Perception of two-dimensional, simulated ego-motion trajectories from optic flow

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Abstract

A veridical percept of ego-motion is normally derived from a combination of visual, vestibular, and proprioceptive signals. A previous study showed that blindfolded subjects can 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 whether vision allows for better path perception in that situation, 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 perceive 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. © 2000 Elsevier Science Ltd. All rights reserved.

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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; Lee, 1974, 1980; Koenderink, 1986), 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; Barinaga, 1991; Lee, 1991; Wang & Frost, 1992; Lee, Davies, Green &

Weel, 1993; Wylie, Bischof & Frost, 1998; Bremmer, Kubischik, Pekel, Lappe & Hoffmann, 1999; Lappe, Bremmer & van den Berg, 1999). But also arthropods, especially insects rely on it in many and often remarkably similar ways (Götz, 1975; Wehner & Lanfranconi, 1981; 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 quite accurately determine their heading direction of linear ego-motion from short optic flow presentations (Warren, Morris & Kalish, 1988; Warren, Blackwell, Kurtz, Hatsopoulos & Kalish, 1991a; Royden, Banks & Crowell, 1992; van den Berg, 1992; Crowell & Banks, 1993; van den Berg & Brenner, 1994a,b; Warren & Saunders, 1995; Banks, Ehrlich, Backus & Crowell, 1996; Royden & Hildreth, 1996; van den Berg, 1996; Grigo & Lappe, 1999; Lappe et al., 1999). They can also detect their heading direction on circular trajectories (Rieger, 1983; Warren et al., 1991a; Warren,

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Mestre, Blackwell & Morris, 1991b; Turano & Wang, 1994; Stone & Perrone, 1997). Ambiguous optic flows however seem to require additional visual or even non-visual information in order for the simulated movement to be perceived correctly. For example, the flow resulting from a linear translation while making a horizontal eye or head or whole-body rotation resembles very closely the flow resulting 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 (Warren & Hannon, 1990; Warren et al., 1991a; Royden et al., 1992; Royden, 1994; Royden, Crowell & Banks, 1994; Banks et al., 1996; Crowell, 1997; Cutting, Vishton, Flückiger, Baumberger & Gerndt, 1997; van den Berg, 1996).

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 tell us 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, Banks, Shenoy & Andersen, 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, Howard & Ohmi, 1995).

Recent work from our group (Ivanenko, Grasso, Israël & Berthoz, 1997a,b) showed that subjects can perceive aspects of linear and curvilinear movements when displaced blindfolded on a mobile robot. 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 visually perceive simulated, passive ego-movement following 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* consecutive instantaneous heading perceptions to form a coherent perception of the travelled path[1]? Virtual real-

ity 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, 742 × 230 pixels, 60 Hz 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; uniform, random distribution) on a surface (50 × 50 m; visible up to 15 m ahead) 1 m below eye-level (see Fig. 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 2 s stationary period followed by 8 s of simulated movement followed by another 2 s 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 × 6 in.: resolution 22 860 × 15 240 pixels) that they held on their knees. A custom-made input device was manipulated by the subject, 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 customary 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 Fig. 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.

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[1] *Path integration* sensu strictu; not implying the maintenance of a 'return vector' pointing to the starting point!
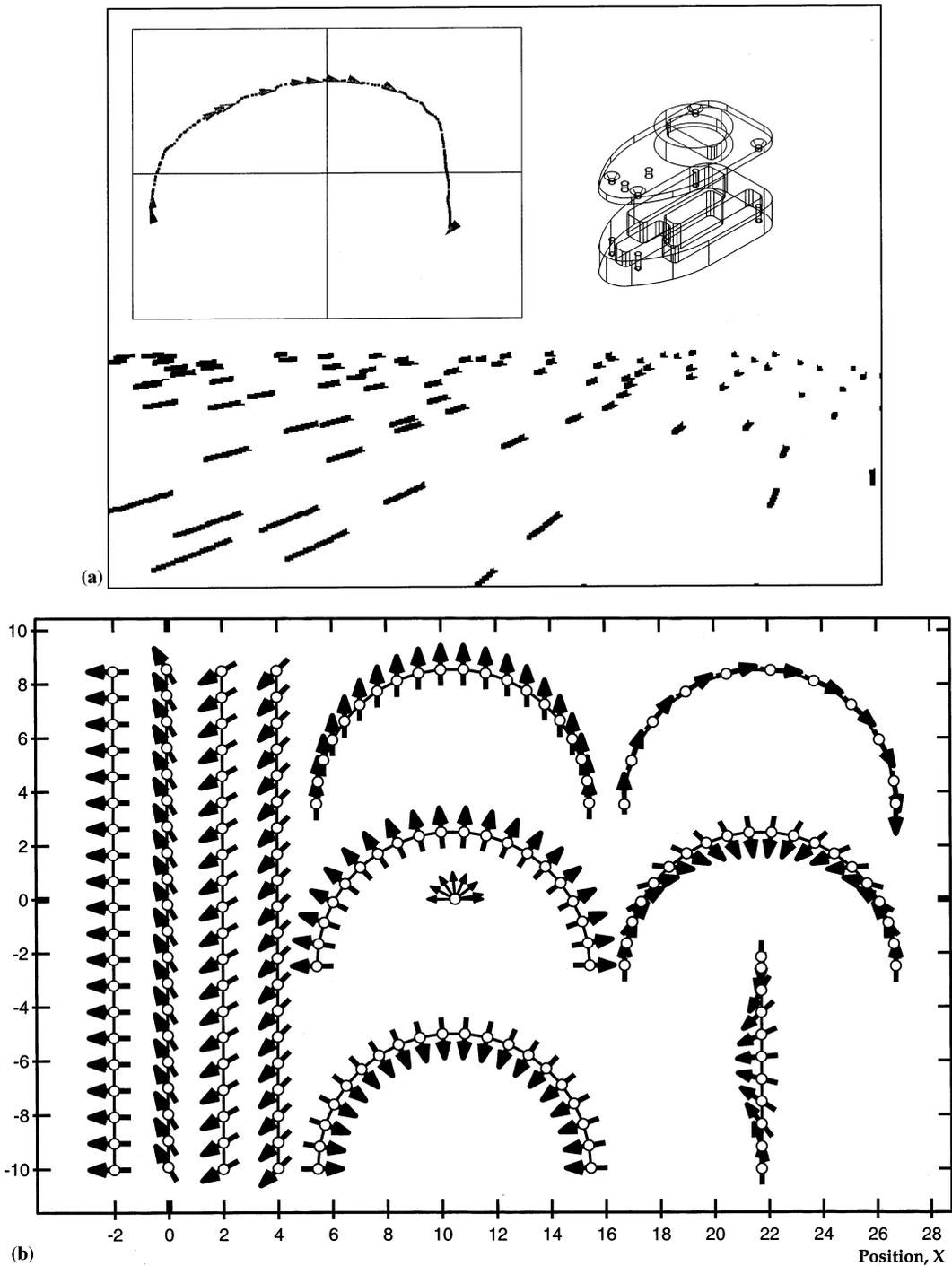
Fig. 1. (a) Optic flow impression. The figure shows the first moments of the large radius condition *semicircle no-turn* ⊞ . In the experimental conditions, only single dots were seen to be moving, with a slightly higher density and otherwise identical geometry and field of view. For this figure, the dots left 'trails' to give an impression of the distribution of dot speed. 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 (Φ_o). 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* (◳; $\Phi_r = 90°$); the *rotation in place* (⊡), and *semicircle inward* (◲; $\Phi_r = -90°$); (right): *semicircle forward* (◱; $\Phi_r = 0°$), *semicircle full-turn* (⊞) and *linear half-turn* (⊞). (c) Explication of the indices used in the quantitative analyses. Ψ_p, the average rotation of the path is calculated from the average difference between the tangents to the trajectory in two consecutive (resampled) points, multiplied by the number of segments per curve (19). The total yaw Ψ_o is calculated by (non circular) summation over Φ_o, minus the initial orientation; thus, two full observer turns give $\Psi_o = 720°$. The average orientation relative to the path, $<\Phi_r>$, is calculated as the average difference between Φ_o and Φ_p 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), $\Psi_o = 180°$, $\Psi_p = -180°$ and $<\Phi_r> = 179.7° \pm 109.8°$.
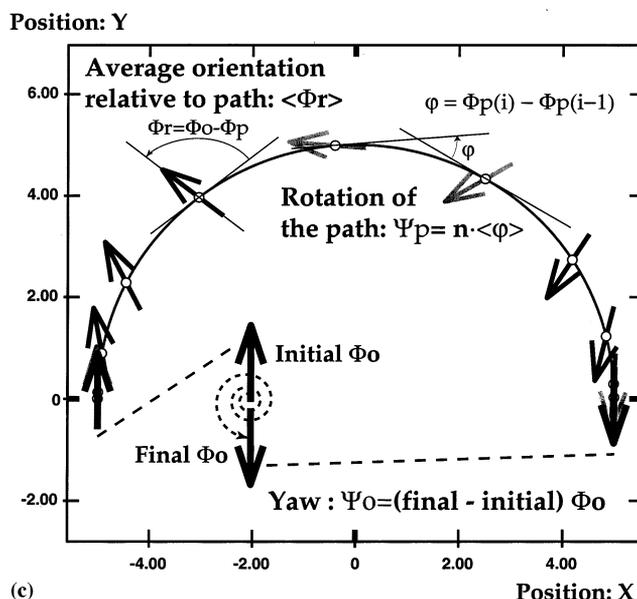
Fig. 1. (*Continued*)

