Reconstructing passively travelled manoeuvres: Visuo-vestibular interactions.

R.J.V. Bertin, I. Israël, A. Berthoz

Collège de France/LPPA

11, place Marcelin Berthelot; 75005 Paris; France

email: (**rene.bertin,**isabelle.israel,alain.berthoz)@college-de-france.fr

Abstract

We recently published a study of the reconstruction of passively travelled trajectories from optic flow. Perception was prone to illusions in a number of conditions, and not always veridical in the other conditions. Part of the illusionary reconstructed trajectories could be explained if we assume that the subjects based their reconstruction on the ego-motion percept obtained during the stimulus' initial moments. In the current paper, we test this hypothesis using a novel paradigm. If indeed the final reconstruction is governed by the initial percept, then additional, extra-retinal information that modifies the initial percept should predictably alter the final reconstruction. We supplied extra-retinal stimuli tuned to supplement the information that was underrepresented or ambiguous in the optic flow: the subjects were physically displaced or rotated at the onset of the visual stimulus. A highly asymmetric velocity profile (high acceleration, very low deceleration) was used. Subjects were required to guide an input device (in the form of a model vehicle; we measured position and orientation) along the perceived trajectory. We show for the first time that a vestibular stimulus of short duration can influence the perception of a much longer lasting visual stimulus. Perception of the ego-motion translation component in the visual stimulus was improved by a linear physical displacement; perception of the ego-motion rotation component by a physical rotation. This led to a more veridical reconstruction in some conditions, but it could also lead to less veridical reconstructions in other conditions.

A more detailed version of this paper is to appear in Exp. Brain Res.

1— Introduction

There is an ongoing debate about the relative importance of different sensory systems in the perception and control of ego-motion, and the interactions between these modalities. It has long been thought that navigation and orientation were mainly subserved by visual ego-motion perception. In particular, the direction of heading — where we are going — was supposed to be retrieved from the optic flow (Gibson, 1950; Koenderink, 1986; Lappe, Bremmer et al., 1999) and/or from other visual sources of information (Rushton, Harris *et al.*, 1998). A renewed interest in the role and function of other sensory modalities in the perception of ego-motion, orientation and navigation — often in relation to virtual reality — is supplying evidence that the visual system is less dominant than thought.

1.1 Where are we going?

Studies addressing orientation and navigation using the optic flow have typically looked at the perception of heading direction, that is: "Where are we going?". It is well established that humans can perceive their heading direction from optic flow patterns, with high accuracy and almost instantaneously. It is also known that perceptual illusions can occur in this task, inducing large errors. A famous example of such an ambiguous optic flow field is the flow that represents a straight trajectory, but that is perceived as a curved path (the *rotation problem*: Royden, Crowell *et al.*, 1994; Crowell, Banks *et al.*, 1998; Wann, Swapp *et* *al.*, 2000; Li and Warren, Jr., 2000). This optic flow stimulus simulates an observer moving along a straight line while making a horizontal eye- or head movement (rotation), e.g. to fixate an object at eye-height to the side of the path. It is generally thought that the illusion occurs because information is missing from, or underrepresented in, the optic flow. Information can be added via several sensory modalities to disambiguate this stimulus. When the observer actively makes an eye- or head movement corresponding to the one simulated, the illusion disappears and heading perception becomes more veridical (Crowell, Banks, Shenoy, and Andersen, 1998) — but not when the subject is full-body rotated passively. The illusion can also be made to disappear by increasing the amount of visual information available, for instance by presenting a structured visual environment (Li and Warren, Jr., 2000) instead of a virtual landscape consisting only of white dots, or even by adding a single landmark to such a "dotscape" (Bertin and Israël, 2002).

