# Perception and reconstruction of two-dimensional, simulated ego-motion trajectories from optic flow.

**R.J.V. Bertin†, I. Israël†, M. Lappe‡**

**Abstract**
A veridical percept of ego-motion is normally derived from a combination of visual, vestibular, and proprioceptive signals. In a previous study, blindfolded subjects could accurately perceive passively travelled straight or curved trajectories provided that the orientation of the head remained constant along the trajectory. When they were turned (whole-body, head-fixed) relative to the trajectory, errors occurred. We ask here whether vision allows for better path perception in similar tasks, to correct or complement vestibular perception. Seated, stationary subjects wore a head mounted display showing optic flow stimuli which simulated linear or curvilinear 2D trajectories over a horizontal ground plane. The observer's orientation was either fixed in space, fixed relative to the path, or changed relative to both. After presentation, subjects reproduced the perceived movement with a model vehicle, of which position and orientation were recorded. They tended to correctly perceive ego-rotation (yaw), but they perceived orientation as fixed relative to trajectory or (unlike in the vestibular study) to space. This caused trajectory misperception when body rotation was wrongly attributed to a rotation of the path. Visual perception was very similar to vestibular perception.

Key words: path perception, ego-motion; optic flow; linear heading, circular heading, vision; vestibular.

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# 1— Introduction

Vision provides a wealth of information about our whereabouts in the external world. Much of the information concerning position and (ego)movement can be gleaned from the *optic flow* (Gibson, 1950; Gordon, 1965; Koenderink & van Doorn, 1977,1987; Koenderink, 1986; Lee, 1974,1980), the distribution of local velocities over the visual field arising when we move through the world. It has been shown that this information is used throughout much of the animal kingdom. Vertebrates (birds and mammals including humans) use optic flow information in many tasks involving ego-motion (Lee & Young, 1985; Judge, 1990; Lee, 1991; Barinaga, 1991; Lee *et al.*, 1993; Wang & Frost, 1992; Wylie *et al.*, 1998; Lappe & Bremmer, 1999a; Lappe *et al.*, 1999b). But also arthropods, especially insects rely on it in many and often remarkably similar ways (Wehner & Lanfranconi, 1981;(Wehner & Lanfranconi, 1981) Götz, 1975; Krapp & Hengstenberg, 1996), notably ants and bees for estimating travelled distance (Collett, 1996; Schöne, 1996).

There is a substantial body of literature providing psychophysical evidence which shows that humans can accurately determine their heading direction of linear ego-motion from short optic flow presentations (Warren *et al.*, 1988; Warren, Blackwell *et al.*, 1991; Crowell & Banks, 1993; Royden *et al.*, 1992,1996; van den Berg, 1992,1996; van den Berg & Brenner, 1994a,b; Warren & Saunders, 1995 Banks *et al.*, 1996; Grigo & Lappe, 1999; Lappe *et al.*, 1999a; ). They can also detect their heading direction on circular trajectories (Rieger, 1983; Turano & Wang, 1994; Stone & Perrone, 1997; Warren, Blackwell *et al.*, 1991; Warren, Mestre *et al.*, 1991(Rieger, 1983; Turano & Wang, 1994; Stone & Perrone, 1997; Warren *et al.*, 1991; Warren *et al.*, 1991)). In some cases, additional visual or even non-visual information is required if the simulated movement is to be perceived correctly: this is the case when the optic flow is ambiguous. For example, the flow that results from a linear translation concurrent with a horizontal eye or head or whole-body rotation resembles very closely the flow that results from a tangential, curvilinear movement (for short presentations and/or small rotations). In absence of disambiguating extra information, such a flow may give rise to a perception of travelling along a curved path (Banks *et al.*, 1996; Crowell,

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1997; Cutting *et al.*, 1997; Royden, 1994; Royden *et al.*, 1992,1994; van den Berg, 1996; Warren & Hannon, 1990; Warren, Blackwell *et al.*, 1991).

Vision is not the only source of ego-motion information we have. Efference copies provide information about intended movements. Proprioception and inertial information coming from the somatosensory and vestibular systems inform about movements actually being made. Combinations of information from these sources can indeed disambiguate the optic flow given as an example above. When making the appropriate eye movements, or when moving the head relative to the trunk in the appropriate way, observers correctly perceive to be moving along a straight path (Royden *et al.*, 1994; Crowell *et al.*, 1998). Finally, in absence of visual information, the vestibular (and somatosensory) system can be relied upon to estimate movement, as long as velocity is not constant (Telford *et al.*, 1995).

Recent work from our group (Ivanenko *et al.*, 1997a,b) showed that subjects can perceive aspects of linear and curvilinear movements when displaced blindfolded on a mobile robot, in some cases correctly reproducing (with pen and paper) the perceived travelled trajectory. In addition, they are capable of updating their angular position relative to a previously seen landmark, even in the absence of semicircular canal input (i.e. with their orientation [yaw] fixed in space). They do not, however, seem to use this information about their orientation to improve their perception of the trajectory.

In the present paper, we study whether subjects can perform the same task based on visual input, in our case optic flow, alone. That is, we address the question whether human observers can correctly perceive visually simulated, passive ego-movement along 2D trajectories. The visual literature cited above show that humans are capable of *instantaneous* perception of heading from short optic flow stimuli. The problem we will study here is whether they can also *integrate* successive instantaneous heading perceptions to form a coherent percept (*reconstruction*) of the travelled path[1]? Virtual reality was used to simulate movement of the subjects, after which they were asked to reproduce the movement they had perceived. To this end they could manipulate a model vehicle of which position and orientation were recorded. Several simulated 2D movements were presented; linear and semicircular trajectories, with the observer's orientation fixed relative to either the trajectory, to the external world, to both or to neither. We compare the results with those obtained in the vestibular study (*op. cit.*).

# 2— Methods

### 2.1- Experimental set-up.

Optic flow stimuli were generated on a Silicon Graphics Indigo[2]/Extreme workstation using the Performer 2.1 libraries, and displayed in a Virtual Research VR4 head mounted display (HMD; FOV 48° horizontal × 36° vertical, 742x230 pixels, 60Hz refresh) worn by the subject. Both eyes saw the same, monochrome, image. The image represented a virtual observer's view through the helmet on a dark (black) environment with white dots (4800; homogeneous, random distribution) on a surface (50x50m; visible up to 15m ahead) 1m below eye-level (see figure 1a). Optic flow was created by simulating movements of the observer through the virtual environment, of which between 150 and 200 points were visible at any given moment. Each stimulus consisted of a 2s stationary period followed by 8s of simulated movement followed by another 2s stationary period.

Subjects were required to reproduce their perception of the simulated movement after stimulus presentation. Their responses were digitised online by means of a CalComp DrawingSlate II tablet (9"x6": resolution 22860x15240 pixels) that they held on their knees. They manipulated a custom-made input device, containing the coil, switches, circuit board and batteries that were removed from the stylus that came with the tablet. The device's instantaneous position (X,Y) and orientation ($\Phi o$; resolution approx. 4°) were read from the tablet using custom-written software running on the Indigo, and saved to disk. During the reproduction, a cursor was presented in the VR helmet, showing the device's current position and orientation, and a trace showing its trajectory. Horizontal and vertical lines intersecting in the centre of the image were also shown as a frame of reference (inset in figure 1a). Buttons on the device allowed the subjects to erase unsatisfactory reproductions and accept (save) only those that best represented their percept. Subjects were instructed to remove the device from the tablet during stimulus presentation. A post-hoc compensation was made for the slight difference in aspect ratio between the VR helmet and the tablet.

### 2.2- Experimental procedure.

Subjects were seated on a standard office chair. The experimenter gave a brief introduction to the experiment, stating that the images they were to see would give the impression of being moved passively, for instance on a chair on wheels that can turn around its vertical axis. A few possible movements not used in the experiment were demonstrated (with the chair) to familiarise the subjects with the fact that yaw need not be yoked to the path. The input device was presented to the subjects as a vehicle capable of this kind of movements, e.g. a boat or hovercraft (or a helicopter restrained to horizontal movement); it will be referred to hereafter as the vehicle. Subjects were allowed to get comfortable with the vehicle and tablet and to train in the reproduction of circular, tangential, movements and rotations in place, both before and after donning the helmet. This also allowed to check if and to what extent they had grasped the idea of reproducing movements (2D, 3 degrees of freedom) with the vehicle.

Subjects were required to reproduce, with the vehicle, on the tablet, their perception of the simulated movement. That is, they were to guide the vehicle through the movement they had just perceived. They

[1] Path integration *stricto sensu*; not implying the maintenance of a "return vector" pointing to the starting point!

were instructed to concentrate on reproducing the perceived movement's spatial geometry, and to make optimal use of the tablet's surface (resolution optimisation). After validating their response, they could ask for re-presentations of the same stimulus, until they were entirely satisfied with their reproduction. To minimise response errors due to either memory or drawing artefacts, subjects were asked whether they required a re-presentation when they seemed unsure about their perception. Similarly, when drawing/reproduction problems were noticed, subjects were asked to assess their result (via the image in the