2.2. Experimental procedure

Subjects were seated on an 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 on a chair on wheels that can turn around its vertical axis. A few possible movements not used in the experiment were demonstrated to familiarise the subjects with the fact that yaw need not be fixed relative 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 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 of the movement. 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 HMD), and to either erase and redraw it, or view another presentation and redo the reproduction. Experiments generally did not last longer than 1 h, depending on the time spent in familiarising with the set-up, and on the number of re-presentations requested.

The simulated movements (Fig. 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 $11.46°/s^2$ (0.2 rad/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 (Φ_o; independent of the trajectory), the orientation of the trajectory (Φ_p: the angle in space of the tangent to the trajectory) and the observer's orientation relative to the trajectory, $\Phi_r = \Phi_o - \Phi_p$. Similarly, we will distinguish two types of rotation (change in orientation): Ψ_o (yaw) and Ψ_p (the rotation of the trajectory). Angles are expressed in degrees, with positive values indicating clockwise rotation.

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

Stimuli with the observer's orientation (yaw) fixed in space:

1. Linear translation with the observer's orientation oblique at $\Phi_r = \Phi_o = 30°$ (condition *linear oblique 30°* ▣), $\Phi_o = 135°$ (condition *linear oblique 135°* ▣) and $\Phi_o = 120°$ (condition *linear oblique 120°* ▣). Linear acceleration was 1.18 m/s², average translation speed 2.33 m/s. (In these stimuli, orientation is also fixed relative to the trajectory.)
2. Semicircular trajectory with $\Phi_o = 0°$ (condition *semicircle no-turn* ▣ , condition III in *op.cit.*). Stimuli with the observer's orientation fixed relative to the trajectory:
3. Semicircular trajectory with the observer looking outward ('centrifugal': $\Phi_r = 90°$; condition *semicircle outward* ▣).
4. Semicircular trajectory with the observer looking inward ('centripetal': $\Phi_r = -90°$; condition *semicircle inward* ▣).
5. Semicircular trajectory with tangential orientation ($\Phi_r = 0°$; condition *semicircle forward* ▣ ; condition II in *op.cit.*). The average speed of rotation (Ψ_o) in III, IV and V was $-22.5°/s$. Stimuli with the observer's orientation changing in space and relative to the trajectory:
6. Semicircular counter-clockwise trajectory with a full rotation ($\Psi_o = 360°$, starting at 0°; condition *semicircle full-turn* ▣; condition V in *op.cit.*)[2]. The average speed of rotation (Ψ_o) was 45°/s.
7. Linear translation with $\Psi_o = 180°$ starting at 0°, (Fig. 1d; condition *linear half-turn* ▣; condition VI in *op.cit.*).
8. A $\Psi_o = -180°$ clockwise *rotation in place* (▣ ; condition **I** in *op.cit.*). The average speed of rotation (Ψ_o) was $-22.5°/s$.

The semicircular conditions were all presented with a large (5 m) and a small (1.5 m) radius. In these conditions, the average speed of translation was 0.59 m/s for the small, and 1.96 m/s for the large radius, while the direction of translation rotated at an average speed of $\pm 22.5°/s$. Condition *linear half-turn* was also presented in two lengths: 7.8 and 4.7 m. In the short version, simulated acceleration was 0.3 m/s², and the average speed of translation 0.59 m/s. In the long version, acceleration was 0.5 m/s², and the average speed of translation 0.98 m/s. Both had an average speed of rotation (Ψ_o) 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 ($\Phi_o = 90°$: 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].

Twenty-three subjects (aged 20–50 years 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 seven 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, differing only in the velocity profile — which was either triangular or constant, but of 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 three frames to approx. 85–100 frames. Where necessary, we will refer to these two sub-populations as Group 1 and 2, 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 manipulating 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 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. Figs. 1 and 2) with side-by-side X, Y and Φ_o time-series: (1) as leading or trailing horizontal lines on the time-series; 2) as random variations in X and Y with Φ_o 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].

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[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, due to the size of the field of view and the closeness of the screens.

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

Fig. 2.

