



# Evidence in Human Subjects for Independent Coding of Azimuth and Elevation for Direction of Heading from Optic Flow

GIOVANNI D'AVOSSA,\* DANIEL KERSTEN†‡

Received 3 July 1995; in revised form 23 November 1995

We studied the accuracy of human subjects in perceiving the direction of self-motion from optic flow, over a range of directions contained in a 45 deg cone whose vertex was at the viewpoint. Translational optic flow fields were generated by displaying brief sequences (<1.0 sec) of randomly positioned dots expanding in a radial fashion. Subjects were asked to indicate the direction of perceived self-motion at the end of the display. The data were analyzed by factoring out the constant component of the error by means of a linear regression analysis performed on the azimuthal and elevational components of the settings. The analysis of the variable error revealed that: a) the variance of the settings is 3–45% greater along elevation than azimuth for five observers; b) azimuth and elevation correspond, on average, to the principal components of the error in the settings; c) there are differences in the variances of azimuthal and elevational errors between upper and lower visual fields. Moreover, the distribution of the errors for azimuth and elevation in the upper and lower hemifields is not the same. All of the above evidence supports the hypothesis that heading information is represented centrally in terms of its azimuthal and elevational components. Copyright © 1996 Elsevier Science Ltd.

Heading    Optic flow    Periphery    Motion

## INTRODUCTION

Most animals are able to rely on the optic flow (Gibson, 1950), namely brightness changes taking place over time and space in the retinal image, to determine their own instantaneous trajectory and the relative distance and shape of objects in the surrounding environment. While the estimation of heading usually depends upon the integration of multisensory inputs, including vestibular, kinesthetic, and other visual cues (Israël & Berthoz, 1989; Roy *et al.*, 1992), there are circumstances when human subjects estimate their direction of self-motion relying mostly upon optic flow, such as when driving along a straight trajectory at a constant speed.

Given the importance of optic flow information for heading, one can ask two key questions: Can the relevant information be extracted from optic flow? How is the information for heading encoded in the human visual system? Regarding the first question, it is well-known that the focus of the radially expanding flow field provides direct information regarding heading for an

observer undergoing translation without a simultaneous rotation (Gibson, 1950). Under general observer motion, however, it is necessary to discount the rotational component of optic flow to estimate heading. Theoretically, it has been shown that given the presence of a wide visual field and “sufficient” depth changes in the environment (Koenderink & van Doorn, 1987), the optic flow contains enough information to make the estimation of heading a well-posed problem (Longuet-Higgins & Prazdny, 1980) even in the presence of rotational motion of the observer. Experimental data have provided evidence that for low rates of rotation, optic flow may be sufficient for the reliable estimation of direction of self-motion by human observers (Warren & Hannon, 1988). Additional information from proprioception may become increasingly important at higher rotational speeds (Royden *et al.*, 1992).

There are relatively few studies regarding the second question, namely how direction of heading from optic flow is encoded centrally. One of the issues which has been considered recently is whether there exist visual field specializations for particular optic flows and what influence eccentricity has on the accuracy of perceived heading (Warren & Kurtz, 1992; Crowell & Banks, 1993). Data on heading accuracy as a function of eccentricity are particularly relevant to the understanding of the neural mechanisms involved in the computation of heading since they bear upon the scaling of central representations of the

\*Neuroscience Program, University of Minnesota, Minneapolis, U.S.A.

†Department of Psychology, 75 East River Road, University of Minnesota, MN 55455, U.S.A.

‡To whom all correspondence should be addressed *E-mail* kersten@eye.psych.umn.edu].

optic flow and heading direction. Nevertheless, such scaling has been investigated only along the azimuthal direction. In fact, all published data report the accuracy of human subjects in determining the azimuthal component of direction of heading while keeping the elevational component constant. We fill this gap in current knowledge by reporting measurements of heading judgments for directions spanning more than one dimension. The results bear directly on the issue of how two-dimensional heading information may be centrally encoded and computed from the optic flow. In particular we address the question of whether distinct neural representations exist for the components of heading. The notion of separate neural mechanisms for encoding aspects of directional information has precedents in the work done on other organisms and domains. Neurophysiological work dealing with sensory and motor systems has provided numerous examples of directional information being coded in dedicated nervous structures (Knudsen *et al.*, 1987). We report the first experimental evidence supporting the independent coding of azimuth and elevation for direction of self motion by the brain. We measured the accuracy of heading judgments over a two-dimensional region of the visual field using translational optic flows. The computation of heading is particularly simple when the optic flow arises only from the observer's translation. This case is not uncommon as pure translation occurs naturally when keeping the gaze toward a point at the horizon or when gaze and heading coincide. As such, they are a subset of the set of "ecological flows". Further, if indeed the visual system decomposes the optic flow field into its rotational and translational components, then what we find with translational flows should also hold true when rotational components are present.

## METHODS

The stimuli were generated off-line on a Macintosh IIfx and displayed on a Hitachi (SM-19B), 19", 1280 × 870 high resolution monitor. Sequences of 28 images were displayed at 66 Hz. Images were refreshed every two frames. Each frame contained 400 dots in positive contrast. Two hundred of these dots were newly created in each image while the other two hundred were displaced from their position in the previous image (according to the simulated translational velocity of the observer and the laws of projective geometry) and then were substituted in the next image. The linear dimension of each dot was 6.2' of visual angle.\* It has already been shown by others that such stimuli are able to create an effective percept of heading (Warren *et al.*, 1991).

The initial three-dimensional coordinates of the dots were generated so that the probability that a dot would have a given  $x$ - $y$  position on the screen had a uniform distribution. The virtual distance of each point, that is its

$Z$  coordinate, was chosen by sampling a pseudo-random uniform distribution whose range was from three to seven times the distance of the observer from the screen. We assumed that the simulated acceleration of the observer had a unimodal shape as if the observer was subject to a smooth force pulse. This was done to minimize the abruptness of vection and visuo-vestibular conflict, and it yielded an asymptotically decreasing function for the time to contact with a frontal plane between the front and the back end of the virtual volume containing the dots.

