using binocular and monocular information. *Vision Research, 38*, 499–512.

Graziano, M. S. A., Anderson, R. A., & Snowden, R. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience, 14*, 54–67.

Grzywacz, N. M., Watamaniuk, S. N., & McKee, S. P. (1995). Temporal coherence theory for the detection and measurement of visual motion. *Vision Research, 35*, 3183–3203.

Grzywacz, N. M., & Yuille, A. L. (1990). A model for the estimate of local image velocity by cells in the visual cortex. *Proceedings of the Royal Society of London A, 239*, 129–161.

Gurney, K. N., & Wright, M. J. (1992). A self-organizing neural network model of image velocity encoding. *Biological Cybernetics, 68*, 173–181.

Gurney, K. N., & Wright, M. J. (1996). A biologically plausible model of early visual motion processing. I. Theory and implementation. *Biological Cybernetics, 74*, 339–348.

Hatsopoulos, N. G., & Warren, W. H. (1991). Visual navigation with a neural network. *Neural Networks, 4*, 303–317.

Heeger, D. J. (1987). Model for the extraction of image-flow. *Journal of the Optical Society of America A, 4*, 1455–1471.

Hildreth, E. C., Grzywacz, N. M., Adelson, E. H., & Inada, V. K. (1990). The perceptual buildup of three-dimensional structure from motion. *Perception and Psychophysics, 48*, 19–36.

Hildreth, E. C. (1992). Recovering heading for visually-guided navigation. *Vision Research, 32*, 1177–1192.

Hirahara, M., & Nagano, T. (1993). A neural network model for visual motion detection that can explain psychophysical and neurophysiological phenomena. *Biological Cybernetics, 68*, 247–252.

Hoagling, D. C., Mosteller, F., & Tukey, J. W. (1983). Introduction to more refined estimators. In D. C. Hoagling, F. Mosteller, & J. W. Tukey (Eds.), *Understanding robust and exploratory data analysis* (pp. 283–296). New York: John Wiley.

Hoyle, F. (1957). *The black cloud* pp 26-27. London: Penguin.

Johnston, A., Benton, C. P., & Morgan, N. G. (1999). Concurrent measurement of perceived speed and speed discrimination using the method of single stimuli. *Vision Research, 39*, 3849–3854.

Kim, N. G., Turvey, M. T., & Carello, C. (1993). Optical information about the severity of upcoming contacts. *Journal of Experimental Psychology, 19*, 179–193.

Koenderink, J. J. (1986). Optic flow. *Vision Research, 26*, 161–179.

Koenderink, J. J., & van Doorn, A. J. (1976). Local Structure of movement parallax of the plane. *Journal of the Optical Society of America, 66*, 717–723.

Krekelberg, B., & Lappe, M. (1999). Temporal recruitment along the trajectory of moving objects and the perception of position. *Vision Research, 39*, 2669–2679.

Lappe, M., & Rauschecker, J. P. (1994). Heading detection from optic flow. *Nature, 369*, 712–713.

McKee, S. (1981). A local mechanism for differential velocity detection. *Vision Research, 21*, 491–500.

McKee, S. P., Silverman, G. H., & Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Research, 26*, 609–619.

Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature, 376*, 507–509.

Orban, G. A., Lagae, L., Verri, A., Raiguel, S., Xiao, D., Maes, H., et al. (1992). First-order análisis of optical flow in monkey brain. *Proceedings of the National Academy of Sciences of the United States of America, 89*, 2595–2599.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442.

Perrone, J. A. (1992). Model for the computation of self-motion in biological systems. *Optical Society of America, 9*, 177–194.

Perrone, J. A. (2004). A visual motion sensor based on the properties of V1 and MT neurons. *Vision Research, 44*, 1733–1755.

Perrone, J. A., & Stone, L. S. (1994). A model of self-motion estimation within primate extrastriate visual cortex. *Vision Research, 34*, 2917–2938.

Perrone, J. A., & Stone, L. S. (1998). Emulating the visual receptive-field properties of MST neurons with a template model of heading estimation. *The Journal of Neuroscience, 18*, 5958–5975.

Perrone, J. A., & Thiele, A. (2001). Speed skills: measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience, 4*, 526–532.

Regan, D. (2000). *Human perception of objects: Early visual processing of spatial form defined by luminance, color, texture, motion, and binocular disparity*. Sinauer Associates.

Regan, D., & Beverley, K. J. (1985). Visual responses to vorticity and the neural analysis of optic flow. *Journal of the Optical Society of America A, 2*, 280–283.

Regan, D., & Hamstra, S. J. (1993). Dissociation of discrimination thresholds for time to contact and for rate of angular expansion. *Vision Research, 33*, 447–462.

Regan, D., & Vincent, A. (1995). Visual processing of looming and time to contact throughout the visual field. *Vision Research, 35*, 1845–1857.

Royden, C. S. (1997). Mathematical analysis of motion-opponent mechanisms used in the determination of heading and depth. *Journal of the Optical Society of America A, 14*, 2128–2143.

Royden, C. S. (2002). Computing heading in the presence of moving objects: a model that uses motion-opponent operators. *Vision Research, 42*, 3043–3058.

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

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology, 79*, 3272–3278.

Schrater, P. R., Knill, D. C., & Simoncelli, E. P. (2000). Mechanisms of visual motion detection. *Nature Neuroscience, 1*, 64–68.

Simoncelli, E. P., & Heeger, D. (1998). A model of neuronal responses in visual area MT. *Vision Research, 38*, 743–761.

Snowden, R. J., & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research, 31*, 907–914.

Tanaka, A., & Satio, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology, 62*, 626–641.

Turano, K., & Pantle, A. (1989). On the mechanism that encodes the movement of contrast variations: velocity discrimination. *Vision Research, 29*, 207–221.

Warren, W. H., & Hannon, D. J. (1988). Direction of self-motion is perceived from optical flow. *Nature, 336*, 162–163.

Warren, W. H., & Hannon, D. J. (1990). Eye movements and optical flow. *Journal of the Optical Society of America A, 7*, 160–169.

Warren, W. H., Morris, M. W., & Kalish, M. (1988). Perception of translational heading from optical flow. *Journal of Experimental Psychology—Human Perception and Performance, 14*, 646–660.

Watamaniuk, S. N., McKee, S. P., & Grzywacz, N. M. (1995). Detecting a trajectory embedded in random-direction motion noise. *Vision Research, 35*, 65–77.

Watamaniuk, S. N., Sekuler, R., & Williams, D. W. (1989). Direction perception in complex dynamic displays: the integration of direction information. *Vision Research, 29*, 47–59.

Welch, L., & Bowne, S. F. (1990). Coherence determines speed discrimination. *Perception, 19*, 425–435.

Werkhoven, P., & Koenderink, J. J. (1993). Visual size invariance does not apply to geometric angle and speed of rotation. *Perception, 22*, 177–184.

Yuille, A. L., & Grzywacz, N. M. (1998). A theoretical framework for visual motion. In T. Watanabe (Ed.), *High-level motion processing—computational, neurobiological, and psychophysical perspectives* (pp. 187–211). Cambridge, Massachusetts: MIT Press.