Position; Y

(e)

Position; X

Position; Y

(f)

Position; X

Position; Y

(g)

Position; X

Position; Y

(h)

Position; X

Fig. 2. (*Continued*)

Position; Y

(i)

(j)
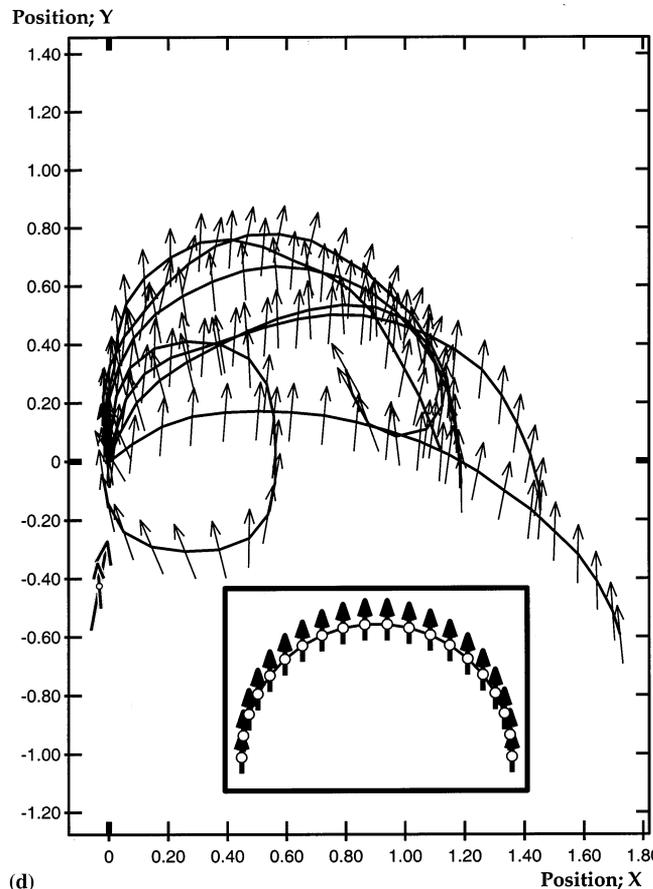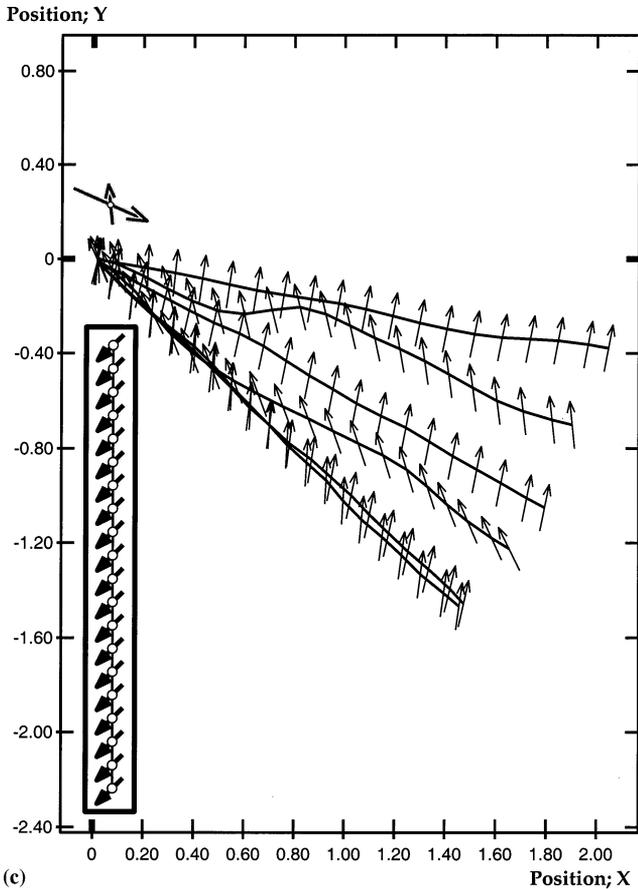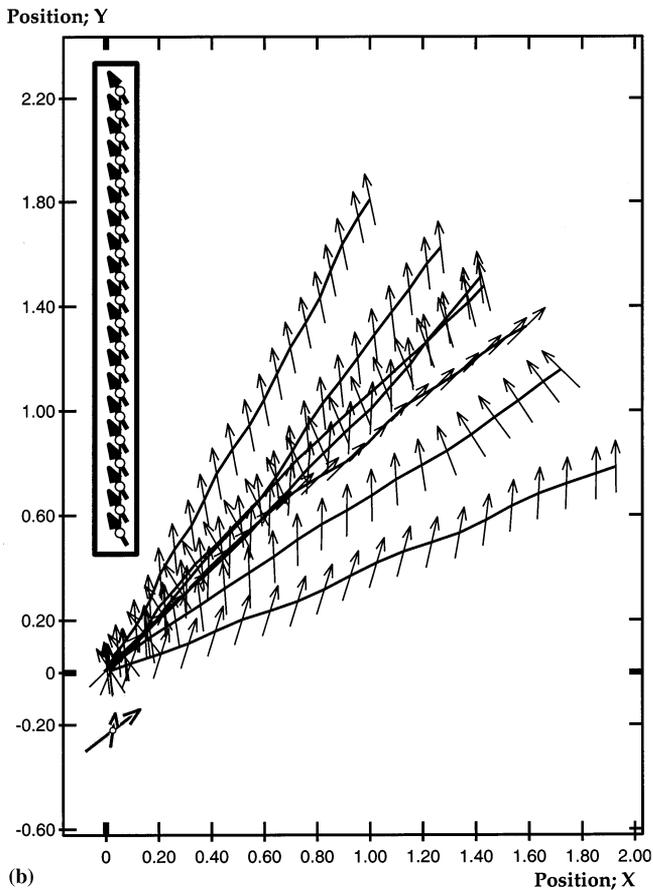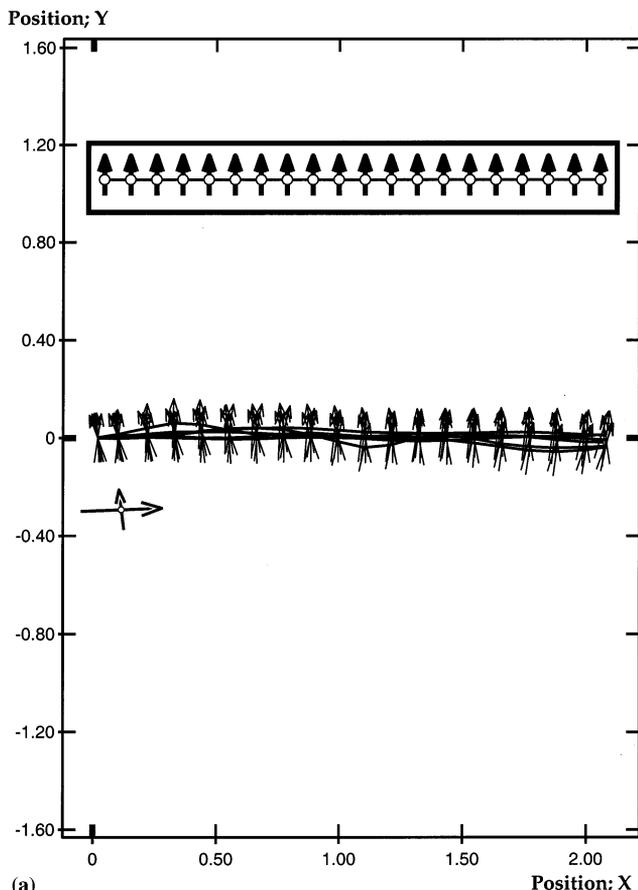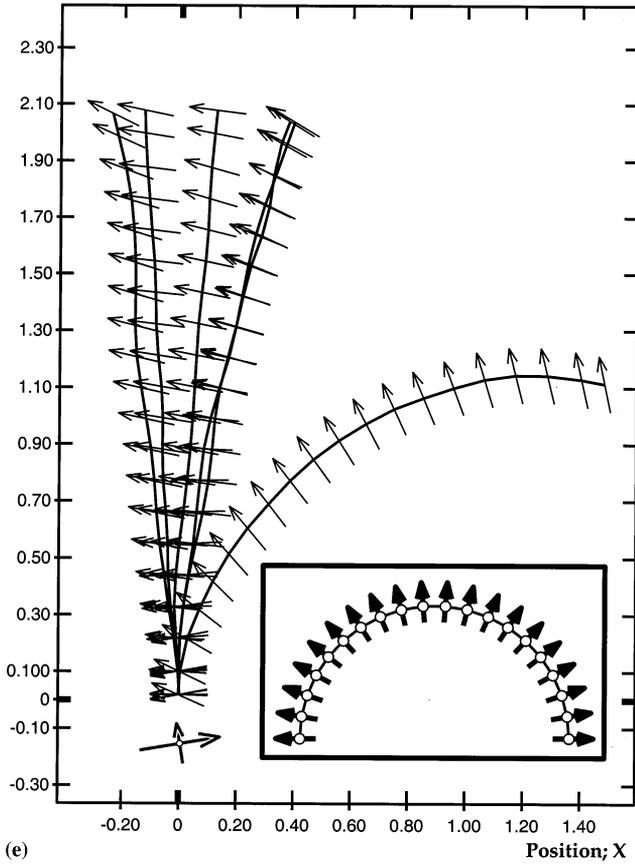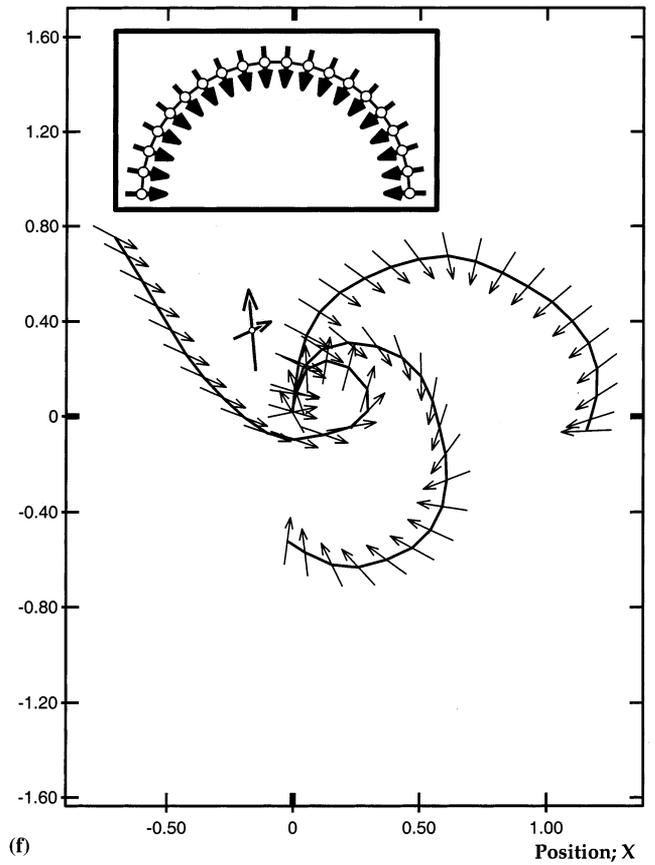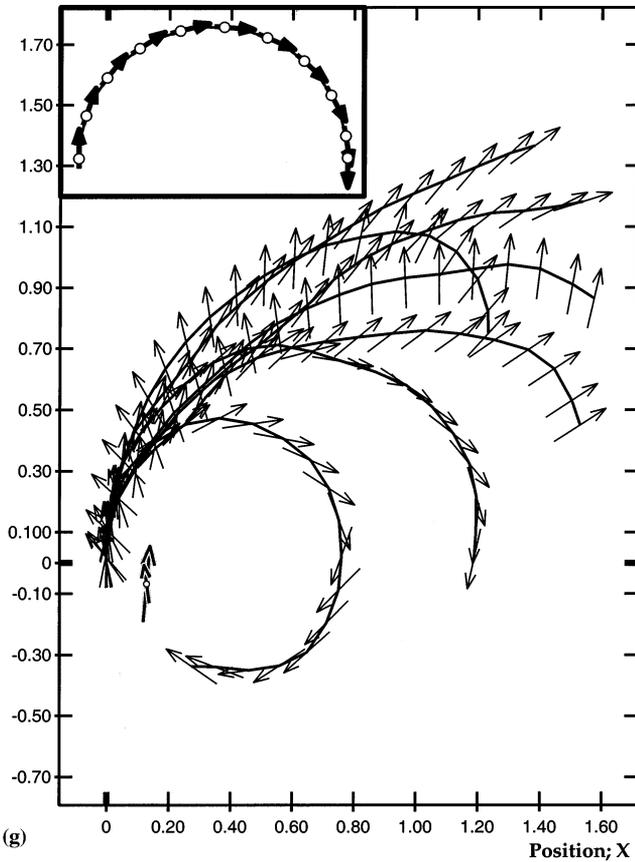
Fig. 2. A selection of reproductions from Group 2 (a–j): all responses to the large/long stimuli with triangular velocity profile. The stimuli are listed in the figures' titles, which also refer to the stimulus enumeration in Section 2. The responses are filtered and resampled as described in Section 2. 