The heading in each trial was chosen in such a way that the probability of its intersection with the image plane had a uniform distribution.

Subjects (the two investigators and three paid naive observers) had a visual acuity of 20/20, with correction if necessary. During the experiments, subjects were comfortably seated on a chair. A bite bar was used to restrain the head. A viewing box with a circular aperture allowed vision of a portion of the screen. At the beginning of each experimental session the subjects had to adjust the position of the bite bar until they had properly aligned their left eye, the circular aperture and their view of the perimeter of a circle, with a diameter of 45 deg, drawn on the screen.

Once the subjects were properly positioned, sessions of 400–500 trials began. Every hundred trials a warning tone and the possibility to rest were given. At the beginning of each trial a fixation cross at the center of the visual field was briefly flashed to warn the subject that a new trial was about to begin. The subjects were instructed to keep fixating the fixation point for the duration of the whole trial. At the end of the display a cursor appeared and the subjects were instructed to place the cursor in the direction of perceived heading by means of a mouse. Clicking on the mouse prompted the beginning of a new trial. During the time between the end of one display and the beginning of the next the dots which had appeared on the last frame of the previous display were left on the screen to maintain light adaptation.

In a control experiment we asked the subjects to match the memorized position of a dot displayed on the screen. The setting procedure was the same as that described above. More precisely, a stationary cross (smaller than the fixation mark) was displayed in a randomly chosen position on the screen. The cross appeared for 0.85 sec (i.e. the same duration of the optic flow stimulus) and then was extinguished. The subjects had to match the position of the cursor to the remembered position of the stimulus.†

\*Adot's image size was not scaled according to its virtual distance from the observer. The rate of size expansion was at most 0.4 deg/sec, corresponding to a change of less than a pixel's width over a dot's two-frame lifetime.

†In these experiments no dotted background was present since textural cues provide rich positional information. In fact, when a textured background is present saccades made to the remembered position of a target are almost errorless (Gnadt *et al.*, 1991) whereas when no textured background is present large systematic and random errors are found in the final position of the eye following saccades made to the memorized position of the targets. We found a similar effect of background texture on the matching accuracy of memorized targets' position, the errors being larger when no textured background was present.

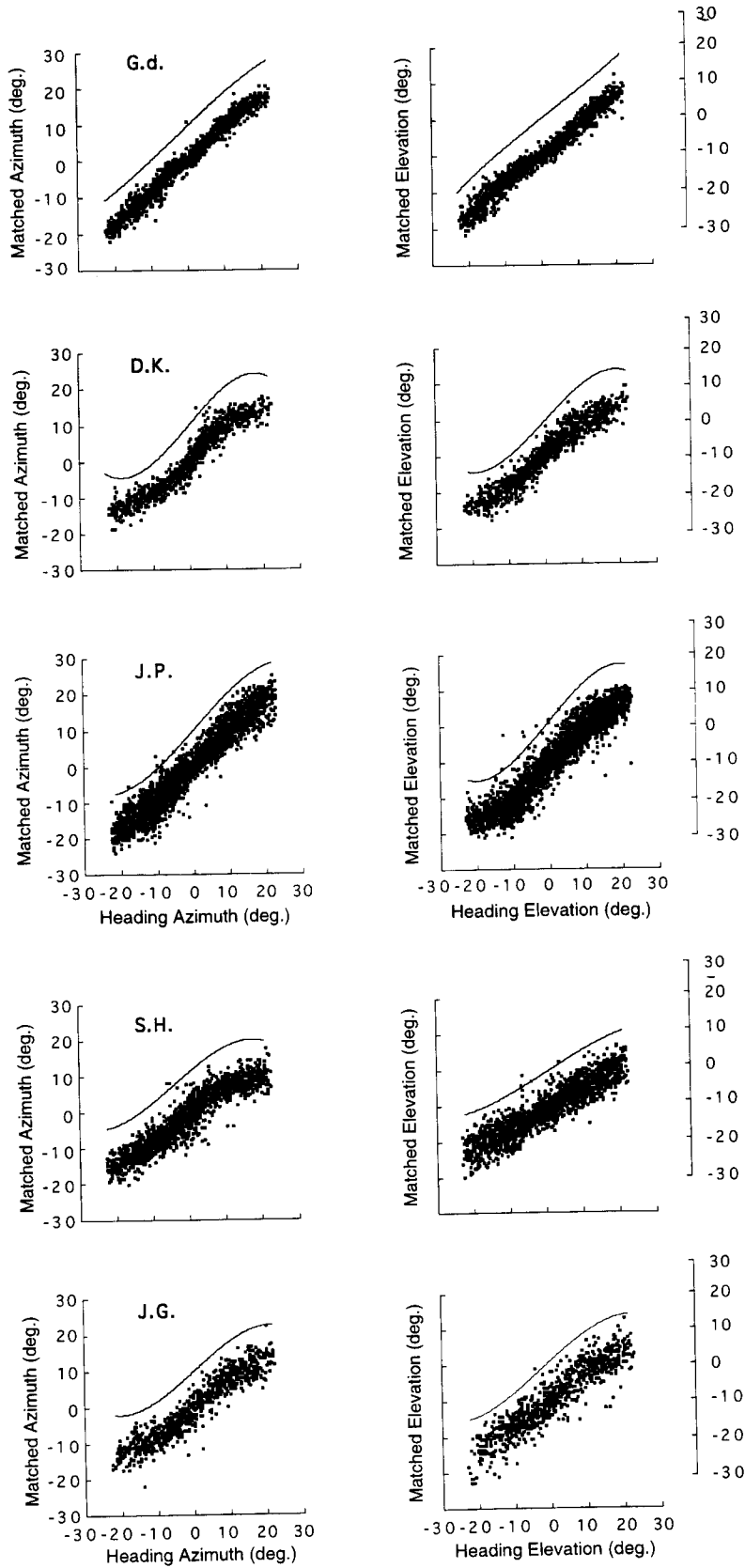


FIGURE 1. The plots show for each subject the relation, in the left column, between the azimuth of the simulated direction of self-motion and the azimuth of the matched direction, and, in the right column, between the elevation of the simulated direction of self-motion and the elevation of the matched direction. Above each set of experimental data, the best-fitting cubic polynomial functions are shown. All the subjects showed a consistent dependence of their setting upon the actual direction of heading. Each point is the result of one trial.