1.2 Where have we gone?

Other authors have studied the perception of travelled distance and/or rotation, that is: "Where (or how far) have we been going?" These authors focussed on the contributions from the visual, vestibular and somatosensory systems (Bakker, Werkhoven *et al.*, 1999; Mergner and Becker, 1990; Hlavacka, Mergner *et al.*, 1996; Mergner, Schweigart *et al.*, 2000; Harris, Jenkin *et al.*, 2000; Loose, Ayan *et al.*, 1999); Probst, Loose *et al.*, 1996; Probst, Loose *et al.*, 1995; Mesland, 1998). These studies clearly indicate that non-visual systems play an important role in ego-motion perception, although it is not yet quite clear which role. One study (Bakker, Werkhoven *et al.*, 1999) found a systematic undershoot in turning through an instructed angle (overestimation of perceived ego-velocity) with better performance when vestibular and kinaesthetic information was used versus when only visual information was available. Another study (Groen, Valenti Clari *et al.*, 2000) found overestimation of the vestibular stimulus in simulators (cf. Pavard and Berthoz, 1977 and Buizza, Leger *et al.*, 1980), and mentioned systematic underestimation of visually perceived ego-velocity (that also occurs when driving a car via a video-link!). Harris and co-workers (Harris, Jenkin *et al.*, 2000; Redlick, Jenkin *et al.*, 2001) found undershoot of the instructed distance when providing only a visual display consisting of properly scaled representations of well-known environments. Jürgens (Jürgens, Boβ *et al.*, 1999) found a range effect (undershoot of large rotations, overshoot of small rotations) when subjects were to estimate rotations using only vestibular information. One suggestion emerging from many of these studies is that the vestibular system dominates the visual system, at least in simulators (e.g. Groen, Valenti Clari *et al.*, 2000; Harris, Jenkin *et al.*, 2000; Redlick, Jenkin *et al.*, 2001), with instructed distances being undershot when only visual information is available, but (slightly) overshot when the corresponding vestibular information is also provided. Other studies have suggested the possibility of a "max rule" where the brain "listens to" the sensory system indicating the biggest travelled distance or turned angle (von der Heyde, Riecke *et al.*, 2001; Lambrey, Viaud-Delmon and Berthoz, in press).

1.3 How did we get there?

In an earlier series of experiments, we studied the reconstruction of passively travelled manoeuvres in the plane; from optic flow information alone, or with a single landmark (Bertin, Israël *et al.*, 2000; Bertin and Israël, 2002). We define a *manoeuvre* as a specific *trajectory* (path) combined with a specific *orientation* (yaw) at any given point along that trajectory; orientation need not be yoked to the path. Among the simulated manoeuvres that we presented, several generated flow fields known to be ambiguous – including the straight path + yaw manoeuvre mentioned above. Until recently, this illusion had been shown to occur only for short stimulus durations, simulating relatively small angular displacement of the eye or head (not more than a few degrees). Our stimuli simulated much larger rotation: between 90 and 360 degrees. Nevertheless, the majority of our subjects perceived themselves to be travelling along a circular trajectory, with orientation more or less (tangentially) fixed relative to that path. That is quite an impressive illusion! Somehow, the fact that all these displays contained a phase of sideways motion, in most cases evolving into backward motion, and so forth, had gone unnoticed. It is often claimed that there is a strong resemblance between this kind of stimulus, and the flow corre sponding to the illusory, perceived manoeuvre, thus explaining the illusion (e.g. Royden, Crowell, and Banks, 1994, but cf. Kim and Turvey, 1998 and Wann and Schwapp, 2000). There is indeed a resemblance between the two flows, but is easy to see that it cannot last longer than a fraction of the duration of our stimuli, as they simulate much larger rotation (see also Ehrlich, Beck et al., 1998).

How then could we explain the fact that the illusion still occurs? We proposed that the initial percept is of crucial importance. It is conceivable that a naive, inexperienced but efficient subject/observer would only update an existing, robust ego-motion percept — e.g. the initial percept — when some qualitative change occurs in the stimulus. In between such events, which don't occur in our stimuli, they would then simply extrapolate that established percept. Such a strategy would explain our result, because, in the stimuli being discussed, the initial percept certainly is the illusory perception of a circular path. This argument is supported by the fact that the few more veridical responses were made by subjects who reported having seen the different phases of motion described above.

Thus, it is our hypothesis that the initial percept is important in ego-motion perception tasks involving the reconstruction of travelled trajectories. We can then ask if it is possible to modify the *final* percept by altering the *initial* impression. During the initial stimulus phases, one could add the information that is ambiguous or underrepresented in the optic flow — for instance by physically displacing the subjects at stimulus onset. If this extra, non-retinal information improves the initial percept's veracity, then the final percept (the reconstructed manoeuvre) should be more veridical if indeed determined by the initial percept. The additional information should be present only at the stimulus onset, thus calling for an impulse-like vestibular stimulus: high acceleration followed by sub-threshold deceleration.