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 Φ_o (in the stimulus; Fig. 2a–d), th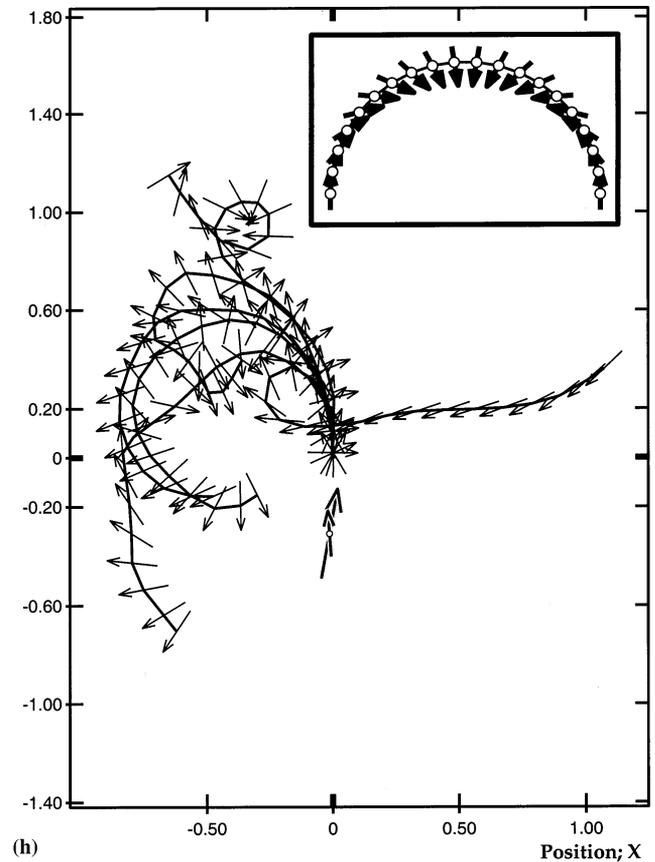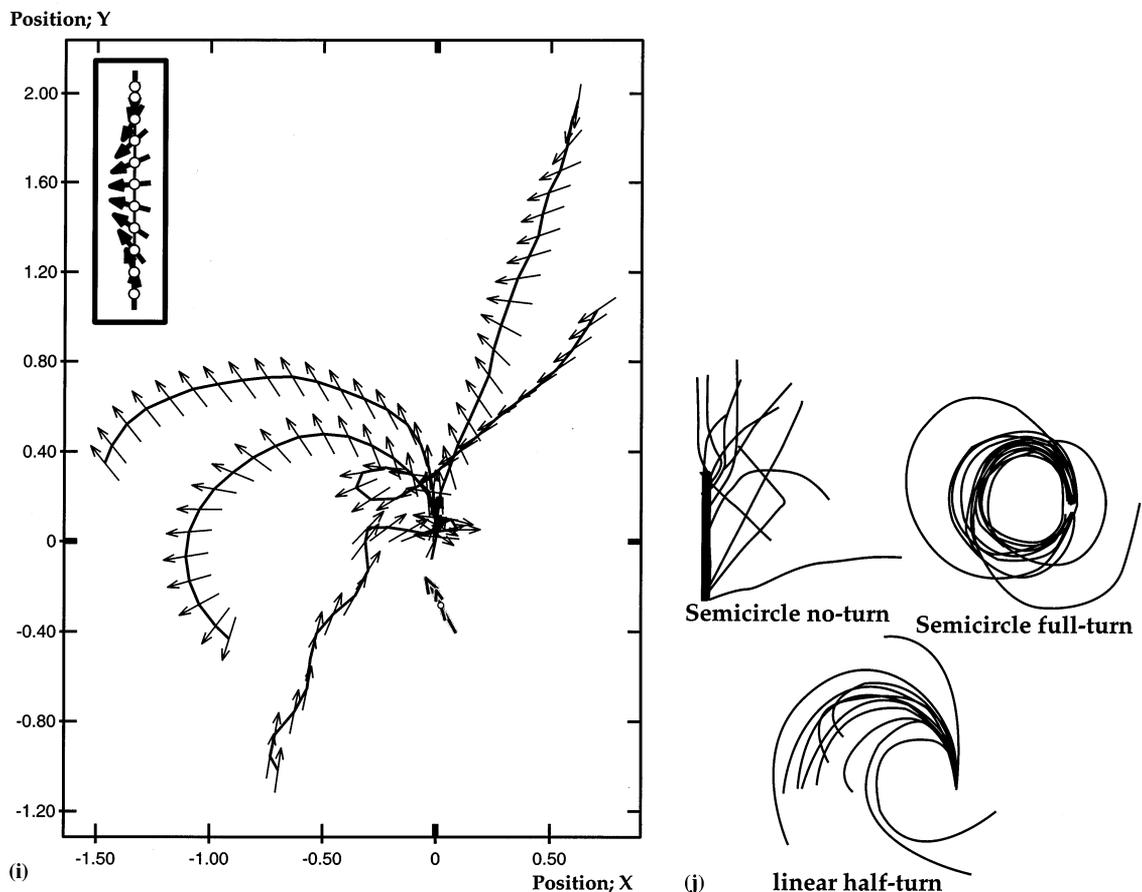e individual reproductions were all rotated over the same angle, such that the resulting orientation averages to 0°. In the other conditions, the reproductions were rotated such that the 1st trajectory segment is oriented at 0°. Finally, the reproductions received additional smoothing. The 'clock face' display of two arrows indicates the average initial Φ_p (the longer arrow) and the average initial Φ_o (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*: $< \Phi_r > = 90.52 \pm 5.833$; $\Psi_p = -3.836 \pm 7.634$; $\Psi_o = -15.89 \pm 8.222$. (b): Ib, *Linear oblique 30°*: $< \Phi_r > = 46.52 \pm 5.659$; $\Psi_p = -1.167 \pm 7.498$; $\Psi_o = 7.137 \pm 17.12$. (c): Ic, *Linear oblique 135°*: $< \Phi_r > = 121.4 \pm 6.059$; $\Psi_p = 3.255 \pm 2.950$; $\Psi_o = -4.797 \pm 