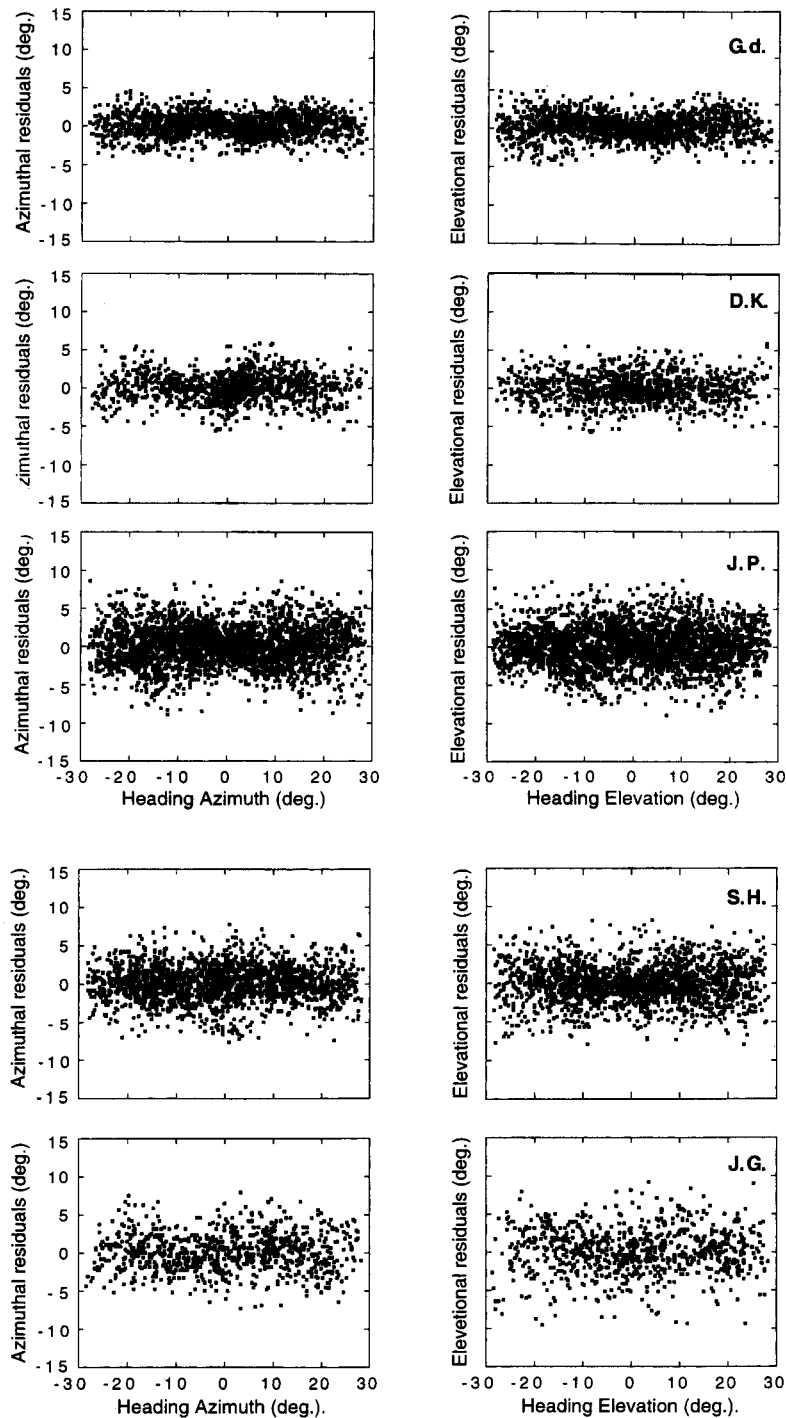


FIGURE 2. The plots of the residuals of the cubic regressions demonstrate that for both the azimuthal (left column) and elevational errors (right column), most of the constant component is accounted for by the polynomial regression.

## RESULTS

### *Constant and variable error in direction of heading*

All of our subjects were able to perform the task, but with different degrees of accuracy. As shown in Fig. 1 there is a monotonic relationship between the azimuth and elevation of the simulated direction of self-motion and the azimuth and elevation of the settings. It is also clear that there are consistent deviations from a purely linear relation between the simulated heading and the matched directions.

The existence of systematic differences between the actual heading and the perceived one has been previously reported by other investigators (Warren & Kurtz, 1992). We thought that this bias might arise because the paucity of static visual cues may not provide the observers with a reliable reference frame. This motivated the control experiment (see Methods) in which subjects also made settings using a procedure similar to the one used in the first experiment; however, instead of matching the simulated heading they had to match the remembered