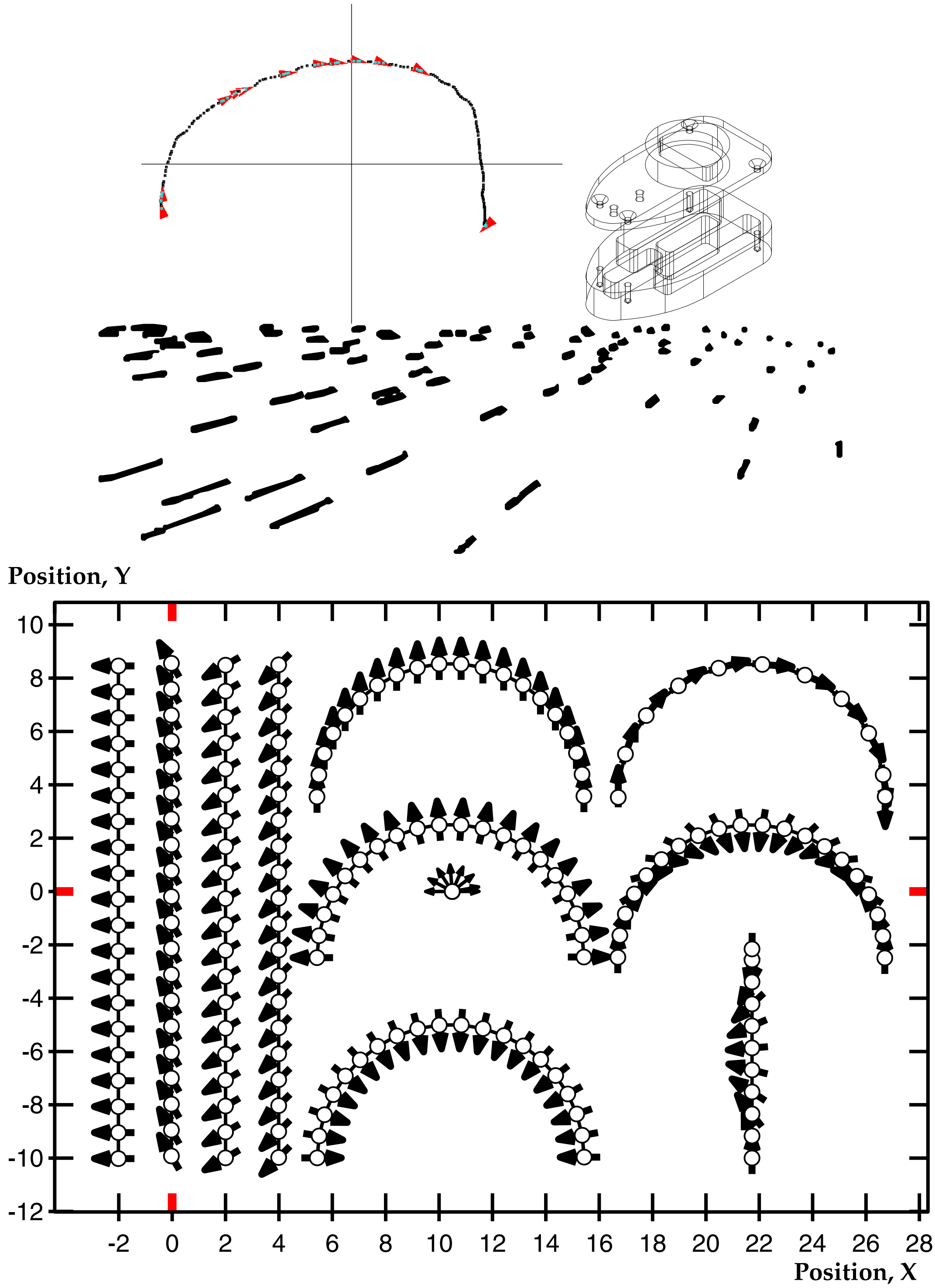



Figure 1. *(a)* Optic flow impression. The figure shows the first moments of the large radius condition semicircle no-turn). In the experimental conditions, only single dots were seen to be moving, with a slightly higher density and otherwise identical geometry and field of view. The upper left inset shows an example of the reproduction feedback the subjects saw in the HMD: here, the input device was guided through a tangential, curvilinear movement. The upper right inset shows an exploded view of the "vehicle", the input device manipulated by the subjects. Vehicle and vehicle drawing © 1998,1999 M. Ehrette. *(b)* Representation of the different stimuli presented. Each curve represents a trajectory (X,Y), the arrows point in the direction of the orientation (Φo). The figure shows only the large conditions, from left to right, top to bottom; (left): **linear lateral** (), **linear oblique 30°** (), **linear oblique 120°** () and **linear oblique 135°** (); (middle): **semicircle no-turn** (), **semicircle outward** (; Φr=90°); the **rotation in place** (), and **semicircle inward** (; Φr=-90°); (right): **semicircle forward** (; Φr=0°), **semicircle full-turn** () and **linear half-turn** ().

HMD), and to either erase and redraw it, or view another presentation and redo the reproduction. Experiments generally did not last longer than one hour, depending on the time spent in familiarising with the set-up, and on the number of re-presentations requested.

The simulated movements (figure 1b) were based on the movements presented in Ivanenko *et al.* (1997b); some were actual simulations thereof. Thus, triangular velocity profiles starting from zero velocity were used, both for linear and angular speed. The angular acceleration was always either 11.46°/$s^2$ (0.2rad/$s^2$) or zero. The figure shows the actual scale (in meters) of the simulated movements. The simulated movements were presented in random order to the subject. Iconic representations (pictograms) will be used throughout to simplify recognition; the tables in the appendix only use pictograms.

We will distinguish three orientations: the orientation of the observer in space (Φo; independent of the trajectory), the orientation of the trajectory (Φp: the angle in space of the tangent to the trajectory) and the observer's orientation relative to the trajectory, Φr = Φo -Φp. Similarly, we will distinguish two types of rotation (change in orientation): Ψo (yaw) and Ψp (the rotation of the trajectory). Angles are expressed in degrees, with positive values indicating clockwise rotation.

The stimuli fall into 3 distinct classes, as listed below:

<u>Stimuli with the observer's orientation (yaw) fixed in space:</u>

I. Linear translation with the observer's orientation oblique at Φr=Φo=30° (condition **linear oblique 30°**), Φo=135° (condition **linear oblique 135°**) and Φo=120° (condition **linear oblique 120°**). Linear acceleration was 1.18m/$s^2$, average translation speed 2.33m/s. (In these stimuli, orientation is also fixed relative to the trajectory.)

II. Semicircular trajectory with Φo=0° (condition **semicircle no-turn**, condition **III** in *op.cit.*).

<u>Stimuli with the observer's orientation fixed relative to the trajectory:</u>

III. Semicircular trajectory with the observer looking outward ("centrifugal": Φr=90°; condition **semicircle outward**).

IV. Semicircular trajectory with the observer looking inward ("centripetal": Φr=-90°; condition **semicircle inward**).

V. Semicircular trajectory with tangential orientation (Φr=0°; condition **semicircle forward**; condition **II** in *op.cit.*)). The average speed of rotation (Ψo) in III, IV and V was -22.5°/s.

<u>Stimuli with the observer's orientation changing in space and relative to the trajectory:</u>

VI. Semicircular counterclockwise trajectory with a full rotation (Ψo=360°, starting at 0°; condition **semicircle full-turn**; condition **V** in *op.cit.*)[2]. The average speed of rotation (Ψo) was 45°/s.

VII. Linear translation with Ψo=180° starting at 0°, (figure 1d; condition **linear half-turn**; condition **VI** in *op.cit.*).

VIII. A Ψo=-180° clockwise **rotation in place** (; condition **I** in *op.cit.* ). The average speed of rotation (Ψo) was -22.5°/s.

The semicircular conditions were all presented with a large (5m) and a small (1.5m) radius. In these conditions, the average speed of translation was 0.59m/s for the small, and 1.96m/s for the large radius, while the direction of translation rotated at an average speed of ±22.5°/s. Condition **linear half-turn** was also presented in two lengths: 7.8m and 4.7m. In the short version, simulated acceleration was 0.3m/$s^2$, and the average speed of translation 0.59m/s. In the long version, acceleration was 0.5m/$s^2$, and the average speed of translation 0.98m/s. Both had an average speed of rotation (Ψo) of 22.5°/s. In the vestibular experiment, only the small/short conditions were used.

These experimental trials were preceded by 1) a simple forward translation and 2) a lateral translation (Φo=90°: condition **linear lateral**). For these two stimuli, the subjects were given feedback to arrive at the correct interpretation of the simulated movements; this served as a final check whether they completely grasped the task, and to help them get used to the optic flow and its presentation in the helmet[3].

23 Subjects (aged 20 to 50 approximately) participated in the experiment. All subjects saw the stimuli presented above. Of these, 16 subjects saw an additional set of stimuli (containing landmarks) that will be reported on in a future paper. The other 7 subjects saw a stimulus set designed to test for a possible influence of the stimuli's velocity profiles. To rule out such an effect, all stimuli were presented twice to these subjects: once with the triangular velocity profile and once with constant velocity (and with identical duration) — intermingled in random order. To mask the abrupt transition from stationary to movement in the constant velocity stimuli, dots had a limited lifetime during the initial stationary period, increasing from 3 frames to approx. 85-100 frames. Where necessary, we will refer to these two sub-populations as Group 1 (with 16 subjects) and Group 2 (with 7 subjects) respectively.

After the experiment subjects were asked for their general impression of the stimuli and of their task. The subjects in Group 2 were also asked if they had remarked that each movement had been presented in two different ways (that is, with a triangular and a constant velocity profile).

**2.3- Data analysis.**

Some subjects showed better manual skills at manipu-

[2] This kind of movement occurs on certain *merry-go-rounds* (carousels); it was included in the vestibular study because it stabilises the observer's orientation "relative to the rotating linear acceleration vector" (*op.cit.*).

[3] The VR4 has some cushion distortion in the corners of its view. This is an overly common problem with HMDs, probably due to the size of the field of view and the closeness of the screens.

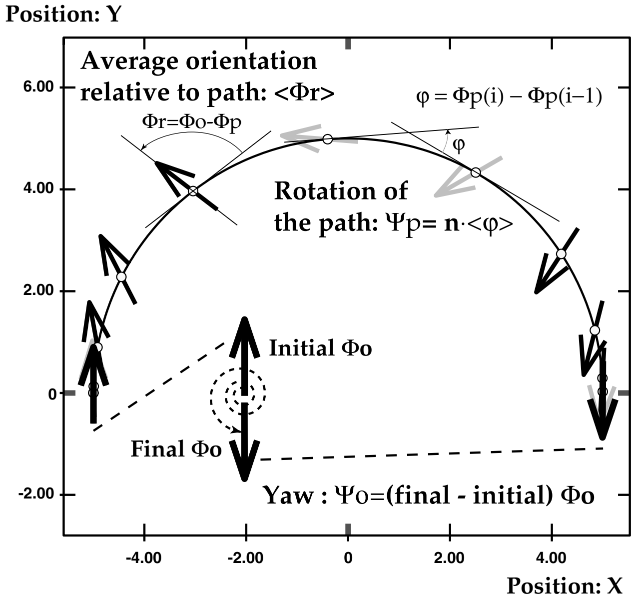



Figure 1. (*c*) Explication of the indices used in the quantitative analyses. Ψp, the average rotation of the path is calculated from the average difference between the tangents to the trajectory in 2 consecutive (resampled) points, multiplied by the number of segments per curve (19). The total yaw Ψo is calculated by (non circular) summation over Φo, minus the initial orientation; thus, 2 full observer turns give Ψo=720°. The average orientation relative to the path, <Φr>, is calculated as the average difference between Φo and Φp in the 20 resampled points. All these measures are expressed in degrees and averaged over subjects. In this example (clockwise semicircle with counterclockwise yaw; not used in the experiments), Ψo=180°, Ψp=-180° and <Φr>=179.7°±109.8°.

lating the vehicle than others, and thus the responses cannot directly be compared amongst each other or to the stimuli. The traces were therefore filtered to remove clutter from the initial positioning of the vehicle and jerk movements due to (transient) individual problems with the vehicle's handling. Such artefacts are easy to recognise and include: 1) samples with the device resting in the same location and orientation for prolonged periods, 2) clutter resulting from putting the vehicle in the desired starting position and/or orientation and 3) abrupt movements caused by lifting the vehicle to validate a reproduction. These are all easily identifiable by comparing response plots (cf. figures 1 and 2) with side-by-side X, Y and Φo time-series; 1) as leading or trailing horizontal lines on the time-series, 2) as random variations in X and Y with Φo approaching the intended value (up to the moment when X and Y start changing systematically and smoothly) and 3) as a sharp jump in X and/or Y, in extreme cases followed by a return to the desired position[4].