7.220$. (d): II, *Semicircle no-turn*: $< \Phi_r > = 93.49 \pm 61.62$; $\Psi_p = -225.0 \pm 93.42$; $\Psi_o = 1.100 \pm 9.242$. (e): III, *Semicircle outward*: $< \Phi_r > = 83.98 \pm 7.169$; $\Psi_p = -23.65 \pm 37.63$; $\Psi_o = -30.15 \pm 15.87$. (f): IV, *Semicircle inward*: $< \Phi_r > = -98.40 \pm 60.11$; $\Psi_p = -294.1 \pm 64.57$; $\Psi_o = -199.2 \pm 70.01$. (g): V, *Semicircle forward*: $< \Phi_r > = 31.20 \pm 16.12$; $\Psi_p = -159.4 \pm 75.77$; $\Psi_o = -117.2 \pm 92.82$. (h): VI, *Semicircle full-turn*: $< \Phi_r > = -97.48 \pm 50.63$; $\Psi_p = 196.8 \pm 263.4$; $\Psi_o = 158.7 \pm 269.7$. (i): VII, *Linear half-turn*: $< \Phi_r > = -142.7 \pm 72.51$; $\Psi_p = 128.3 \pm 172.7$; $\Psi_o = 115.6 \pm 60.17$. (j): The trajectory drawings from the vestibular experiment, conditions *Semicircle no-turn*, *Semicircle full-turn* and *Linear half-turn*.