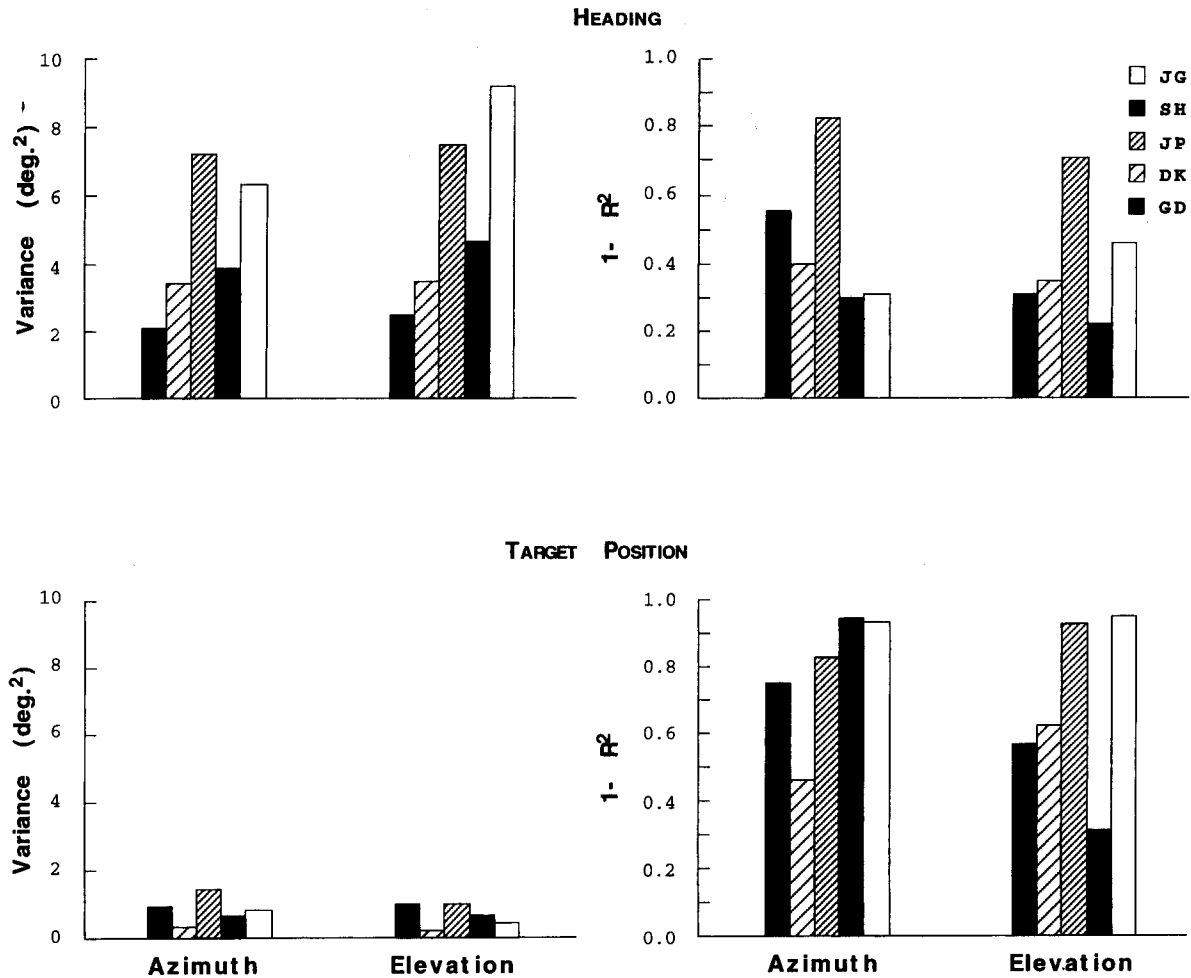


FIGURE 3. The bar graphs on the left depict the magnitude of the variance of the variable error along azimuth and elevation in the heading (top) and control experiments (bottom). In the heading experiments the azimuthal variance is smaller than the elevational variance for all of the subjects. This is not the case in the control experiment. Moreover, the azimuthal and elevational variances are consistently smaller when the subjects had to match the location of a memorized target on the screen. The bar graphs on the right show the proportion of the Mean Squared Error (MSE) due to the variable error. The portion of the total error (MSE) accounted for by the variable error is larger when subjects had to match the direction of the memorized target's position than when they matched heading.

location of a marker displayed on the screen. For both experiments, the differences between the matched azimuth ( $\chi_m$ ), the matched elevation ( $\phi_m$ ) and the actual values of these components, that is the azimuth ( $\chi$ ) and the elevation ( $\phi$ ) were fitted with a third degree polynomial in  $\chi$  and  $\phi$ :

$$\chi_m(\chi, \phi) - \chi = a_0 + a_1\chi + a_2\phi + a_3\chi^2 + a_4\phi^2 + a_5\chi * \phi + a_6\chi^3 + a_7\chi^2 * \phi + a_8\chi * \phi^2 + a_9\phi^3$$

$$\phi_m(\chi, \phi) - \phi = b_0 + b_1\chi + b_2\phi + b_3\chi^2 + b_4\phi^2 + b_5\chi * \phi + b_6\chi^3 + b_7\chi^2 * \phi + b_8\chi * \phi^2 + b_9\phi^3$$

The component of the error accounted for by the regression will be referred to as the constant error and the part of the error not accounted for by the regression, namely the residuals, the variable error. In the analysis to follow, only the residuals that are within 3.0 standard

deviations will be considered. In doing so, 1–2% of the trials (depending on the subject) had to be discarded. Figure 2 shows, for each subject, the residuals of the regression for direction of heading experiments. The plot demonstrates that the regression accounts for most of the constant error.

The upper and lower bar graphs on the left of Fig. 3 show the variance of the variable error for the settings along azimuth and elevation when matching the direction of heading and when matching the memorized position of a target. For all the subjects the variance of the variable error for both azimuth and elevation is smaller when the subjects had to match the position of the target. In fact, the variance in heading judgments is, depending on the subject, ~3.0 to ~10.0 times as large.

In the heading experiments the variance of the errors along the elevation is greater than the variance along the azimuth for all the subjects. Moreover, this difference is

TABLE 1. The ratios ( $F$  value) of the variance of the elevational (V.Err.El.) and the azimuthal error (V.Err.Az.) are reported for each subject as well as probability of these ratios being equal to one, that is, the probability that the variances have the same value

<hr/>		
<i>Subject Gd</i>		
V.Err.El. $\neq$ V.Err.Az.	$F(1385,1385) = 1.181, P < 0.01$	
<i>Subject DK</i>		
V.Err.El. $\neq$ V.Err.Az.	$F(1074,1074) = 1.030, P > 0.1$	
<i>Subject JP</i>		
V.Err.El. $\neq$ V.Err.Az.	$F(2558,2558) = 1.038, P > 0.1$	
<i>Subject SH</i>		
V.Err.El. $\neq$ V.Err.Az.	$F(1582,1582) = 1.155, P < 0.05$	
<i>Subject JG</i>		
V.Err.El. $\neq$ V.Err.Az.	$F(776,776) = 1.453, P < 0.001$	
<hr/>		