Here, we report on a study that addressed this question. We selected 3 different manoeuvres from our previous experiment, and presented them at different scales. One of these was the "linear+yaw" manoeuvre (**linear 180-turn**) discussed at length above. The other 2 were both semicircles, one with tangential observer orientation (observer "looking in the direction of movement": **semicircle forward**), the other with outward observer orientation (observer oriented with the back towards the circle's centre; **semicircle outward**). The **semicircle forward** condition had been generally well perceived, but with frequent rotation-in-place (RIP) responses for the small radius, and yaw was often undershot. The **semicircle outward** condition had been generally mistaken for a lateral, linear displacement in the large radius version, with again many RIP responses in the small radius version. In the **semicircle forward** conditions, additional information would thus have to bolster the linear component: we therefore physically displaced the subjects over a short, linear trajectory. In the **semicircle outward** conditions, the angular component had been undershot or overlooked; hence we physically rotated the subjects (yaw). Finally, in the **linear 180-turn** conditions, neither component was undershot or overlooked, but yaw had been attributed to a rotation of the path, such that the linear nature of the path was ignored. Thus, we also displaced the subjects over a linear trajectory in these conditions. Note that we added either purely linear motion, or purely angular motion, and not a combination of the two (as we could have done e.g. in condition **semicircle forward**). Whereas this choice possibly induced mild visuo-vestibular conflict, it had the advantage that it excited either the linear or the angular vestibular acceleration sensors but not both. It also provided a means to add supplementary information that was minimal and controllable to the best possible extent (e.g. avoiding interactions among semicircular canals and otoliths).

2— Materials and Methods

2.1 Subjects

A total of 14 subjects participated in this study, 8 males and 6 females. All subjects were in their early twenties to mid-thirties, and gave their informed consent before the experiment was run. The experimental protocol was in accordance with institutional and national ethics guidelines and conform to the Helsinki Convention.

2.2 Apparatus: physical displacements

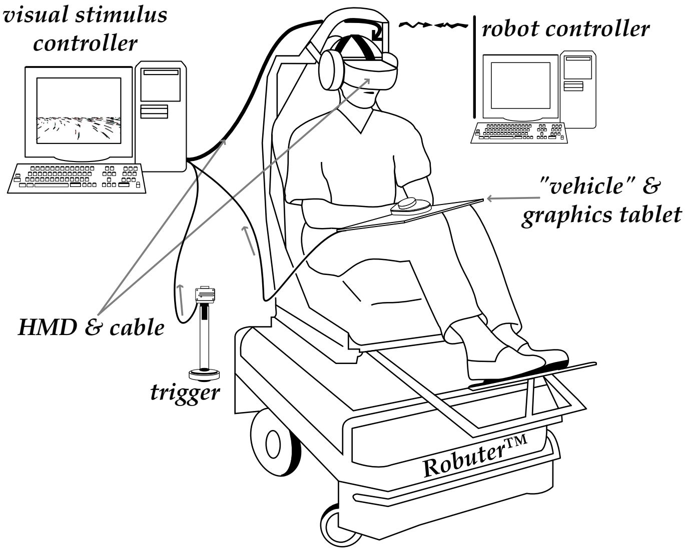

Figure 1: Experimental set-up. The Robuter™; its controller host and the visual stimulus generator (an SGI O2 workstation running Performer software under Irix 6.3) driving an NVision Datavisor LCD HMD. The Robuter is controlled via a radiographic serial link. Synchronisation between physical and visual stimulation is on the onset of the robot's movement. The subject manipulated a vehicle-like input device for the reconstruction of the perceived manoeuvres. Position and orientation of this model vehicle were recorded by a graphics tablet and sent to the O2, where a separate programme stored this information, and presented a stylised view in the HMD for feedback.

For the physical displacements, we used a mobile robot, the Robuter™: figure 1. This is a remotely controlled moving platform, onto which a racing car seat has been mounted. Subjects were seated on this seat throughout the experiment, and secured with three-point safety belts. A foot rest provided support for their feet, such that they were in a comfortable position to perform the required task (see below). The robot was controlled from a dedicated PC computer via radiographic modems. The Robuter was capable of a maximum accelerations of 1 m/s^2 and 1 rad/s^2, with maximum speeds of 1 m/s and 1 rad/s. The best way to present an impulse-like vestibular stimulus with this apparatus was to use a highly asymmetric velocity profile, quickly attaining a maximum velocity, and decelerating to standstill as slowly as possible. Standstill was programmed to occur after the end of the visual stimulation, in order to avoid a "stop signal" during the visual stimulus. The initial acceleration was maximised to ensure that the following deceleration could be the lowest and "smoothest" possible, with the smoothest possible transition from acceleration to deceleration. Odometric data was recorded from the Robuter after each trial. The linear displacements are shown in figure 2a (acceleration of 0.87m/s^2 attained after 0.5s; deceleration of 0.025m/s^2, total displacement of about 1m). The angular displacements are shown in figure 2b (acceleration of around ±54°/s^2 attained after 0.73s, deceleration of around ±2°/s^2, total rotation slightly under ±90°)[1]. A walkman playing white noise (controlled by the subject on the experimenter's indications) masked the sound from the robot's servo motors and other possible sound cues, but could not prevent that almost all subjects could reliably distinguish trials "with robot" from trials "without robot". This did not have any fundamental consequences.