After filtering, the data were resampled to 20 equidistant points per trace. This was done with an interpolating algorithm using cubic splines. Individual splines were fitted to the $X_i$, $Y_i$ and $\Phi o_i$ co-ordinates, using $L_i$ — the length of a trace from its beginning (*i.e.* the travelled distance) up to ($X_i$,$Y_i$) — as the independent variable; where $i$ is the sample/point number ($i$=1…$n$). Resampling was then achieved by taking the "splined" $X^*_j$, $Y^*_j$ and $\Phi o^*_j$ at 20 points $L^*_j$, with $L^*$ linear and between $L^*_1 = L_1 = 0$ and $L^*_{20} = L_n$.

Our protocol does not allow us to analyse reproduced speeds, nor scale. We thus focus our quantitative analyses on orientation (Φ) and change in orientation (rotation; Ψ) only. The three orientations and the two types of rotation that we can distinguish have been introduced above. Of these, we use the following observables as indices to quantify or results: Ψp, Ψo and the average orientation relative to the path <Φr>; cf. figure 1c. Ψp is computed as the average difference between two consecutive tangent measures, times the number of segments in the curve. Its value is zero for a straight line, or 180° for a semicircular trajectory. Its standard deviation measures the constancy of path rotation. The standard deviation is 0 for e.g. a perfectly straight line or for a perfect semicircle. The perceived yaw Ψo is calculated by summing the Φo values in the resampled points, minus the initial orientation (such that for 2 observer turns, Ψo=720°). Finally, <Φr> is computed as the average of the difference between orientation and heading (orientation *minus* heading, where heading is the tangent to the reproduced path). This measure gives 0 for a correct reproduction of a tangential movement, and a zero standard deviation for an orientation remaining perfectly fixed relative to the trajectory. For this index, Φp, Φo and their difference are all expressed as values between [-180°,180°].

# 3— Results

### 3.1- General observations.

Integration of instantaneous self-motion information from optic flow proves to be possible — at least to a certain degree — but it is certainly not always an easy task. In fact, subjects found the task quite difficult, but did not experience discomfort caused by the stimuli. Most subjects indicated that they had experienced the impression of ego-motion, but that this impression had not been equally strong in all conditions.

Several different "strategies" for reproducing the movement were observed. For instance, some subjects made reproducing movements with the vehicle during the stimulus presentation. A few subjects asked for a large number of re-presentations to verify a representation of the path they had perceived. Most subjects, however, did not ask for more than 2 presentations, and were satisfied with a single presentation for most of the stimuli. Their perception mostly did not differ very much between presentations of the same stimulus. They did however forget the direction of (especially) Ψo rather frequently, and corrected this in a 2nd presentation.

Figure 2 (panels a through j) shows a selection of subjects' reproductions. It can be seen that the variability among subjects' responses depends on the stimulus. Generally speaking, optic flow fields simulating what are apparently simple movements give rise to correct responses (at least as far as the trajectories' form is concerned), with little variation between subjects. Such is

[4] In most instances of 2) and 3), the sampling rate is (much) higher than during the actual reproduction (sampling rate peaks at 120Hz and depends on the device's speed of displacement).

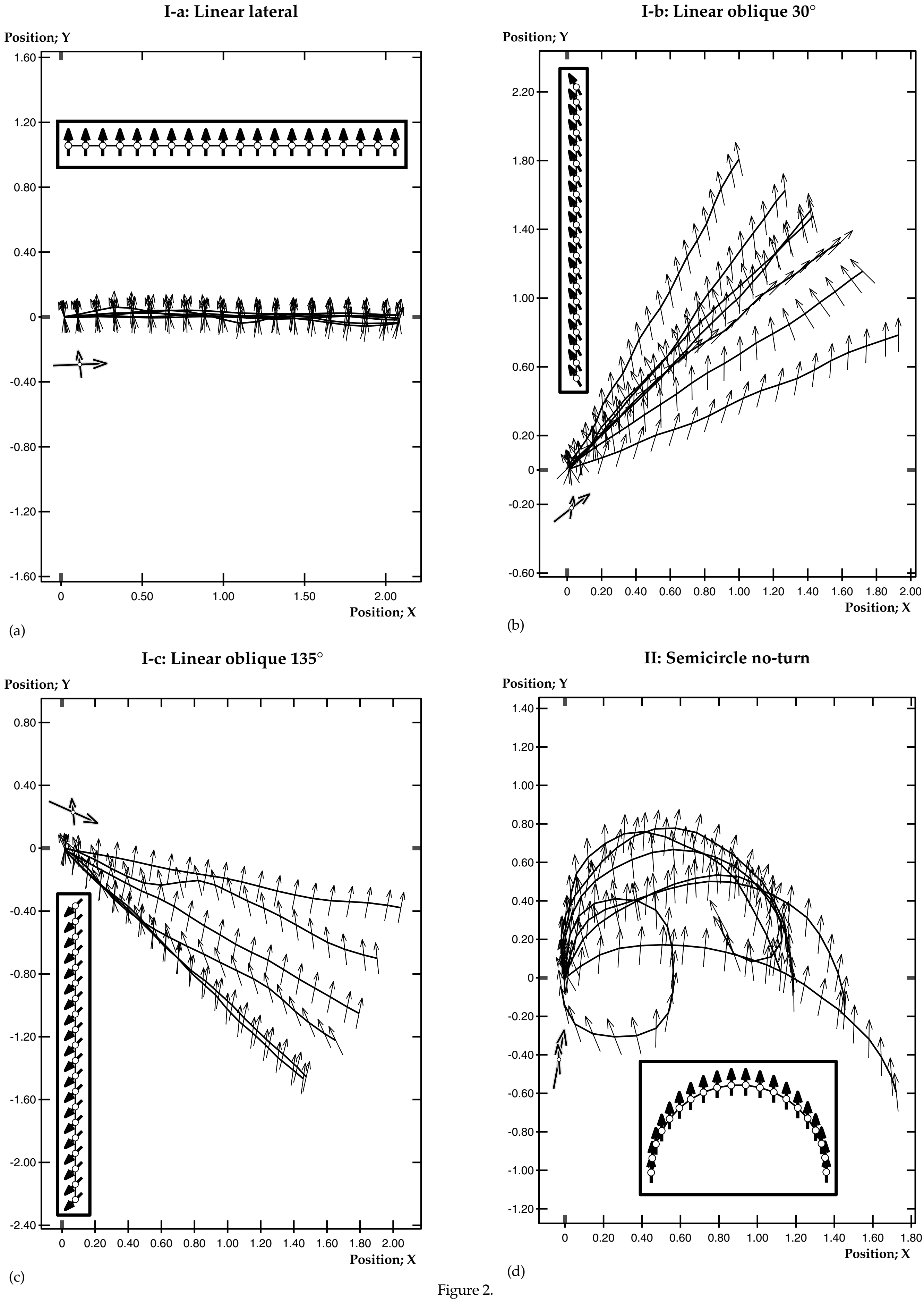

I-a: Linear lateral
Position; Y
1.60
1.20
0.80
0.40
0
-0.40
-0.80
-1.20
-1.60
0
0.50
1.00
1.50
2.00
Position; X
(a)
I-b: Linear oblique 30°
Position; Y
2.20
1.80
1.40
1.00
0.60
0.20
0
-0.20
-0.60
0
0.20
0.40
0.60
0.80
1.00
1.20
1.40
1.60
1.80
2.00
Position; X
(b)
I-c: Linear oblique 135°
Position; Y
0.80
0.40
0
-0.40
-0.80
-1.20
-1.60
-2.00
-2.40
0
0.20
0.40
0.60
0.80
1.00
1.20
1.40
1.60
1.80
2.00
Position; X
(c)
II: Semicircle no-turn
Position; Y
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0
-0.20
-0.40
-0.60
-0.80
-1.00
-1.20
0
0.20
0.40
0.60
0.80
1.00
1.20
1.40
1.60
1.80
Position; X
(d)

Figure 2.