For three subjects, Gd, DK, and JG, the values of the variance along azimuth and elevation are significantly different.

statistically significant for three subjects (see Table 1) and cannot be attributed to a difference in the sampling of heading directions along the two orientations (see also Methods). In fact, a Kolmogorov–Smirnov test comparing the distributions of the azimuthal and elevational values of headings yielded a  $P > 0.1$  for all of the subjects. Furthermore, in the control condition three subjects displayed a larger variance along the azimuthal component and only two subjects showed a larger variance along the elevational component. Therefore, when subjects estimate heading, the elevational component is judged less reliably than the azimuthal one, whereas no consistent difference between the azimuthal and elevational variances exist when matching the memorized position of a target.

The bar graphs on the right of Fig. 3 show the proportion of the total error due to the variable error. These values were obtained by computing the difference between the total squared error, normalized to the value of 1.0, and the squared value of the coefficient of determination for the cubic regressions. The variable error accounts for a larger portion of the total error when the subjects had to replicate the memorized position of a target. In other words the constant error in judging heading is in absolute and relative terms greater than the constant error when the target position matching task is performed. Figure 4 shows the raw data for one subject where the azimuthal and elevational errors are plotted against the homologous dimension of the simulated heading, on the left, or target position, on the right. The figure clearly shows that when this subject had to match the memorized target position she made little or no error, while her judgments of heading show both a systematic underestimation of the true direction of heading and higher variability. Hence, the paucity of landmarks in the visual field cannot account by itself for the presence of a relatively large constant error in judgments of heading.

#### *Azimuthal and elevational errors are uncorrelated*

So far we have parametrized direction of self-motion in terms of its azimuthal and elevational components, however, we have not established whether this particular

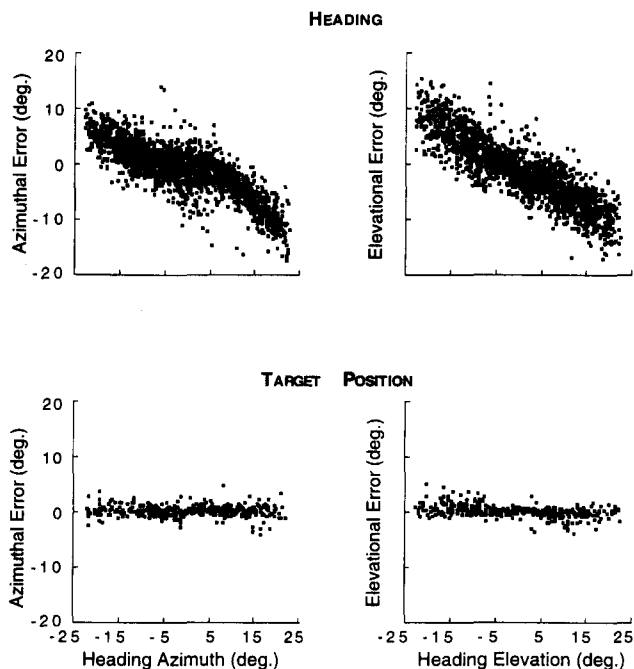


FIGURE 4. The figure shows the signed difference between the azimuth and elevation of the matched and the actual direction, in the heading experiments on the top, and for the static target direction on the bottom. For the one subject, whose data we show, while there is a large underestimation of heading's azimuth and elevation (the difference between perceived and actual heading being positive for negative values of both azimuth and elevation, and negative for positive values of azimuth and elevation), little bias exists when matching the target's location.

choice of the coordinate system is the most meaningful. To this end, we employed Principal Component Analysis (PCA) to search for an orthogonal basis spanning the space of the data such that the correlation among the values of the data along those coordinates is zero. While PCA is generally used to provide a manageable description of high dimensional data, our purpose was to find which pair of axes results in the largest decorrelation of the errors.

We computed the values of the projections of the errors on pairs of orthogonal axes rotated away from the orientation of the azimuthal and elevational axes. Figure 5 shows the correlation between the projection of the errors as a function of the angle by which each pair of axes has been rotated. It is found that the value of the correlation crosses the zero, going from positive to negative values, when the angle of the component accounting for the largest variance is, depending on the subject, between 100 and 60 deg. Figure 6 shows for each subject the orientation of the first principal component, that is the one accounting for most of the variance. These components are on average quite close to the orientation of elevation with a slight bias toward a rightward rotation. While the number of subjects is too small to determine whether this rightward bias is statistically significant, it should be stressed that the orientations of the principle component span a rather small range of the