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 Φ_{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 Φ_{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: Ψ_p, Ψ_o and the average orientation relative to the path $< \Phi_r >$, cf. Fig. 1c. Ψ_p 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 Ψ_o is calculated by summing the Φ_o values in the resampled points, minus the initial orientation (such that for two observer turns, $\Psi_o = 720°$). Finally, $<\Phi_r>$ 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, Φ_p, Φ_o 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 two 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) Ψ_o rather frequently, and corrected that in a second presentation.

Fig. 2 (panels a–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 (apparently) simple movements give rise to correct responses — at least the trajectories' form — with little variation between subjects. Such is the case for stimuli in which the simulated speed of translation is high relative to the simulated rotation speed (Fig. 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. For instance, 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 counter-clockwise semicircle with $\Psi_o = 360°$), a globally correct response would be a counter-clockwise curvilinear trajectory with the orientation changing in counter-clockwise direction relative to the trajectory. The initial orientation (e.g. 0°, or $\pm 90°$) cannot be derived from our stimuli. Thus, we only consider whether the initial orientation with respect to the initial orientation of the path, but we disregard the absolute, space-relative initial orientation and initial direction of reproduced movement. In other words, for the condition *semicircle outward*, a circular path starting at an angle of 0° forward with the observer oriented 80° outward is equally correct as a circular path starting at an angle of $-40°$ (rightward) with the observer oriented 40° outward.

Fig. 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
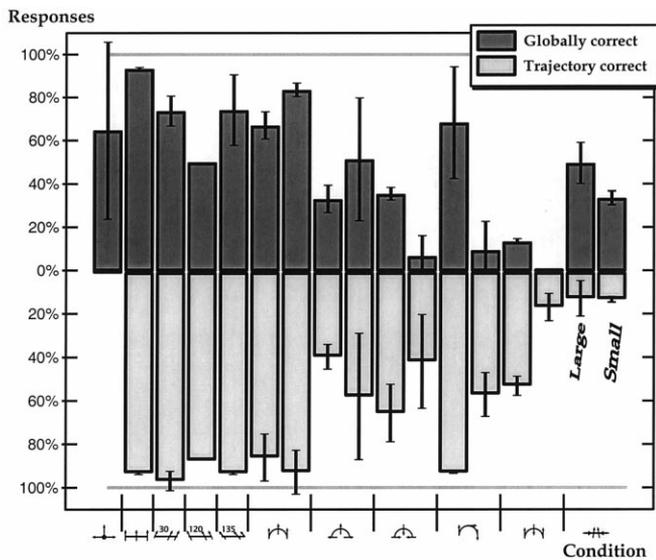
Fig. 3. Performance observations: globally correct responses and responses with the correct type of trajectory, each expressed as a percentage of the number of observations. Percentages shown are calculated over all subjects. The errorbars show the standard deviation in the mean of the per-group performances. Stimulus *linear oblique 120°* (⊡) was not presented to Group 2. Compare with Table 2, 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.

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 Figs. 4 and 5. The detailed results are listed in Table 3. The table also lists the initial heading (the orientation of the trajectory's 1st segment), in addition to the values of the three indices introduced above, Ψ_p, Ψ_o and $<\Phi_r>$. All these observables are averaged over subjects, per condition. Average initial orientation is given for the 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) linear trajectories with Ψ_o in the right direction in condition *semicircle full-turn* ⊞; and (3) curvilinear trajectories with Ψ_o in the right direction in condition *linear half-turn* ⊞ . $<\Phi_o>$ is undefined for rotations in place, so for condition ⊞ we give only the initial heading and the average Ψ_o (for all responses), and Ψ_p for responses that are not rotations in place.

For ease of interpretation, we give *ideal values* of all observations, obtained by performing the same filtering, resampling (see Section 2) and analyses on the *true movements*. True movements are generated by the stimulus program as recordings of the simulated movements (see Section 2.1). Differences between measured re-

are more globally correct responses to the large/long stimuli than to the small/short (e.g. the two conditions *semicircle forward* ⊟).
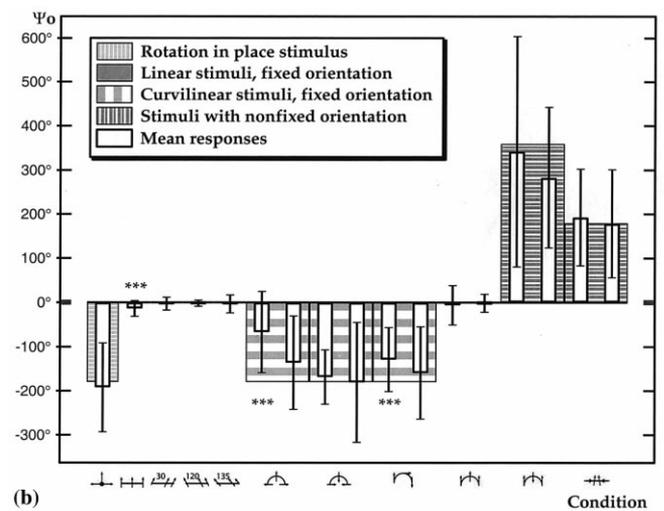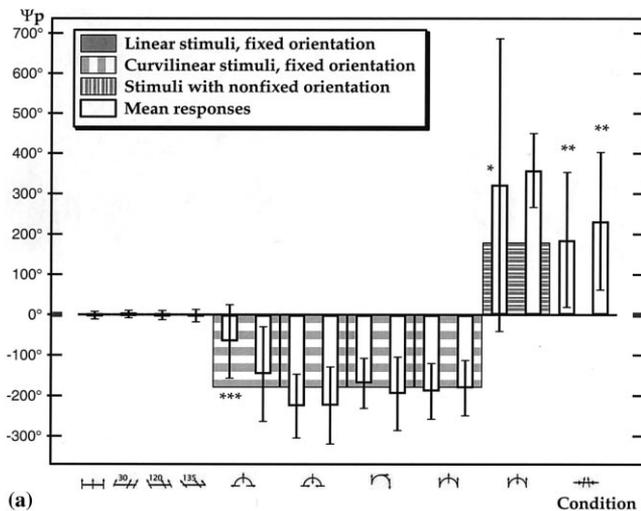
Fig. 4. (a) Ψ_p for all conditions but the *rotation in place*. Shaded, striped bars show the expected (i.e. stimulus) values. Errorbars show standard deviation of the mean. Asterisks indicate significant differences from the expected values, determined by t-tests using mean and average standard deviation; * $P < 0.05$, ** $P < 0.005$, *** $P < 5 \times 10^{-4}$ (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) Ψ_o for all conditions. The *rotation in place* condition is shown leftmost. All presentation details as in (a).