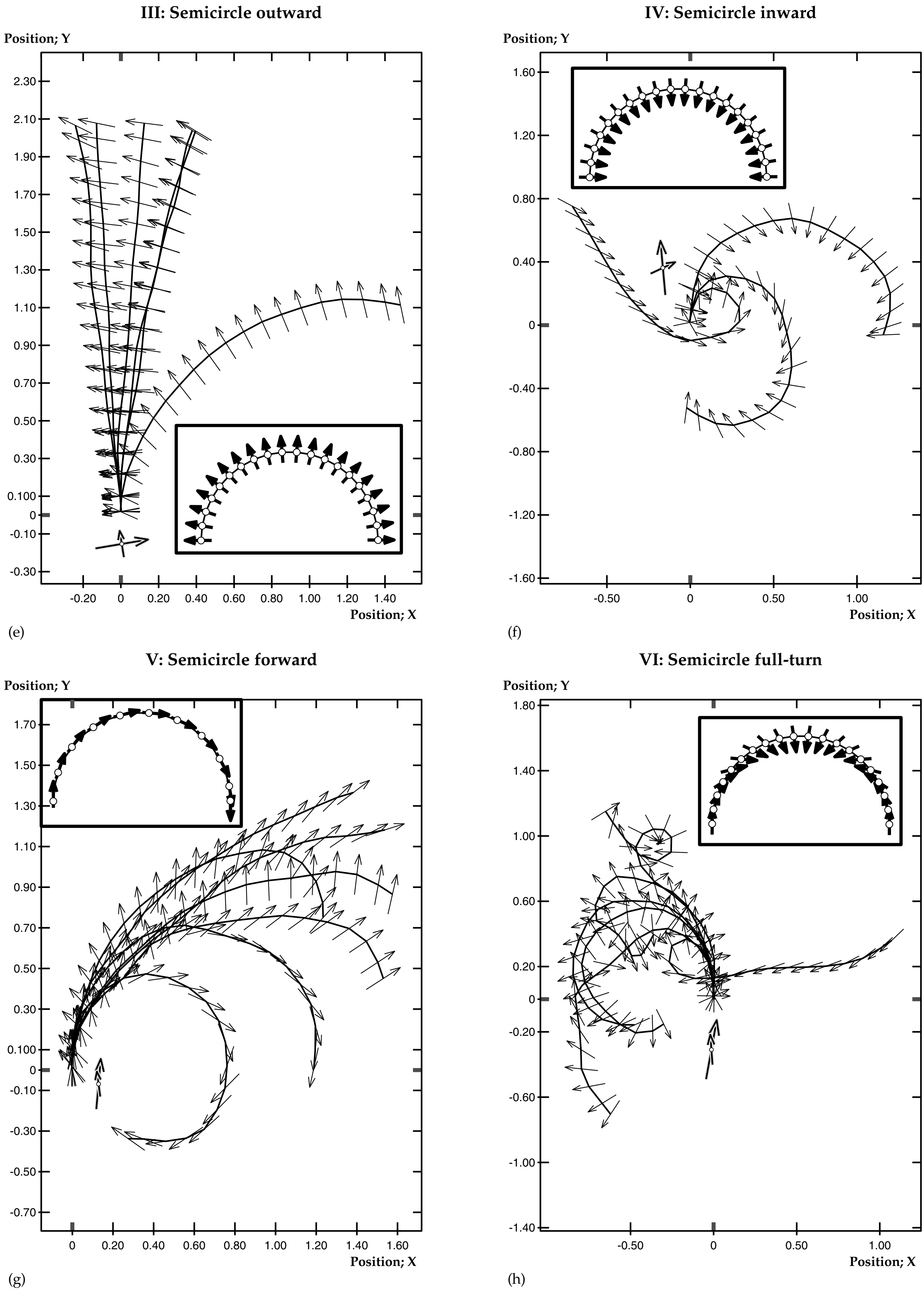
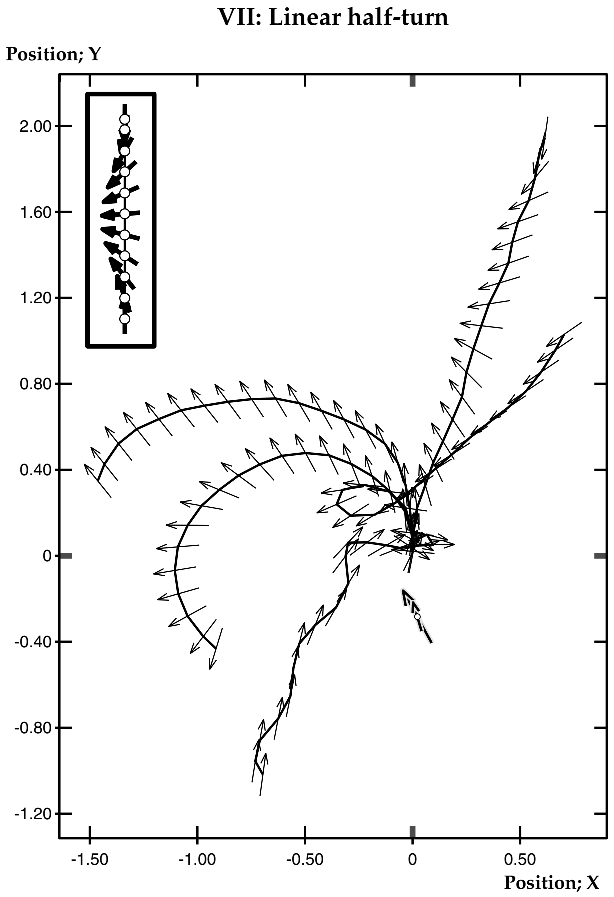
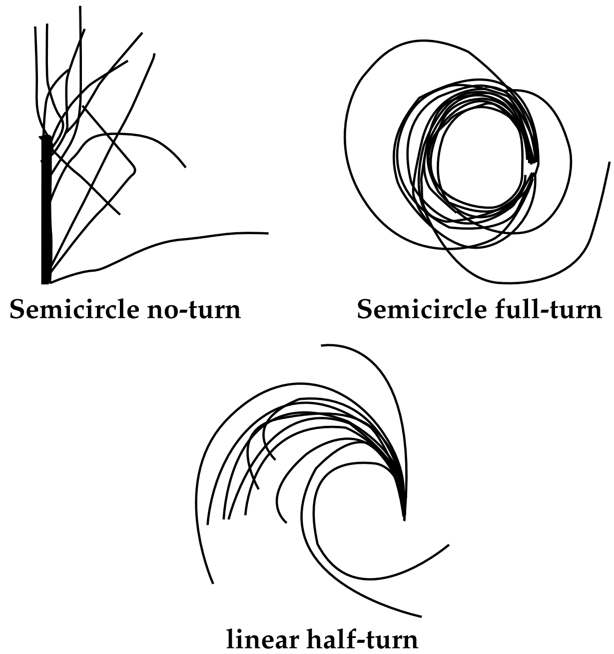



Figure 2 *(continued)*.




(i)




(j)

Figure 2. A selection of reproductions from Group 2 (a-j): all responses to the large/long stimuli with triangular velocity profile. The stimuli are listed in the figures' titles, which also refer to the stimulus enumeration in the Methods. The responses are filtered and resampled as described in the Methods. To clarify the presentation, the trajectories were then translated to start in the origin and normalised to uniform length, and the responses were rotated as follows. For the conditions with fixed Φo (in the stimulus; figures 2a through d), the individual reproductions were all rotated over the same angle, such that the resulting orientation averages to 0°. In the other conditions, the reproductions were rotated such that the 1st trajectory segment is oriented at 0°. Finally, the reproductions received additional smoothing. The "clock face" display of two arrows indicates the average initial Φp (the longer arrow) and the average initial Φo (the smaller arrow). The insets show the stimulus. The indices for the sets shown in the panels are (all values in degrees): (a) Ia, **linear lateral**: <Φr>= 90.52 ± 5.833; Ψp= -3.836 ± 7.634; Ψo= -15.89 ± 8.222; (b) Ib, **linear oblique 30°**: <Φr>= 46.52 ± 5.659; Ψp = -1.167 ± 7.498; Ψo = 7.137 ± 17.12; (c) Ic, **linear oblique 135°**: <Φr>= 121.4 ± 6.059; Ψp = 3.255 ± 2.950; Ψo = -4.797 ± 7.220; (d) II, **semicircle no-turn**: <Φr>= 93.49 ± 61.62; Ψp = -225.0 ± 93.42; Ψo = 1.100 ± 9.242; (e) III, **semicircle outward**: <Φr>= 83.98 ± 7.169; Ψp = -23.65 ± 37.63; Ψo = -30.15 ± 15.87; (f) IV, **semicircle inward**: <Φr>= -98.40 ± 60.11; Ψp = -294.1 ± 64.57; Ψo = -199.2 ± 70.01; (g) V, **semicircle forward**: <Φr>= 31.20 ± 16.12; Ψp = -159.4 ± 75.77; Ψo = -117.2 ± 92.82; (h) VI, **semicircle full-turn**: <Φr>= -97.48 ± 50.63; Ψp = 196.8 ± 263.4; Ψo = 158.7 ± 269.7; (i) VII, **linear half-turn**: <Φr>= -142.7 ± 72.51; Ψp = 128.3 ± 172.7; Ψo = 115.6 ± 60.17; (j) The trajectory drawings from the vestibular experiment, conditions **semicircle no-turn**, **semicircle full-turn** and **linear half-turn**.

the case for stimuli in which the simulated speed of translation is high relative to the simulated rotation speed (figure 2a-d). In the case of more complicated movements, subjects increasingly detect (or reproduce) only certain properties of the simulated movement. Quite often subjects report a rotation in place rather than a movement that contains translation.

A remarkable result is that none of the subjects in Group 2 noticed that there were two different velocity profiles. In addition, there is no significant difference in perception of the stimuli with triangular velocity profile, and those with constant velocity. In the following text we will therefore make no distinction between data from conditions with a triangular or constant velocity profile.

Once a stimulus has been associated with a certain movement, ("understood", whether correctly, or not), it is recognised almost all the time.

### 3.2- Response classification.

As mentioned above, the degree of correctness of the subjects' responses (performance) varies between conditions and subjects. We assess performance qualitatively by scoring globally correct responses, and responses with the correct type of trajectory. A globally correct response is one that retains the crucial components of the actually presented movement. Thus, for a lateral (oblique) translation, a reproduced movement is globally correct when it is clearly intended to be linear, has the correct direction and the observer's orientation oblique to the path. For a complex movement such as condition **semicircle full-turn** (a counterclockwise semicircle with Ψo=360°), a globally correct response would be a counterclockwise curvilinear trajectory with the orientation changing in counterclockwise direction relative to the trajectory. The initial observer orientation and the initial direction of movement (e.g. 0°, or ±90°, in

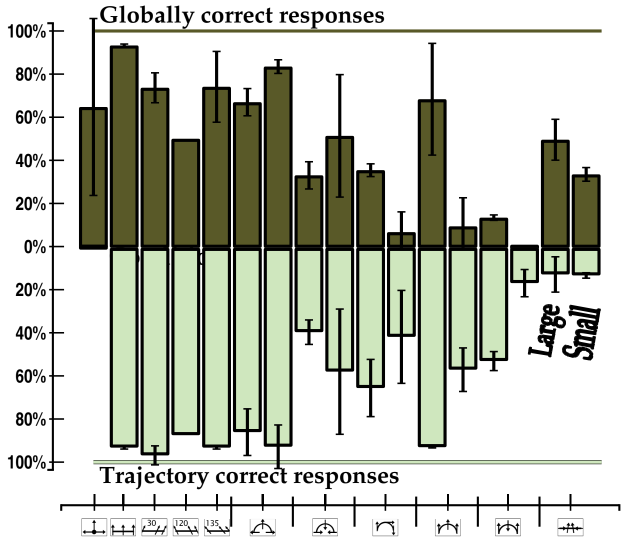



Figure 3. Performance observations: globally correct responses and responses with the correct type of trajectory, each expressed as a percentage of the number of observations. Percentages shown are calculated over all subjects. The errorbars show the standard deviation in the mean of the per-group performances. Stimulus linear oblique 120° ( ) was not presented to Group 2. Compare with Table 2 in the Appendix, which lists absolute values and numbers of observations. Conditions are labelled with iconified representations of the stimuli. For conditions that were presented in two sizes, the responses to the large/long stimulus are always shown as the leftmost bar, as indicated in the graph. See the text for the remaining details.

space) cannot be derived from our stimuli. Thus, we only consider the initial orientation with respect to the initial orientation of the path, but we disregard the absolute, space-relative initial orientation and the initial direction of the reproduced movement. In other words, for the condition **semicircle outward**, a circular path starting at an angle of 0° forward with the observer oriented approximately perpendicularly outward (say, 80°) is equally correct as a circular path starting at an angle of -40° ("north-eastward") with the observer oriented 40° outward.