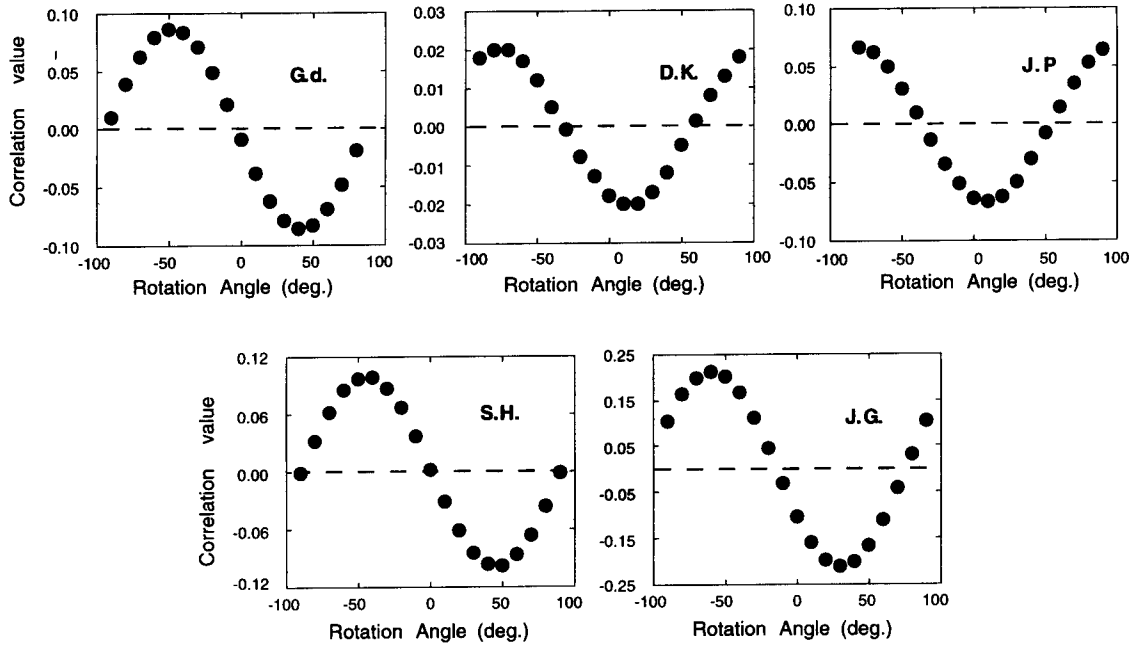


FIGURE 5. The correlations between the errors in different orthogonal coordinates are plotted as a function of those coordinate's orientation angle relative to azimuth and elevation. The angle where the correlation coefficient turns from negative to positive values is approximately the same (within 37 deg) for all of the subjects (Gd, -6.8; DK, -30.6; JP, -35.8; SH, +0.6; JG, -19.0 deg).

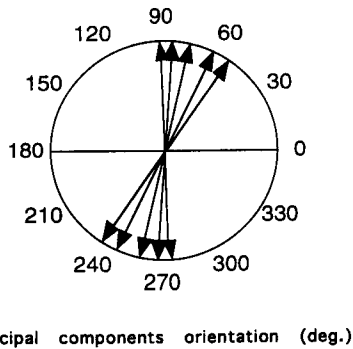


FIGURE 6. The directions of the first principal component of the variable error (oriented arrows) cluster in a range of directions closely centered around the orientation of the elevational component.

possible values (40 out of 180 deg). This lends support to our initial choice of azimuth and elevation as the coordinates most appropriate to parametrize the settings. In fact, the correlation between the projections of the errors on these axes is close to zero.

Table 2 reports the *P*-values of the Kolmogorov-Smirnov test for normality performed on the distributions of the variable portion of the errors. In some instances these values suggest that the distribution of the errors is equal to a distribution generated by a Gaussian process. There is evidence that the distribution of the errors, when obtained from more than one direction of heading (as in our case) can be best described as the superposition of

Gaussian distributions with unequal spreads. This fact can justify the observed deviations from normality and supports the hypothesis that the errors may follow a Gaussian distribution, at least for any one given direction of heading. If so, azimuthal and elevational errors not only are uncorrelated but statistically independent.\*

*Visual field differences*

We ascertained whether there are visual field differences in the variance of the errors when judging azimuth and elevation. The existence of visual field differences

TABLE 2. The values of the Kolmogorov-Smirnov test on the significance of the differences between the distribution of the variable errors and a normal distribution are reported

Subject		Max. difference	<i>P</i> value
Gd	V.Err.Az	0.027	0.018
	V.Err.El	0.027	0.016
DK	V.Err.Az	0.030	0.024
	V.Err.El	0.026	0.016
JP	V.Err.Az	0.014	0.289
	V.Err.El	0.016	0.117
SH	V.Err.Az	0.026	0.014
	V.Err.El	0.022	0.067
JG	V.Err.Az	0.021	0.534
	V.Err.El	0.031	0.071

\*Two variables with a zero correlation and a Gaussian distribution are independent.

For two subjects, JP and JG the difference is not significant, whereas for the other three subjects it is significant at the 0.05 level (with the exception of the elevational error in SH).

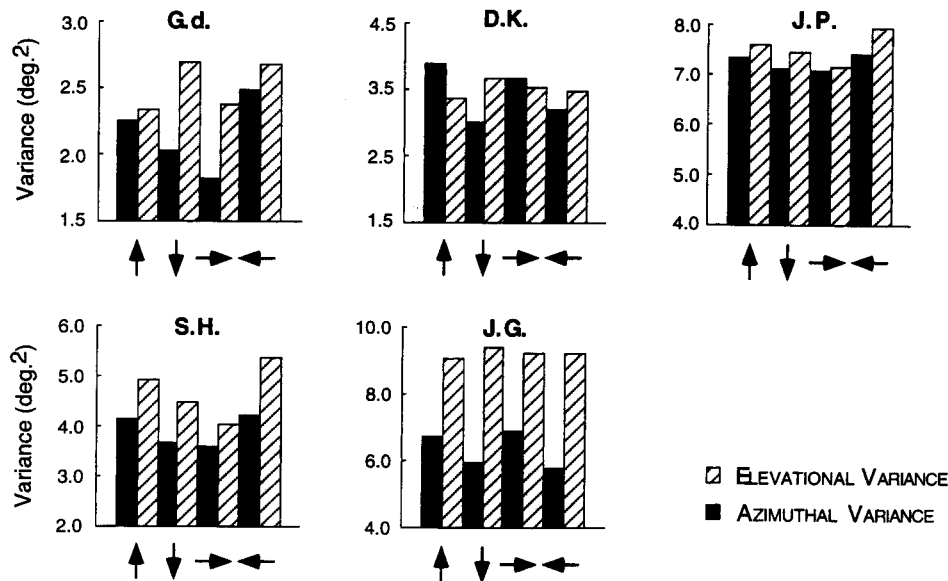


FIGURE 7. The bar graphs, one for each subject, show the variance of the azimuthal and elevational variable error in the different hemifields. In particular, the upward oriented arrows indicate the upper visual field, the downward oriented arrows the lower visual field, the rightward oriented arrows the right visual field and the leftward oriented arrows the left visual field. For a description of the differences the reader should refer to the main text.