The visual stimulus was synchronised to the vestibular stimulus by means of a trigger apparatus that, using an infrared photodiode on a serial link, detected the onset of the robot's displacement with a precision

---

[1] This deceleration is not sub-threshold, but was the lowest smooth deceleration we could attain, and much weaker than the preceding acceleration.

of not more than a millimetre. Upon arrival of the synchronisation signal, the movement of the optic flow generating dotscape (that was already visible) started a single frame (1/60s) later.

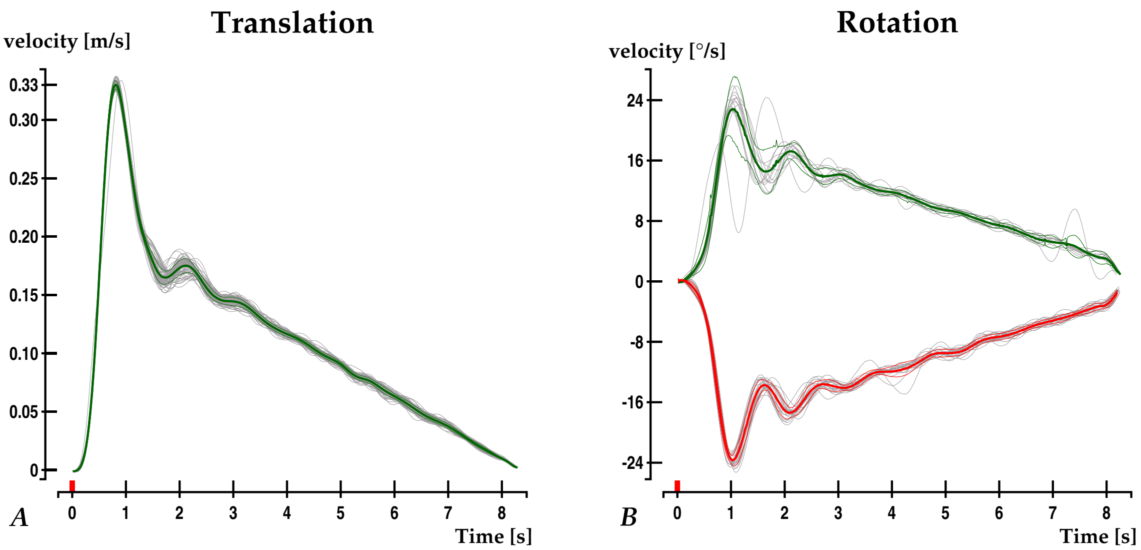

Figure 2: physical displacement velocity profiles (vestibular stimuli).

a) Velocity profile of the linear displacements. The dark, fat trace shows the average and standard deviation of the individual profiles that are shown in light grey. Speed was calculated from the robot's position signal.

b) Velocity profiles of the angular displacements. Display as described for figure 2a. Positive speeds (angles) indicate counter-clockwise rotations, negative speeds (angles) clockwise rotations.

2.3 Apparatus: visual stimulation & response

The set-up of the visual stimulation and the response apparatus have been described elsewhere in more detail (Bertin, Israël *et al.*, 2000; Bertin and Israël, 2002). Visual stimuli were generated on a Silicon Graphics O2 workstation, using the Performer 2.1 libraries, and consisted of "dotscapes" of white dots distributed on a horizontal ground plane in an otherwise dark (black) environment (a total of 3000 dots [pfLPointStates] on a 25x25m plane). The position of the ground plane was calibrated to match the actual position of the ground as seen from the subject's position on the robot; on average around 1.25m below eye-level. Optic flow was generated by simulating movement of the virtual observer (viewpoint) along the desired manoeuvres (remember that we call a manoeuvre a specific type of trajectory combined with a specific orientation at any given point along that trajectory; yaw need not be yoked to the path). Constant velocity manoeuvres were used. These displays were presented to the subject via an NVision Datavisor LCD HMD (FOV 48° horizontal x 36° vertical, 640x480 true VGA resolution at 60Hz). Stimuli were generated on the O2 in a 640x480 window that was captured by the O2's dedicated hardware, sent as NTSC format S-Video to a Blackbox video-to-VGA converter, and sent to the HMD. (This extra step was necessary in order preserve some screen "real estate" for the experimenter, and to create comparable conditions with earlier experiments.) Figure 3 shows time exposure snapshots of the different types of optic flow.