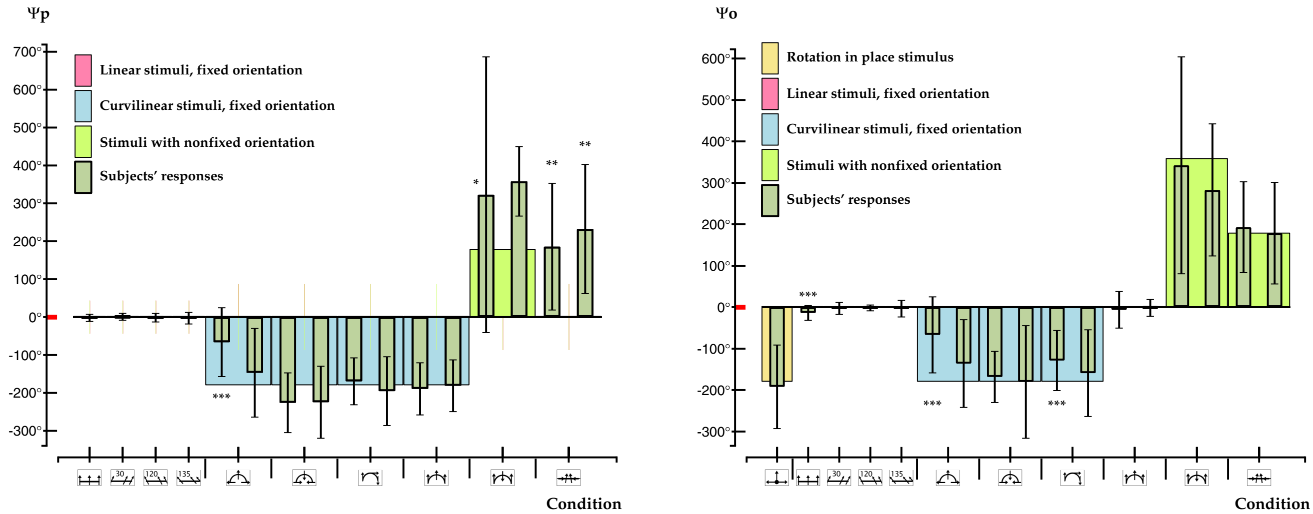
Figure 3 shows a classification of our data according to these principles. For completeness, the "raw" data are listed in Table 2, which also lists the number of samples per condition and group. The figure and the table also list a score of responses in which the type of trajectory reproduced was correct, *i.e.* trajectories that preserve *a)* the curvilinearity of the stimuli **semicircle inward**; **semicircle forward**; **semicircle no-turn** and **semicircle full-turn**, or *b)* the linearity of the stimuli **linear lateral**, **linear oblique** , , and **linear half-turn**. The table also lists the number of rotation in place responses observed.

When the observer's orientation is fixed in space, performance is generally good. This is much less the case for the conditions in which the orientation is fixed only relative to the trajectory, or not at all. Two general observations can be made for these stimuli: *1)* there are many rotation in place responses; *2)* in general, there are more globally correct responses to the large/long stimuli than to the small/short (e.g. the two conditions **semicircle forward**).

Some more detailed observations will be made in the presentation of the results below.

### 3.3- Quantitative analyses.

The results of the quantitative analyses are shown in figures 4 and 5. The detailed results are listed in Table 3. The table also lists the initial heading (the orientation of the trajectory's 1$^{st}$ segment), in addition to the values of the three indices introduced above, Ψp, Ψo and <Φr>. All these observables are averaged over subjects, per condition. Average initial orientation is given for the




(a) (b)

Figure 4. *(a)* Ψp for all conditions but the rotation in place. Shaded, striped bars show the expected (i.e. stimulus) values. Asterisks indicate significance of difference with the expected values. Errorbars show standard deviation of the mean. Asterisks indicate significant differences from the expected values, determined by t-tests using mean and average standard deviation; * ≡ p< 0.05, ** ≡ p< 0.005, *** ≡ p< 5·10-4 (Student's t). For the conditions that were shown in two sizes, the response to the large/long stimulus is shown in the left-hand bar, the small in the right-hand bar. There is a significant undershoot for the large **semicircle outward**: this stimulus is often seen as a lateral translation. It can clearly be seen that a change of orientation relative to trajectory and space is often attributed to a rotation of the path instead (**semicircle full-turn** and **linear half-turn**). *(b)* Ψo for all conditions. The **rotation in place** condition is shown leftmost. All presentation details as in figure 4a.

stimuli, and also averaged over all subjects' responses. Only responses that were not rotations in place, and without rotation in the wrong direction are included in the analysis. The number of responses retained is listed in the table. This excludes responses that are clearly uncorrelated with the stimulus, but includes the following frequent misinterpretations: *1)* lateral translations in condition **semicircle outward**; *2)* more-than-180°-arc (|Ψp| >180°; full circle, spiral, …) trajectories[5] with Ψp and Ψo in the right direction in condition **semicircle full-turn** and *3)* curvilinear trajectories with Ψo in the right direction in condition **linear half-turn**. <Φo> is undefined for rotations in place, so for condition we give only the initial heading and the average Ψo (for all responses), and Ψp for responses that are not rotations in place.

Differences between measured responses and the presented (ideal) values, and between per-condition responses are tested with Student's t-tests.

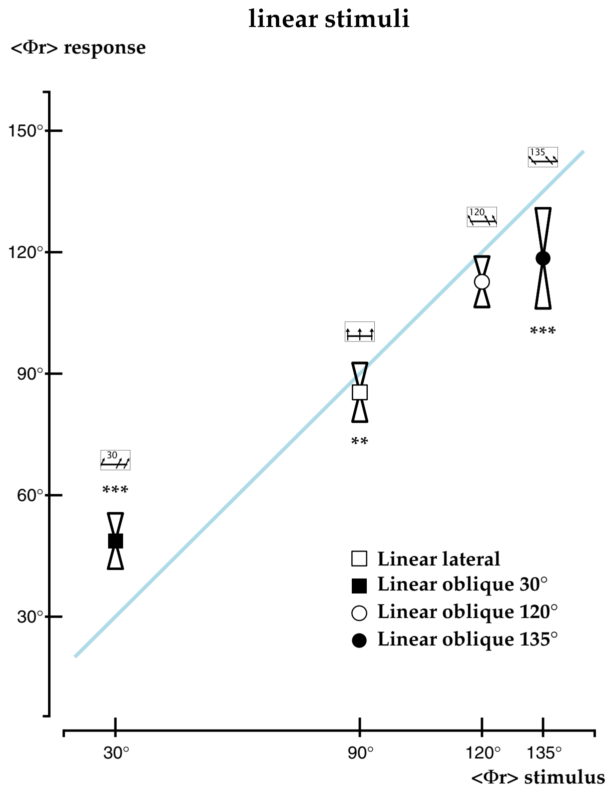
The rotation of the path (Ψp) and the reported yaw (Ψo) are shown in figures 4a and 4b respectively (narrow bars with heavy outline), together with the presented values (broader bars with light outline). Both properties generally seem to be well perceived. Figure 5 shows <Φr>, reported versus presented, for the conditions with fixed Φr. Correct responses would fall on the shaded line.

A quick glance at these figures would suggest that — albeit considerable variability — the task is on average well performed by our subjects. However, not all responses were included in the computation of the quantitative results (compare the **N** columns in Tables 2 & 3), and we have not yet considered the reported initial heading and orientation. Therefore we will now proceed to a condition-per-condition analysis, referring to the qualitative observations where appropriate.

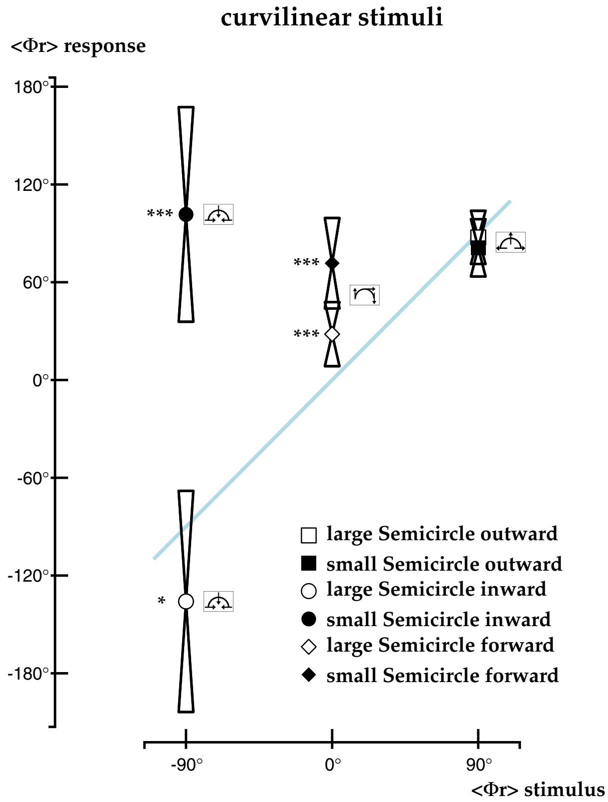
In the **linear lateral** condition, responses are near perfect (figure 2a). Subjects maintain almost the correct Φr (<Φr> ≈ -90°) and they reproduce trajectories which are close to linear on average (|Φp| < 5°). However, since they assume an initial Φo=0°, their initial heading is approximately 90° to the right. A similar type of response can be observed in the other linear stimuli, conditions **linear oblique 30°** (figure 2b); **120°** and **135°** (figure 2c). Here, there is overshoot of the smaller angle (approximately 60%; **linear oblique 30°**) and up to 12% undershoot of the larger angles (**linear oblique 120°** and **135°**). Thus, in these conditions, in which orientation is fixed relative to the trajectory and in space, perceived orientation is approximately correct relative to the trajectory, but not in space. As a result, condition **linear oblique 30°** is perceived as a forward movement, and conditions **linear oblique 120°** and **135°** as backward (initial heading less than 90° rightward and more than 90° rightward respectively). This is not erroneous or inaccurate perception; our stimuli do not contain any information whatsoever about the initial orientation.

In the case of condition **semicircle no-turn** (figure

[5]NB: This corrects the statement "linear trajectories with Ψo in the right direction..." in the version published in Vision Research! There were only two such responses.




(a)




(b)

Figure 5. *(a)* Observed vs. presented (i.e. stimulus) <Φr> values, for the 4 linear stimuli with fixed Φo. Errorbars show average standard deviation (averaged over per-subject values). Correct responses would fall on the grey line. All values in degrees. Asterisks indicate levels of significance of difference with presented value: * ≡ p< 0.05, ** ≡ p< 0.005, *** ≡ p< 5·10-4 (Student's t). *(b)* Observed vs. presented (i.e. stimulus) <Φr>, for the semicircular conditions with fixed Φr. Presentation as in figure 5a.

| **trajectory only** | **Ψo [°]** | | | **Ψp [°]** | | | **<Φr> [°]** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **h 1** | **h 2** | **p** | **h 1** | **h 2** | **p** | **h 1** | **h 2** | **p** |
| **semicircle full-turn:** | 180 | 180 | | 90 | 90 | | 42.6 | 132.4 | |
| **response, large version:** | 145.4 | 188.4 | 0.078 | 131.3 | 181.9 | 0.054 | -18.9 | -55.7 | 0.075 |
| **linear half-turn:** | 90 | 90 | | 0 | 0 | | 42.6 | 132.4 | |
| **response, long version:** | 85.7 | 116.7 | 0.068 | 92.6 | 84 | 0.77 | -27.8 | -4.78 | 0.2 |
| **response, short version:** | *77.3* | *104.2* | *0.017* | 117 | 104.1 | 0.69 | -29.5 | -23.9 | 0.7 |

Table 1.The three quantitative measures calculated for the first (h1) and second (h2) halves of the conditions with orientation changing relative to space and to the trajectory, presented and subjects' responses. The p values indicate the significance of the difference between the first and second halves of the subjects' responses. The small condition **semicircle full-turn** is excluded because of an insufficient number of observations.