TABLE 3. The variances of the azimuthal error in the upper visual field (Az.Up) and the lower visual field (Az.Lo) are compared through the computation of the  $F$  statistic, and so for the variances of the azimuthal error in the left visual field (Az.Lft) and right visual field (Az.Rgt)

<i>Subject Gd</i>	
Az.Up $\neq$ Az.Lo	$F(682,703) = 1.109, P > 0.1$
El.Up $\neq$ El.Lo	$F(682,703) = 1.156, P < 0.05^*$
Az.Lft $\neq$ Az.Rgt	$F(758,627) = 1.360, P < 0.01$
El.Lft $\neq$ El.Rgt	$F(758,627) = 1.126, P < 0.1$
<i>Subject DK</i>	
Az.Up $\neq$ Az.Lo	$F(556,518) = 1.291, P < 0.01$
El.Up $\neq$ El.Lo	$F(556,518) = 1.101, P > 0.1^*$
Az.Lft $\neq$ Az.Rgt	$F(580,494) = 1.145, P < 0.1^*$
El.Lft $\neq$ El.Rgt	$F(580,494) = 1.011, P > 0.1^*$
<i>Subject JP</i>	
Az.Up $\neq$ Az.Lo	$F(1331,1227) = 1.041, P > 0.1$
El.Up $\neq$ El.Lo	$F(1331,1227) = 1.019, P > 0.1$
Az.Lft $\neq$ Az.Rgt	$F(1288,1270) = 1.045, P > 0.1$
El.Lft $\neq$ El.Rgt	$F(1288,1270) = 1.104, P < 0.1$
<i>Subject SH</i>	
Az.Up $\neq$ Az.Lo	$F(821,761) = 1.335, P < 0.001$
El.Up $\neq$ El.Lo	$F(821,761) = 1.031, P > 0.1^*$
Az.Lft $\neq$ Az.Rgt	$F(794,788) = 1.036, P > 0.1$
El.Lft $\neq$ El.Rgt	$F(794,788) = 1.241, P < 0.01$
<i>Subject JG</i>	
Az.Up $\neq$ Az.Lo	$F(396,380) = 1.293, P < 0.05$
El.Up $\neq$ El.Lo	$F(396,380) = 1.036, P > 0.1^*$
Az.Lft $\neq$ Az.Rgt	$F(391,385) = 1.200, P < 0.1^*$
El.Lft $\neq$ El.Rgt	$F(391,385) = 1.011, P > 0.1$

The same is done for the variance of the elevational error in the four hemifields. Note that the value of the variance on the left of the table is always larger than the one on the right, unless an asterisk (\*) is placed next to the  $P$ -value.

has been reported for the onset and magnitude of linear vection (Telford & Frost, 1993). Our starting hypothesis is that if a single mechanism encodes both components and if indeed differences in accuracy are found among nonoverlapping parts of the visual field, such inhomogeneities should be coincident for azimuthal and elevational errors. On the other hand if azimuth and elevation are coded by distinct mechanisms we should not necessarily find the same pattern of inhomogeneities.

To this end, the variance of the errors in azimuth and elevation was computed for headings in the lower, upper, right and left visual hemifields, respectively. Figure 7 shows the variance of the variable error in the various hemifields. For all subjects the variance of the azimuthal errors is smaller in the lower than in the upper visual hemifield. On the other hand, for three subjects the elevational variance is smaller in the upper visual field (see also Table 3, subjects Gd, DK, and JG), while for two subjects it is smaller in the lower visual field even though the difference between upper and lower hemifields is less than that found for the azimuthal component (subjects JP and SH). Moreover, the elevational component has a smaller variance in the right than the left visual hemifield for four subjects (Gd, JG, JP, and SH), and in three subjects the azimuthal variance is found to be smaller in the right visual hemifield (all the previous subjects except JG).

In summary, consistent differences are found across the horizontal meridian for the azimuthal component. Moreover, the inhomogeneity does not seem to coincide for azimuth and elevation and thus lends further support to the hypothesis that estimation of azimuth and elevation



of self-motion direction might depend upon distinct processes.

## DISCUSSION

Analysis of the variable component of the errors made by subjects while judging their direction of self-motion from optic flow provides strong indications that heading azimuth and elevation are coded independently by the central nervous system. This conclusion has been reached given three lines of converging evidence.

Firstly, despite the fact that the radially symmetric stimuli provided the same amount of information for the estimation of the two components of heading (see Methods), the variance of the errors is larger along the elevation in all of our subjects. Moreover, in control experiments, in which we asked the subjects to replicate the position of a target briefly presented on a screen, we found no consistent difference between the variance of the settings along azimuth and elevation; thus, this difference may be specific to heading judgments.

Secondly, the first principal component of the errors, that is the visual meridian along which the errors have the largest variance, is collinear with the elevation. This result follows from the fact that the errors along azimuth and elevation are uncorrelated. We conclude that both the class of orthogonal (rotations) and possibly nonlinear transformations of the azimuthal and elevational coordinates are unlikely candidates for the central representation of heading.

Thirdly, the variance in judging azimuth is consistently smaller in the lower visual field than in the upper visual field. This is in contrast with judgments of elevation which are more reliable in the upper visual field in three out of five subjects. Note that while judgments of elevation are more accurate in the lower visual field for two subjects, the difference in accuracy is nevertheless smaller than the one found for the azimuth. This result would not be expected if a single mechanism coded both components because then the visual field inhomogeneities would have to be the similar for azimuth and elevation.

The independent coding of heading azimuth and elevation could be implemented using existing algorithms for heading estimation. In fact, Heeger and Jepson (1990) have proposed an algorithm for the computation of direction of heading based upon local linear filtering of the optic flow. In their model the first stage of the computations consists of matching the input data (that is, the optic flow) to a set of mechanisms each defining a constraint line for the direction of self-motion. Independent coding of azimuth and elevation could then be easily implemented if the constraint lines were chosen to be collinear with azimuth and elevation.