$<\Phi_r>$ response

Linear lateral ☐
Linear oblique 30° ■
Linear oblique 120° ○
Linear oblique 135° ●

(a)

$<\Phi_r>$ stimulus

$<\Phi_r>$ response

large Semicircle outward ☐
small Semicircle outward ■
large Semicircle inward ○
small Semicircle inward ●
large Semicircle forward ◇
small Semicircle forward ◆

(b)

$<\Phi_r>$ stimulus

Fig. 5. (a) Observed versus presented (i.e. stimulus) $<\Phi_r>$ values, for the four linear stimuli with fixed Φ_o. 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: * $P < 0.05$, ** $P < 0.005$, *** $P < 5 \times 10^{-4}$ (Student's t). (b) Observed versus presented (i.e. stimulus) $<\Phi_r>$, for the semicircular conditions with fixed Φ_r. Presentation as in (a).

sponses and true movements, and between per-condition responses are tested with Student's t-tests.

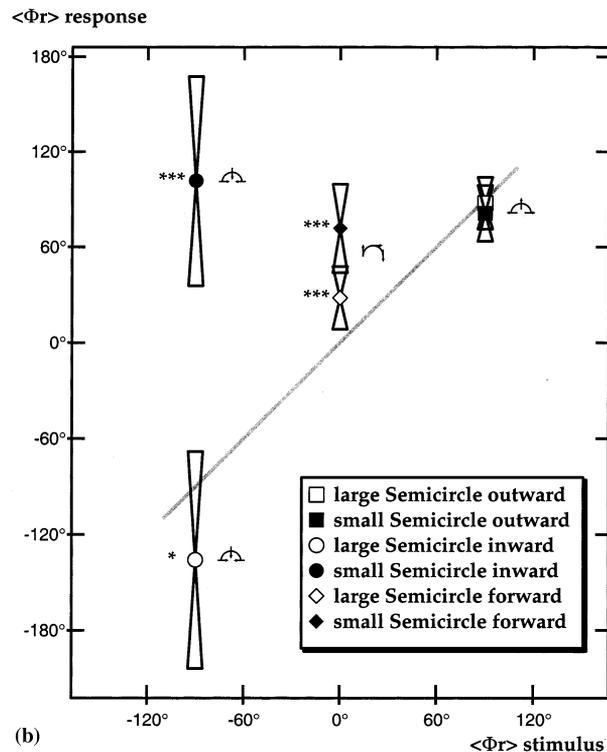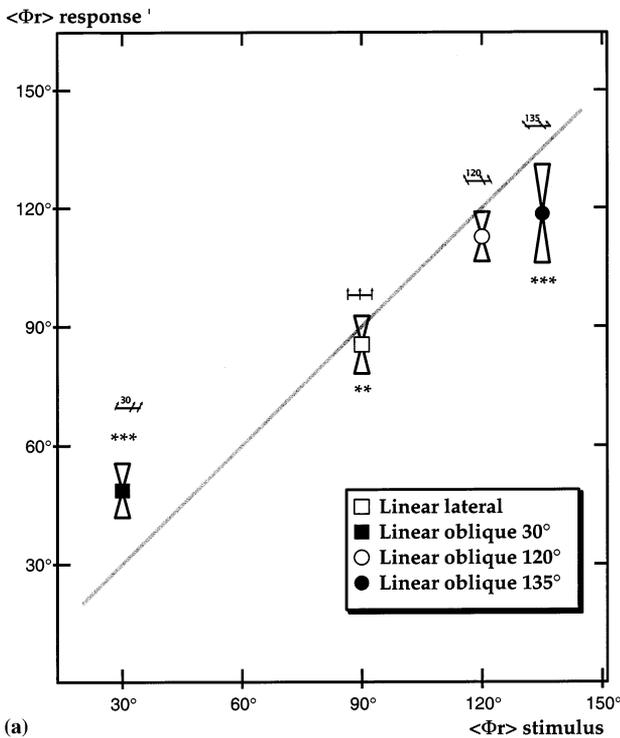The rotation of the path (Ψ_p) and the reported yaw (Ψ_o) are shown in Fig. 4a and b, respectively (narrow, white bars), together with the *true movement* values (broader, shaded bars). Both properties generally seem to be well perceived. Fig. 5 shows $<\Phi_r>$, reported versus presented, for the conditions with fixed Φ_r. 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 and 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 (Fig. 2a). Subjects maintain almost the correct Φ_r ($<\Phi_r> \approx -90°$) and they reproduce trajectories which are close to linear on average ($|\Phi_p| < 5°$). However, since they assume an initial $\Phi_o = 0°$, 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°* ▭(Fig. 2b); *120°* ▭ and *135°* ▭ (Fig. 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* ▭ (Fig. 2d), the quantitative results repeat what was already evident from the qualitative results in Fig. 3: these stimuli are perceived correctly. The differences from the expected values are all non-significant.

In condition *semicircle outward* ▭ (Fig. 2e), $<\Phi_r>$ 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. Ψ_p confirms this: for the large radius, $|\Psi_p| < 180°$ ($P < 0.001$); for the small radius, $|\Psi_p|$ is more than $2\times$ larger at $P \approx 0.08$. This difference also shows in Ψ_o, which approximates Ψ_p and is thus too small (significant at $P < 10^{-5}$ for the

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[a]

	Ψ_o (°)			Ψ_p (°)			$<\Phi_r>$ (°)		
	h1	h2	P	h1	h2	P	h1	h2	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

[a] 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.

large radius; larger for the small radius[$P < 0.03$]). Initial heading is mostly to the right, even for the correct responses.

Condition *semicircle inward* ⊞ (Fig. 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 (Φ_o or Φ_r), but for the small radius version, curvilinear responses typically have either a 'centrifugal' $\Phi_r \approx 90°$, or, in some cases, Φ_o fixed in the environment. The large radius stimulus is perceived as a backwards movement ($|<\Phi_r>| > 90°$; $P < 0.02$). There is also a tendency to perceive a trajectory spanning more than half a circle ($|\Psi_p| > 180°$). Ψ_o is approximately correct, however.

A large number of the curvilinear trajectories reproduced for condition *semicircle forward* ⊡ (Fig. 2g) maintain a fixed Φ_r — only oriented outwards, 'centrifugal' ($<\Phi_r> > 0°$; almost all for the small radius; almost 50% for the large radius in Group 2). This causes a significant undershoot of Ψ_o ($P < 0.001$). Perception is better for the stimulus with the large radius (Fig. 3). Indeed, $<\Phi_r>$ 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 (Fig. 3).