2d), the quantitative results repeat what was already evident from the qualitative results in figure 3: these stimuli are perceived correctly. The differences from the expected values are all non-significant.

In condition **semicircle outward** (figure 2e), <Φr> is perceived correctly, although there is more variability than in the linear conditions. In the stimulus with the large radius, the optic flow resembles much more the laminar flow of a lateral translation than in the small radius stimulus. Indeed approximately half the subjects reproduce linear trajectories. Ψp confirms this: for the large radius, |Ψp|< 180° ($p< 0.001$); for the small radius, |Ψp| is more than 2x larger at $p\approx 0.08$. This difference also shows in Ψo, which approximates Ψp and is thus too small (significant at $p< 10^{-5}$ for the large radius), although less so (larger) for the small radius ($p< 0.03$). Initial heading is mostly to the right, even for the correct responses.

Condition **semicircle inward** (figure 2f) is clearly difficult. Most of the subjects who perceive a movement other than a rotation in place see a curvilinear trajectory. There is no consistent perception of ego-orientation (Φo or Φr), but for the small radius version, curvilinear responses typically have either a "centrifugal" Φr ≈ 90°, or, in some cases, Φo fixed in the environment. The large radius stimulus is perceived as a backwards movement (|<Φr>|> 90°; $p< 0.02$). There is also a tendency to perceive a trajectory spanning more than half a circle (|Ψp|> 180°). Ψo is approximately correct, however.

A large number of the curvilinear trajectories reproduced for condition **semicircle forward** (figure 2g) maintain a fixed Φr — only oriented outwards, "centrifugal" (<Φr> > 0°; almost all for the small radius; almost 50% for the large radius in Group 2). This causes a significant undershoot of Ψo ($p< 0.001$). Perception is better for the stimulus with the large radius (figure 3). Indeed, <Φr> is smaller ($p< 10^{-6}$) and the initial heading is on average more forward ($p< 0.002$) for the large than for the small radius. Also, a larger number of curvilinear trajectories are perceived in the *large* radius condition (figure 3).

Subjects have the greatest problems with the conditions in which orientation is not fixed at all; **semicircle full-turn** (figure 2h) and **linear half-turn** (figure 2i). The reported <Φr> is actually negative instead of 90°. In addition, Ψp is too large; between 50% and 150% in condition **semicircle full-turn** ($p< 0.02$; $p< 0.0001$ in **linear half-turn**). Ψo is more or less correct, though[6]. This combination of approximately the right amount of yaw combined with a too curved trajectory explains the negative <Φr> values: Ψo "trails" relative to Ψp (see figures 2h and 2i). In condition **linear half-turn**, Ψp is on average closer to the amount of simulated Ψo than to the actually simulated Ψp = 0°. This hints at what probably happens: subjects seem to attribute Ψo to Ψp. This also explains the overshoot of the Ψp in condition **semicircle full-turn**.

Our results thus suggest that subjects assume that the rotation they perceive is due to a rotation of their trajectory, at least for a large part. Do they at some point notice the difference between stimulus and perception that will inevitably be caused by this illusion, or do they stick to their initial perception? To test this, we calculated our measures independently for the two halves of each response, and tested for differences using analyses of variance (subjects x conditions x halves). When tested over all conditions, there was no significant difference between the first (h1) and the second (h2) half of the responses, in neither of the 3 measures. There are differences however for the large **semicircle full-turn**, and the long and short **linear half-turn**: see Table 1.

Subjects report significantly more yaw in the second half of their response than in the first (Ψo main effect: $F(1,12)=6.33$, $p< 0.027$). In condition **semicircle full-turn**, the reported trajectory is also more curved in the second half (Ψp), whereas the larger value for <Φr> would suggest that the subjects do indeed perceive that their orientation changes relative to the trajectory.

# 4— Discussion

We studied the perception of ego-movement during visually simulated passive 2D displacements in the horizontal plane. The displacements simulated straight or curved trajectories, with in some cases ego-rotation relative to the trajectory and/or in space. Specifically, we asked whether human observers can perceive (reconstruct) such displacements from long (8s) optic flow presentations. It is well documented that humans can perceive instantaneous heading from short optic flow presentations (generally less than 1s); perception of our longer simulated movements could e.g. be based on integration of the instantaneous perception of heading. We investigated the subjects' reproductions of their percep-

[6] Group 1 overshoots yaw in the long condition **linear half-turn** by some 44%, p≈0.003 .

tion of both orientation (ego-rotation, yaw), and displacement (trajectory). We compared the results with an earlier study addressing vestibular perception of identical, physical displacements in blindfolded subjects.

Our results show that under certain restraints that depend on the stimulus, the *type* of displacement can be perceived; directions, the form of trajectory ($\Psi p$) and the average orientation relative to the trajectory ($<\Phi r>$). As the optic flow does not provide information on absolute linear ego-motion speed, an absolute judgement of the travelled distance cannot be made. This is also the case for the vestibular system where the double integration of the otolith-provided acceleration signal does not yield a correct measure of distance travelled (Glasauer & Israël, 1993; Israël *et al.*, 1993): subjects do not correctly estimate the length of linear trajectories travelled passively. But human observers are quite capable to make relative based distance judgements from optic flow (Bremmer & Lappe, 1999; Bremmer *et al.*, 1999).

### 4.1- Perception of trajectory.

Generally speaking, trajectories were correctly perceived when the simulated movement contained relatively little rotation, or none at all. Thus, perception of the trajectories with the observers' orientation ($\Phi o$) fixed in space was good. For the linear trajectories, $<\Phi r>$ was overshot at 30°, while for 120° and 135° it was undershot. This range effect (a common phenomenon, e.g. also observed for angular perception in vestibular studies) is possibly due to errors in the estimation of the vehicle's orientation and/or the drawn trajectory. On the one hand, it has been shown that humans can detect their heading direction with an accuracy of up to 1° although they generally underestimate (verbal report: Cutting, 1986; discrimination: Warren *et al.*, 1988; Warren, Blackwell *et al.*, 1991). But on the other hand, nominal ("sloppy") heading direction judgements might be more useful in everyday life than exact judgements (Cutting *et al.*, 1997)).

The curvilinear trajectories with orientation fixed relative to the trajectory, could also be perceived correctly. In general, perception was better for the larger radius. When the radius was smaller, the simulated movements contained relatively more rotation. As a result, almost half the subjects reported rotations in place. However, the remainder of the subjects perceived curvilinear trajectories, of too high curvature.

Thus, in most of the cases discussed above, subjects perceived a curvilinear trajectory when the stimulus was curvilinear, if they perceived a trajectory at all. Often, they also reported a *semicircular* trajectory. Theoretically, they can detect this from the optic flow because the simulated angular velocity is specified unambiguously. Observation of the subjects during the experiment, and the impressions recorded after the experiment suggest another explanation: trajectories were often judged as more than a quarter arc, but less than a 3/4 or full circle, thus a semicircle was assumed. Subjects applied the same categorisation in vestibular tests, and probably also in the judgement of yaw that will be discussed next.

### 4.2- Perception of orientation.

The optic flow provides absolute angular velocity information, in contradistinction to the information about linear velocity. Humans can use this information to extrapolate a tangential, curvilinear trajectory in order to determine whether they will pass to the left or to the right of a target shown after a stimulus (heading detection on curvilinear trajectories, see e.g. Warren, Mestre *et al.*, 1991; Stone *et al.*, 1997). In our experiment, we also find that in most cases subjects report total amounts of yaw that are not significantly different from the actual values. Again one could argue that this overall good performance is due to the subjects' assumption that we presented only "cardinal" amounts of rotation (0°, ±180° and 360°), such that "too large for 90°" leads to "180°". Large simulated translation speeds can interfere with the correct perception of rotation, though. Such is the case for the large radius outward- and forward-looking movements in which subjects undershot their rotation significantly.

It happens more often, however, that changes in orientation disturb the perception of translation. To such an extent that subjects often lose a coherent perception of translation when the orientation changes in space or in space *and* with respect to the trajectory, and perceive a rotation in place instead.

The effect of large rotation on the perception of translation is clearest in the cases in which the orientation changes with respect to both the world and the trajectory. We presented two such cases, one a semicircle with a full, 360° rotation of the observer, and the other a lin-

Table 2. Summary of results. Results are based on the last response given for each condition (in case the subject asked re-presentations). Per condition, the number of globally correct responses, trajectory correct responses (**trajectory only**) and, where applicable, the number of rotations in place is reported for the 2 groups. Globally correct responses are those which contain a certain minimal set of properties of the correct response: form and direction/orientation of trajectory (thus, these responses are a subset of the trajectory correct responses); type and direction of [change in] orientation. Further specifications are given in the table, per condition. The initial orientation and heading are always disregarded. The total number of responses per group is given in the **N** column. For Group 2, columns are divided in two equal halves, with the left halve listing the observables for the triangular-velocity condition, and the right halve for the constant-velocity condition. Cw indicates clockwise rotation, CCw counterclockwise rotation.

Condition **semicircle outward**: In Group 1, there were 7 linear lateral translations reported for the large stimulus, and 1 for the small. In Group 2, these figures were 5; 3 for the large condition (triangular vs. constant velocity profile), and 2; 0 for the small.

Condition **semicircle no-turn**: one subject in Group 2 systematically reports a full circular movement with constant (space-fixed) orientation.

Condition **linear half-turn**: the linear trajectories reported are all — but 2 — correct responses. In this condition, globally correct responses are not necessarily also trajectory correct responses!