### *Incongruence of anisotropies and inhomogeneities for two-dimensional motion and direction of heading*

So far we have related our findings to the nature of the purported central representation of direction of heading. Though, the anisotropy (i.e. the difference in accuracy in

judging azimuth and elevation) and inhomogeneities (i.e. differences in accuracy across the visual field) for heading could result from anisotropies and inhomogeneities in the discrimination and/or detection of two-dimensional motion (Ball & Sekuler, 1980; van de Grind *et al.*, 1993). At the present time the data on two-dimensional motion detection and discrimination are not consistent enough to warrant a conclusive assessment of the relation between two-dimensional motion perception and the estimation of heading. In particular, no anisotropies or inhomogeneities have been reported when discriminating the direction or the speed of moving dots (Orban *et al.*, 1985) and gratings (Ball & Sekuler, 1979). Moreover, data on thresholds (van de Grind *et al.*, 1993) for the detection of centripetal vs centrifugal motion are in poor agreement with data from reaction time experiments (Ball & Sekuler, 1980). Nevertheless, it is informative to compare the data collected by van de Grind *et al.* (1993) to ours, because these authors have provided the most extensive description of anisotropies and inhomogeneities in two-dimensional motion perception to date.

Their data on two-dimensional motion detection and our data on direction of heading estimation are in agreement in that detection thresholds are greater for vertical than horizontal motion (van de Grind *et al.*, 1993) while the variance of the errors is greater along elevation than azimuth, as shown above. However, our data on the inhomogeneities can be contrasted with those of van de Grind *et al.*, who did not find any noticeable difference in detection threshold between upper and lower visual field. The fact that the van de Grind *et al.* results may not be relevant to understanding visual field inhomogeneities for heading is also suggested by data of Osaka (1988) who has reported the discrimination of self speed to be better in the left visual hemifield (temporal retina).

The observation that the azimuth is judged better in the lower visual field while the elevation is judged better, even though not nearly as consistently, in the upper visual field could depend on the distribution of the neural units involved in the coding of the azimuth and the elevation. In particular, neurophysiological data have been used to suggest that heading is represented in a dedicated cortical area, namely Medio Superior Temporal cortex (Saito *et al.*, 1986). Thus, the prevalence of either the azimuth or the elevation in the internal representation of heading could ultimately be determined by the outcome of a competition for "computational nodes" in such a neural map. If so, oppositely directed gradients in the number of units coding azimuth or elevation in a visuotopically organized neural structure and the resulting perceptual inhomogeneities could be established through competitive learning.

## REFERENCES

- Ball, K. & Sekuler, R. (1979). Masking of motion by broadband and filtered directional noise. *Perception & Psychophysics*, 26, 206-214.
- Ball, K. & Sekuler, R. (1980). Human vision favors centrifugal motion. *Perception*, 9, 317-325.
- Crowell, J. A. & Banks, M. S. (1993). Perceiving heading with

- different retinal regions and types of optical flow. *Perception & Psychophysics*, 53, 325–337.
- Gibson, J. J. (1950). *Perception of the visual world*. Boston: Houghton Mifflin.
- Gnadt, J. W., Bracewell, R. M. & Andersen, R. A. (1991). Sensorimotor transformation during eye movements to remembered visual targets. *Vision Research*, 31, 693–715.
- Heeger, D. J. & Jepsen, A. (1990). Visual perception of three-dimensional motion. *Neural Computation*, 2, 129–137.
- Israël, I. & Berthoz, A. (1989). Contribution of the otoliths to the calculation of linear displacement. *Journal of Neurophysiology*, 62, 247–263.
- Knudsen, E. I., du Lac, S. & Esterly, S. (1987). Computational maps in the brain. *Annual Review of Neuroscience*, 10, 41–65.
- Koenderink, J. J. & van Doorn, A. J. (1987). Facts on optic flow. *Biological Cybernetics*, 56, 247–254.
- Longuet-Higgins, H. C. & Prazdny, K. (1980). The interpretation of moving retinal image. *Proceedings and Philosophical Transactions of the Royal Society*, 208, 385–397.
- Orban, G. A., Van Calenbergh, F., DeBruyn, B. & Maes, H. (1985). Velocity discrimination in central and peripheral visual field. *Journal of the Optical Society of America*, 2, 1836–1847.
- Osaka, N. (1988). Speed estimation through restricted visual field during driving in day and night: naso-temporal hemifield differences. In Gale, A. G., Freeman, M. H., Haslegrave, C. M., Smith, P. & Taylor, S. P. (Eds), *Vision in vehicles—II* (pp. 45–55). Elsevier Science Publishers B.V.: North Holland.
- Royden, C. S., Banks, M. S. & Crowell, J. A. (1992). The perception of heading during eye movements. *Nature*, 360, 583–585.
- Roy, J., Komatzu, H. & Wurtz, R. H. (1992). Disparity sensitivity of neurons in monkey extrastriate area MST. *Journal of Neuroscience*, 12, 2478–2492.
- Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y. & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *Journal of Neuroscience*, 6, 145–157.
- Telford, L. & Frost, B. J. (1993). Factors affecting the onset and magnitude of linearvection. *Perception & Psychophysics*, 53, 682–692.
- van de Grind, W. A., Koenderink, J. J., van Doorn, A. J., Milders, M. V. & Voerman, H. (1993). Inhomogeneity and anisotropies for motion detection in the monocular visual field of human observers. *Vision Research*, 33, 1089–1107.
- Warren, W. H., Blackwell, A. W., Kurtz, K. J., Hatsopoulos, N. G. & Kalish, M. L. (1991). On the sufficiency of the velocity field for perception of heading. *Biological Cybernetics*, 65, 311–320.
- Warren, W. H. & Hannon, D. J. (1988). Direction of heading is perceived from optical flow. *Nature*, 336, 162–163.
- Warren, W. H. & Kurtz, K. J. (1992). The role of central and peripheral vision in perceiving the direction of self-motion. *Perception & Psychophysics*, 51, 443–454.

---

*Acknowledgement*—This research was supported by Grant NSF BNS-9109514.