Subjects have the greatest problems with the conditions with orientation not fixed at all; *semicircle full-turn* ⊞ (Fig. 2h) and *linear half-turn* ⊞ (Fig. 2i). The reported $<\Phi_r>$ is actually negative instead of 90°. In addition, Ψ_p is too large; between 50 and 150% in condition *semicircle full-turn* ($P < 0.02$; $P < 0.0001$ in t_{180}/T_{180}). Ψ_o is more or less correct, though[5]. This combination of approximately the right amount of yaw combined with a too curved trajectory explains the negative $<\Phi_r>$ values: Ψ_o 'trails' relative to Ψ_p (see Fig. 2h and i). In condition *linear half-turn* ⊞, Ψ_p is on

average closer to the amount of simulated Ψ_o than to the actually simulated $\Psi_p = 0°$. This hints at what probably happens: subjects seem to attribute Ψ_o to Ψ_p. This also explains the overshoot of the Ψ_p in condition *semicircle full-turn* ⊞.

Our results thus suggest that subjects assume that the rotation they perceive is due (at least for a large part) to a rotation of their trajectory. 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 × conditions × 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 three 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 (Ψ_o 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 (Ψ_p), whereas the larger value for $<\Phi_r>$ would suggest that the subjects do 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 ego-rotation relative to the trajectory and/or in space in a number of cases. Specifically, we asked whether human observers can perceive such displacements from long (8 s) optic flow presentations. It is well documented that humans can perceive instantaneous heading from short optic flow presentations (generally less than 1 s); perception of our longer

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[5] Group 1 overshoots yaw in condition T_{180} by some 44%, $P \approx 0.003$.

Table 2
Summary of results[a]

condition	globally correct =		trajectory only		rotations in place		N
(icon)	Cw rotation in place		(curvi)linear orthogonal		N/A		
Gr. 1	15		0				16
Gr. 2	2	3	4	3			7
(icon)	rightward linear, lateral Φr		linear		no rotations in place		
Gr. 1	15		15				16
Gr. 2	6	7	6	7			7
(icon) 30	rightward linear, oblique Φr		linear		no rotations in place		
Gr. 1	11		15				16
Gr. 2	5	6	7	7			7
(icon) 120	rightward linear, oblique Φr		linear		no rotations in place		
Gr. 1	8		14				16
(icon) 135	rightward linear, oblique Φr		linear		no rotations in place		
Gr. 1	10		15				16
Gr. 2	6	6	6	7			7
(icon)	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
(icon)	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
(icon)	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
(icon)	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
(icon)	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
(icon)	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

[a] 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 two 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 counter-clockwise rotation. Condition *semicircle outward* ⌧ : In Group 1, there were seven 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 two — 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!

simulated movements could e.g. be based on integration of the instantaneous perception of heading. We investigated the subjects' reproductions of their perception 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, depending on the stimulus, the *type* of displacement can be perceived; directions, the form of trajectory (Ψ_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 distance travelled cannot be made. This is also the case for the vestibular system where the double integration of otolith provided acceleration does not yield a correct measure of distance travelled (Glasauer & Israël, 1993; Israël, Chapuis, Glasauer, Charade & Berthoz, 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).

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 observer's orientation (Φ_o) fixed in space was good. Subjects assumed they were orientated straight ahead in space, i.e. at 0°. For the linear trajectories, $< \Phi_r >$ was overshot at 30°, while for 120° and 135° it was under-shot. 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, 1991a). 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. The remainder of the subjects however 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 et al., 1991b; Stone & Perrone, 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' as-

Table 3
Results of quantitative analyses, sorted by condition and group[a]

condition	$\langle\Phi_r\rangle$ [°]	Ψ_p [°]	initial heading [°]	Ψ_o [°]	N
(icon)	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
(icon 30)	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
(icon 120)	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
(icon 135)	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
(icon)	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
(icon)	-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
(icon)	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

Table 3 Continued

	$\langle \Psi_r \rangle$	Ψ_p [°]	initial heading	Ψ_o	N
[symbol]	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
[symbol]	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
[symbol]	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
[symbol]	N/A	Ψ_p [°]	initial heading [°]	-179.8; 90	
Gr. 1		-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

[a] In Group 2 results are lumped over the stimuli with triangular and constant velocity profile, porting the maximum number of samples to $2 \times 7 = 14$. The $\langle \Psi_r \rangle$ column lists the mean $\langle \Psi_r \rangle \pm$ the mean standard deviation, averaged over all responses per group/condition. The table also lists Ψ_p (the rotation of the trajectory), the average initial heading and Ψ_o, the total change in observer orientation (yaw). The value ± 0.000 represents 'almost zero': values between $\pm 1 \times 10^{-4}$. 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 $\langle \Phi_r \rangle$, Ψ_p and Ψ_o columns indicate significant differences with the true movements. Significant differences between groups: $\langle \Phi_r \rangle$: *linear oblique 30°* ▨, small *semicircle inward* ▨, *semicircle forward* ▨, *semicircle full-turn* ▦ and *linear half-turn* ▦. Ψ_o: large *linear half-turn*. Significance at $P < 0.05$ or better, all determined by t-tests.

sumption 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 the 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 linear 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 condition is a well known phenomenon in optic flow literature: the flow presented in this condition is (initially) similar to the retinal flow corresponding to a forward movement with horizontal eye or head movement (Warren & Hannon, 1990; Warren et al., 1991a; Royden et al., 1992, 1994; Royden, 1994; Banks et al., 1996; van den Berg, 1996; Crowell, 1997; Cutting et al., 1997). 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 et al., 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). 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) rotation of the path (rotation in space of the displacement vector), (b) from a rotation of the observer relative to the path, or (c) 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 two 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 rotation axis has to be estimated. At any instant in time, the momentary flow field contains information about the amount of rotation, which might 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 (Ψ_o, Fig. 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 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 changes 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 rotations in place responses. The reported rotation was often incorrect for these responses (not shown). It is of course possible that in those cases subjects only perceived rotation due to a masking of translation perception by large amounts of rotation. But these responses can also be a sort of 'fallback' responses when the subject is only sure about the experienced rotation, as could result from disorientation, or from a too small field of view. Consider the case of 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.

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 seven 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 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. Fig. 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 Φ_o, although there is variation in the amount of path rotation and length. Also, some subjects visually perceive a 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 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 Φ_o as in condition *semicircle no-turn* .

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 Φ_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 (low-level) process. The movements rather seem to be deduced 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 subjects in Group 2 whether they had remarked that all stimuli had been presented twice (they had), 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. They had only been instructed 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, on 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. 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 two 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 manoeuvres. 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 2.5 m at a display spanning approximately $4.5 \times 3.4°$. She explained 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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