Condition **rotation in place**: the "**trajectory only"** column lists the number of responses consisting of curvilinear or linear trajectories with the orientation orthogonal to the path; there is thus no overlap with the globally correct responses!

| condition | globally correct = | | trajectory only | | rotations in place | | N |
|---|---|---|---|---|---|---|---|
|  | Cw rotation in place | | (curvi)linear orthogonal | | N/A | | |
| Gr. 1 | 15 | | 0 | | | | 16 |
| Gr. 2 | 2 | 3 | 4 | 3 | | | 7 |
|  | rightward linear, lateral Φr | | linear | | no RIPs | | |
| Gr. 1 | 15 | | 15 | | | | 16 |
| Gr. 2 | 6 | 7 | 6 | 7 | | | 7 |
|  | rightward linear, oblique Φr | | linear | | no RIPs | | |
| Gr. 1 | 11 | | 15 | | | | 16 |
| Gr. 2 | 5 | 6 | 7 | 7 | | | 7 |
|  | rightward linear, oblique Φr | | linear | | no RIPs | | |
| Gr. 1 | 8 | | 14 | | | | 16 |
|  | rightward linear, oblique Φr | | linear | | no RIPs | | |
| Gr. 1 | 10 | | 15 | | | | 16 |
| Gr. 2 | 6 | 6 | 6 | 7 | | | 7 |
|  | Cw curvilinear, outward Φr | | curvilinear | | | | |
| **Gr. 1**; large | 6 | | 7 | | 2 | | 16 |
| **Gr. 1**; small | 5 | | 6 | | 9 | | 16 |
| **Gr. 2**; large | 1 | 3 | 1 | 4 | 1 | 0 | 7 |
| **Gr. 2**; small | 5 | 5 | 5 | 6 | 0 | 1 | 7 |
|  | Cw curvilinear, inward Φr | | curvilinear | | | | |
| **Gr. 1**; large | 6 | | 9 | | 6 | | 16 |
| **Gr. 1**; small | 2 | | 4 | | 10 | | 15 |
| **Gr. 2**; large | 2 | 2 | 4 | 5 | 1 | 1 | 6 |
| **Gr. 2**; small | 0 | 0 | 5 | 3 | 0 | 3 | 7 |
|  | Cw curvilinear, tangential Φr | | curvilinear | | | | |
| **Gr. 1**; large | 13 | | 14 | | 0 | | 15 |
| **Gr. 1**; small | 3 | | 8 | | 8 | | 16 |
| **Gr. 2**; large | 4 | 3 | 6 | 7 | 0 | 1 | 7 |
| **Gr. 2**; small | 0 | 0 | 4 | 5 | 2 | 1 | 7 |
|  | Cw curvilinear, space-fixed Φo | | curvilinear | | no rotations in place | | |
| **Gr. 1**; large | 10 | | 15 | | | | 16 |
| **Gr. 1**; small | 13 | | 16 | | | | 16 |
| **Gr. 2**; large | 5 | 5 | 5 | 6 | | | 7 |
| **Gr. 2**; small | 6 | 6 | 6 | 6 | | | 7 |
|  | CCw curvilinear, Φr starting tangentially and changing CCw | | curvilinear | | | | |
| **Gr. 1**; large | 2 | | 9 | | 3 | | 16 |
| **Gr. 1**; small | 0 | | 2 | | 14 | | 16 |
| **Gr. 2**; large | 2 | 0 | 4 | 3 | 1 | 0 | 7 |
| **Gr. 2**; small | 0 | 0 | 2 | 1 | 4 | 5 | 7 |
|  | any, Φr starting tangentially with CCw change and leftward lateral phase | | linear | | | | |
| **Gr. 1**; long | 9 | | 3 | | 2 | | 16 |
| **Gr. 1**; short | 5 | | 2 | | 7 | | 16 |
| **Gr. 2**; long | 3 | 3 | 1 | 0 | 2 | 1 | 7 |
| **Gr. 2**; short | 2 | 3 | 1 | 1 | 1 | 0 | 7 |

Table 2

ear translation with a 180° rotation. In both cases, subjects attributed a large part of the perceived rotation to a rotation of the path, as they did in the vestibular study. Yet our results show that they clearly understood that they were not being transported tangentially along a curvilinear path. In the **linear half-turn** condition, perceived trajectories were approximately semicircles. In the **semicircle full-turn** case, many subjects perceived more than 3/4 of a circular path, or even loops. When this movement was presented with the smaller radius only very few subjects perceived a trajectory at all instead of a rotation in place, and some of these trajectories were in the wrong direction. Note that this is an especially obnoxious stimulus, which in addition gives rise to velocities (of the optic flow elements) that are close to the VR system's limits. Nevertheless, there were correct responses for both types of movement in a few subjects.

The "misperception" of the **linear half-turn** condition is a well known phenomenon in optic flow literature: the flow presented in this condition is initially similar to the retinal flow generated by a forward movement with horizontal eye or head movement (Banks *et al.*, 1996; Crowell, 1997; Cutting *et al.*, 1997; Royden, 1994; Royden *et al.*, 1992,1994; van den Berg, 1996; Warren & Hannon, 1990; Warren, Blackwell *et al.*, 1991). It is known that, for short presentations, subjects perceive such a flow as a curvilinear movement when no extra-retinal information is present (Royden, 1994; Crowell, 1998), or when the visual scene is unstructured (Cutting *et al.*, 1997). However, "neither oculomotor nor static depth cues" seem to be *necessary* to provide the rotational signal for accurate retinocentric heading estimation" (Stone & Perrone, 1997 page 587). Also, more may be at play than just the similarity between the presented flow field, and that of a true curvilinear movement, as we discuss in the following two paragraphs.

Rotational components in the flow field might result from *a)* a rotation of the path (rotation in space of the displacement vector) or *b)* from a rotation of the observer relative to the path, or *c)* from a combination of both. The difference between conditions *a)* and *b)* is that the rotation axis is at the centre of the curve in *a)* but through the position of the observer in *b)*, whereas there are 2 axes, one in each position, in *c)*. Correct discrimination between *a)* and *b)* requires two judgements. First, the amount of rotation has to be determined. Second, the location of the rotation axis has to be estimated. At any instant in time, the momentary flow field contains information about the amount of rotation, which could be determined by decomposition of rotational and translational flow components. Such an instantaneous flow field, however, does not specify the location of the rotation axis. This location can only be extracted through an analysis of the development of the flow fields over time, i.e. from an entire sequence. Hence, two questions must be asked: can one estimate the correct amount of rotation, *i.e.* is decomposition possible? And, if so, does one perceive the correct rotation axis, *i.e.* the correct path? Our results suggest that the first answer is yes and the second is no. The total amount of perceived ego-rotation (Ψo, figure 4b) is on average close to the correct values in most cases. This shows that the rotation is detected and that decomposition is possible. However, in many cases subjects attribute the entire rotation to path rotation, *i.e.* as if no rotation of the observer occurred relative to the path. Hence the difficulties are in the correct interpretation of the rotation that is perceived from the flow field, notably the location of the centre of rotation (or the number of such centres as in *c)* above). We cannot conclude, based on our current results, whether this is because the centre of rotation is correctly perceived, or not. But apparently subjects found it more likely that the perceived rotation results from path rotation than from ego-rotation.

The similarity between the flow fields of a linear path + body rotation and that of a curvilinear path (*the initially perceived path*) disappears in time when the simulated rotation increases. Halfway through the presentation, the **linear half-turn** stimulus has a laterally moving phase, whereas in the end movement is backwards. The fact that many of our subjects mistook the linear path for curvilinear suggests that they based their judgement mostly on the initial phase of the stimulus. We tested for a difference between the first and the second halves of the subjects' reproductions. Such a difference could indicate that the subjects noticed that the movement they initially perceived became "incompatible" with the stimulus later on. In the conditions in which the orientation changed relative to the trajectory, there was indeed such a difference: subjects reported more yaw in the second half. If this was indeed to correct action for their initial misinterpretation, it was not a big improvement of the reproduction or percept.

Stimuli which contained a simulated rotation of the observer often gave rise to rotation in place (RIP) responses. The reported rotation was often incorrect for these responses (not shown). It is of course possible that

Table 3. Results of quantitative analyses, sorted by condition and group. In Group 2 results are lumped over the stimuli with triangular and constant velocity profile, porting the maximum number of samples to 2×7=14. The <Ψr> column lists the mean <Ψr> ± the mean standard deviation, averaged over all responses per group/condition. The table also lists Ψp (the rotation of the trajectory), the average initial heading and Ψo, the total change in observer orientation (yaw). The value ±0.000 represents "almost zero": values between ±10-4. All values in degrees, except the number of observations, **N**.
The ideal values (stimulus values) are listed in bold between the different conditions. Values for stimuli are based on actual stimulus presentations (recordings of simulated (stimulus) position and orientation), and are processed in identical fashion as the subjects' responses. The Ψ**o** column lists the initial heading and Ψ**o** separated by a semicolon (**initial heading;**Ψ**o**); for the stimuli only. Near the bottom of the table, the initial orientation averaged over all subjects' responses is listed in this column; for all conditions, the average initial orientation is not significantly different from this global average value. At the bottom of the table, a number of the observables are listed that are defined also for the **rotation in place**: numbers in square brackets refer to the sample size (*i.e.* the number of non-rotation in place responses).
Values in italics in the <Φr>, Ψp and Ψo columns indicate significant differences with the presented values. Significant differences between groups: <Φr>: **linear oblique 30°**, small **semicircle inward**, **semicircle forward**, **semicircle full-turn** and **linear half-turn**. Ψo: large **linear half-turn**. Significance at $p < 0.05$ or better, all determined by t-tests.

| condition | <Φr> [°] | Ψp [°] | initial heading [°] | Ψo [°] | N |
|---|---|---|---|---|---|
|  | **90** | **0** | **0** | **0; 90** | |
| **Gr. 1** | *84.17 ± 8.575* | 0.2234 ± 10.70 | -86.30 ± 6.713 | *-12.67 ± 22.13* | 16 |
| **Gr. 2** | 86.90 ± 5.597 | -4.340 ± 7.422 | -86.93 ± 4.823 | *-15.30 ± 10.39* | 13 |
|  | **30.00** | **-0.000** | **0.000** | **0; 30** | |
| **Gr. 1** | *54.02 ± 6.722* | 0.7086 ± 8.927 | -58.46 ± 15.85 | -5.649 ± 12.22 | 15 |
| **Gr. 2** | *43.03 ± 6.987* | 1.498 ± 9.807 | -52.42 ± 11.94 | 0.1159 ± 16.30 | 14 |
|  | **120.0** | **0** | **0** | **-0.000; 120** | |
| **Gr. 1** | *112.7 ± 6.244* | -1.445 ± 11.41 | -111.9 ± 21.06 | -1.830 ± 7.000 | 14 |
|  | **135.0** | **0** | **0** | **0.000; 135** | |
| **Gr. 1** | 118.2 ± 17.99 | -5.854 ± 20.47 | -105.9 ± 23.60 | -0.8676 ± 26.36 | 14 |
| **Gr. 2** | *118.8 ± 6.313* | 0.6286 ± 5.926 | -111.8 ± 14.60 | -6.193 ± 10.60 | 13 |
|  | **90.00** | **-179.9** | **-4.733** | **-179.9; 90** | |
| **Gr. 1**; large | 89.36 ± 14.06 | *-48.37 ±64.69* | -85.08 ± 13.15 | *-38.88 ± 58.13* | 12 |
| **Gr. 1**; small | 70.58 ± 20.13 | *-75.32 ± 72.83* | -83.29 ± 19.41 | -120.3 ± 60.38 | 5 |
| **Gr. 2**; large | 85.71 ± 18.44 | *-82.85 ± 109.6* | -69.95 ± 35.30 | *-92.69 ± 110.6* | 13 |
| **Gr. 2**; small | 84.79 ± 16.58 | -174.4 ± 120.9 | -67.25 ± 26.92 | -142.2 ± 120.3 | 13 |
|  | **-90.00** | **-179.9** | **-4.735** | **-179.9; -90** | |
| **Gr. 1**; large | -125.2 ± 76.15 | -191.6 ± 42.54 | 173.0 ± 135.9 | -161.6 ± 55.16 | 9 |
| **Gr. 1**; small | -72.39 ± 57.05 | -158.9 ± 120.9 | 45.51 ± 103.0 | -162.6 ± 38.23 | 4 |
| **Gr. 2**; large | *-158.5 ± 58.50* | *-264.7 ± 94.32* | -9.168 ± 91.31 | -176.1 ± 71.49 | 8 |
| **Gr. 2**; small | *102.3 ± 70.88* | *-261.8 ± 57.56* | -14.17 ± 70.42 | -190.9 ± 172.2 | 7 |
|  | **0.000** | **-179.9** | **-4.735** | **-179.9; 0** | |
| **Gr. 1**; large | *19.73 ± 19.36* | -173.2 ± 57.12 | -1.930 ± 17.46 | *-137.6 ± 63.61* | 15 |
| **Gr. 1**; small | *52.45 ± 26.96* | -188.1 ± 98.38 | -22.20 ± 31.71 | -162.5 ± 94.34 | 8 |
| **Gr. 2**; large | *38.87 ± 20.00* | -165.0 ± 68.90 | -14.02 ± 20.61 | *-118.6 ± 83.05* | 13 |
| **Gr. 2**; small | *86.46 ± 28.49* | -201.8 ± 88.87 | -44.81 ± 32.17 | -156.4 ± 118.6 | 9 |
|  | **89.93 ± 50.53** | **-179.9** | **-4.733** | **0.000; 0** | |
| **Gr. 1**; large | 90.83 ± 60.59 | -172.4 ± 28.68 | -5.631 ± 20.69 | -13.22 ± 60.01 | 15 |
| **Gr. 1**; small | 91.91 ± 60.89 | -177.1 ± 45.01 | -4.091 ± 24.22 | 4.605 ± 21.15 | 16 |
| **Gr. 2**; large | 99.01 ± 68.21 | -207.5 ± 92.72 | -13.49 ± 20.67 | 1.400 ± 15.14 | 14 |
| **Gr. 2**; small | 102.4 ± 57.39 | -185.7 ± 89.48 | -20.13 ± 21.35 | -8.631 ± 17.14 | 14 |
|  | **89.92 ± 50.53** | **179.9** | **4.733** | **359.7; 0** | |
| **Gr. 1**; large | *-43.39 ± 50.67* | 284.7 ± 260.5 | 0.6883 ± 50.16 | 344.9 ± 211.0 | 12 |
| **Gr. 1**; small | 70.47 ± 56.36 | *430.9 ± 36.40* | -149.9 ± 138.3 | 410.9 ± 23.21 | 2 |
| **Gr. 2**; large | *-117.5 ± 59.46* | 370.9 ± 467.2 | 43.05 ± 78.41 | 339.1 ± 324.8 | 10 |
| **Gr. 2**; small | *-94.25 ± 45.82* | 309.7 ± 85.74 | 16.16 ± 78.31 | 197.5 ± 152.1 | 3 |
|  | **89.92 ± 50.53** | **0** | **0** | **179.9; 0** | |
| **Gr. 1**; long | *-18.49 ± 49.95* | *201.3 ± 196.3* | 14.54 ± 16.21 | *259.0 ± 75.52* | 12 |
| **Gr. 1**; short | *-25.96 ± 56.28* | *216.7 ± 153.9* | 31.66 ± 86.47 | 209.6 ± 146.4 | 8 |
| **Gr. 2**; long | *-85.18 ± 61.83* | *169.2 ± 135.8* | 25.20 ± 42.29 | 120.7 ± 96.02 | 11 |
| **Gr. 2**; short | *-103.5 ± 42.64* | *242.0 ± 185.4* | 44.63 ± 58.22 | 159.5 ± 107.4 | 13 |
| **Initial orientation over all subjects' responses:** | | | | 0.8900 ± 23.45 | 349 |

| | | | | | |
|---|---|---|---|---|---|
|  | | Ψp [°] | initial heading [°] | **-179.8; 90** | |
| **Gr. 1** | **N/A** | -144.6 [1] | -12.04 [1] | -200.2 ± 66.27 | 16 |
| **Gr. 2** | | -245.7 ± 201.8 [9] | -51.77 ± 46.96 [9] | -183.1 ± 132.1 | 14 |

Table 3

in those cases subjects actually perceived only rotation, for instance due to a masking of translation by large amounts of rotation. Take for instance the **semicircle full-turn** condition. In this stimulus, a forward or backward movement can be perceived at the start and end of the stimulus, for both radii. However, the large radius version has a higher translation speed than the small version. For the large stimulus we found some globally correct responses, but for the small radius stimulus only two subjects reported a curvilinear movement; the other responses were all rotations in place. But these responses can also be a sort of "fallback" responses when the subject was only sure about the experienced rotation, as could result from disorientation (rotation…) and/or from a too small field of view.

### 4.3- Reproducibility of the results

Because our paradigm allowed us to use each stimulus for only one response, we did not specifically check for the reproducibility of the subjects' responses. However, there are a few indications that lead us to believe that subjects would reply consistently to repeated presentations of the same stimulus. In most cases, subjects that requested a re-presentation made a highly similar reproduction or indicated that their previously made reproduction was indeed correct. In Group 2, there are no significant differences between the responses to the stimuli with either triangular or constant velocity profile. Group 1 saw a series of 7 stimuli in the landmark part of the experiment that consisted of almost identical movements to which they responded with high consistency. And the influence of experience mentioned above suggests that subjects may well be capable of recognising (or learning to recognise) a stimulus, and repeating the reproduction for that stimulus (which was actually observed in Group 1 in the aforementioned series).

### 4.4- Comparison with the vestibular study.

Overall, subjects responded in a similar way to actual, blindfolded displacement (vestibular information) and to visual, optic flow simulation of the 2D movements. A few exceptions occurred in which the visually based perception was (highly) superior — or rather inferior.

Using vestibular information, subjects are able to track their change in orientation and position to a high degree: they can maintain a pointer aligned with a previously seen landmark (Ivanenko *et al.*, 1997a,b). They are able to perform this task even in the absence of rotation about their vertical axis, as in condition **B** (our **semicircle no-turn**). However, in this condition they do not correctly perceive their trajectory (cf. figure 2h): the perception of their orientation with respect to the landmark does not seem to be used to this means. Visually, however, this condition poses little problems; almost all subjects perceive curvilinear trajectories with fixed $\Phi o$, although there is variation in the amount of path rotation and length. Also, some subjects visually perceive partwise linear/curvilinear, or completely linear trajectories. On the contrary, the intuitively simplest curvilinear stimulus, **semicircle forward** (**A** in the vestibular study), seems to pose more problems visually than vestibularly. All but one of the subjects in the visual experiment who perceive a displacement correctly perceive a curvilinear trajectory (as they do in the vestibular study). However, a large number of the ("visual") subjects reproduce movements which do maintain a fixed orientation relative to the path, but at the wrong angle (oriented 90° outward, over at least a part of the trajectory) — a few even report fixed $\Phi o$ as in condition **semicircle no-turn**. Note that the perceived orientation relative to the path was not measured in the vestibular study, but there were no RIP responses neither!

In condition **semicircle full-turn** the "additional" rotation is attributed to the trajectory in almost all (visual and vestibular) cases. Using visual information, some of the subjects draw loops (as some "vestibular" subjects), and some of the experienced subjects correctly detect the changing $\Phi r$ in the large radius version, but assume a linear trajectory.

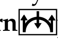
In condition **linear half-turn**, most of the subjects (in both the visual and the vestibular case) also attribute the perceived rotation to a rotation of the path. Thus, they perceive a curvilinear, tangential trajectory. There is more variation in the curvature of the trajectories, however, in the visual case than in the vestibular case. Also, some of our experienced subjects manage to grasp the true nature of the stimulus — not too surprising since after approximately 90° of rotation, the optic flow is very different from the optic flow generated by a curvilinear, tangential path. It is actually more surprising that the percept of a curvilinear trajectory is so persistent in many subjects .

### 4.5- Subjects' impressions.

To our knowledge, this is the first study addressing ego-motion perception of passively travelled 2D trajectories from optic flow. Given the exploratory nature of the study and the methods, we feel it is important to provide some general observations and subjects' impressions.

Subjects generally liked the experiment ("it was fun"), but also found it to be quite difficult. Perception (reconstruction) of travelled trajectories from optic flow does not seem to be a subconscious, automatic or low-level process. The reconstructions rather seem to be made at a conscious level, requiring attention and reasoning: several subjects were observed to reason (aloud) about the stimulus they had just seen: "I started out like this, then I did that, afterwards … and I finished this way". A small number of the subjects were observed making reproducing movements with the vehicle during the stimulus presentation. Could this have helped them in some way to translate instantaneous heading into storable motor commands? If so, it did not give them an advantage with respect to subjects who did not use it.

We asked the subjects who participated in the velocity-profile control experiment (Group 2) whether they had remarked that all stimuli had been presented twice (they had indeed), and whether they had noticed any difference between the two presentations. They did in no case mention the fact that there had been stimuli with acceleration/deceleration, and stimuli with constant velocity. This may not seem overly remarkable. The instruction had only been to concentrate on reproducing the spatial properties of the stimulus — and thus implicitly to ignore stimulus dynamics. And there are indications that perception of heading direction depends mostly on the distribution of directions of the optic flow elements, and not so much on their speed (van den Berg & van de Grind, 1991; Crowell & Banks, 1996). In order to assess the subjective difference between the two velocity profiles, we asked all Group 2 subjects to compare paired presentations of spatially identical stimuli, with triangular and constant velocity profile, directly from the Indigo's screen; notably of the large radius condition **semicircle inward**. None of them succeeded at the first presentation. Instead, they judged that the constant velocity version lasted longer, went slower, and/or turned farther — even though they were told repeatedly that the *geometrical* properties of both stimuli were the same. Many subjects however did notice the difference in velocity profile when presented with one of the lateral translations. This may reflect the low sensitivity for changes in ego-motion speed: it is known that subject need an approximately 50% increase in simulated speed to detect a change in forward ego-speed (Monen & Brenner, 1994).

It has been observed that one can learn to perceive the correct movement if feedback is given, notwithstanding the difficulty of some of the stimuli. (Association of a particular response to a particular stimulus [class] also seems to occur without feedback.) With feedback, one pilot subject got so apt at the task that she managed to get an almost 100% correct score on the conditions here presented even with a limited dot lifetime of 2 frames. This learning effect is certainly enhanced by the fact that 1) there are not that many different movements; 2) in all conditions all components of the movement (translation, rotation of the translation vector, yaw) are present from the beginning, and 3) these components do not change other than in magnitude of speed. Such learning likely plays a role in everyday life, e.g. when we learn to correctly perform delicate manœuvres. The visual experience thus built up can itself influence subject performance. One visitor to the lab immediately interpreted our difficult condition **semicircle full-turn**perfectly, looking from some 2.5m at a display spanning approximately 4.5°x3.4°. She did not find this an exceptional performance, explaining that she had ridden a lot of carousels in her life, which must have provided her with ample experience with the kind of movement and optic flow simulated by this stimulus.

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