Subjects were required to reproduce the manoeuvre they had reconstructed from the optic flow. For this, they could manipulate a vehicle-like input device. A graphics tablet measured position and orientation of this device, and sent this information to the O2 where a separate programme processed and recorded it. For feedback, a stylised representation of the vehicle's current position and orientation, and its travelled path were shown in the HMD: subjects were instructed to guide their reproduction by this information. A cross and a circle were provided to serve as templates for linear and circular trajectories. Buttons on the model vehicle allowed the subject to erase unsatisfactory or "messed up" reproductions, and to save those that optimally represented their percept.

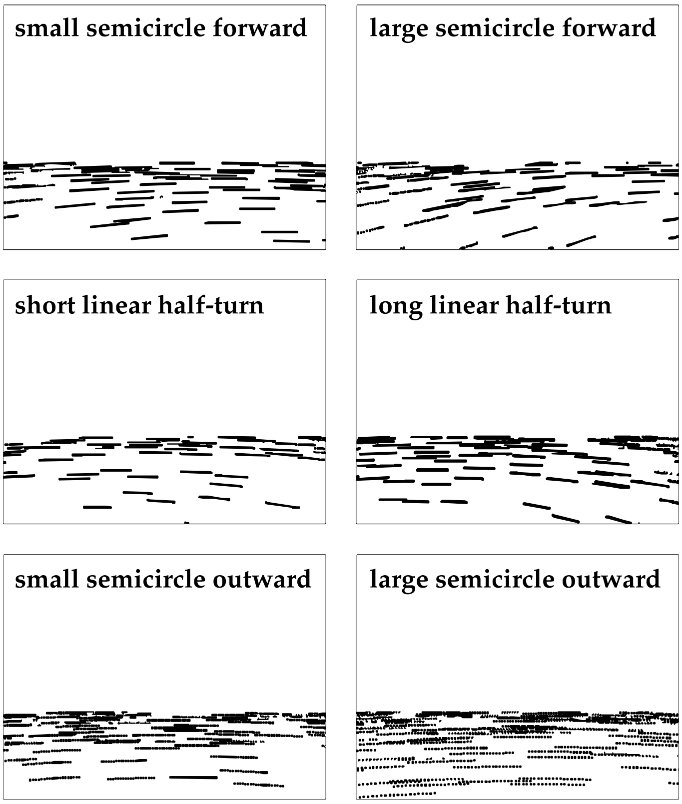

Figure 3: optic flow snapshots, taken after approximately 4s (halfway the stimulus duration), and during approximately 0.3s. The flow generated by the 3 different types of manoeuvre is shown, with in the left column the small/short versions and in the right column the large/long versions.

Top: Conditions **semicircle forward**: tangential, circular movements in clockwise direction.

Middle: Conditions **linear half-turn**: straight translations with 180° yaw rotation in counter clockwise direction.

Bottom: Conditions **semicircle outward**: circular movements with 90° outward orientation.

2.4 Stimuli.

The stimulus conditions fell into three different classes, each visually simulating a particular type of manoeuvre, in different sizes. These conditions were presented either purely visually, or in combination with a vestibular stimulus (see also figure 4):

1. *Tangential semicircles* (the conditions **semicircle forward)** were presented in 3 different radii: R=1.5m, R=3.25m and R=5m. In a circular movement, radius, tangential velocity (Vt) and angular velocity (Va) are related by a simple equation: Vt = R Va. Keeping the stimulus duration constant, one can thus attain different radii in 2 orthogonally different ways. The total travelled angle can be kept constant while increasing tangential velocity to increase the radius. This we call the constant angular velocity (**Va=C**) condition. One can also fix the total travelled distance, decreasing angular velocity to increase the radius. This is the constant tangential velocity (**Vt=C**) condition. All rotations were clockwise (a control experiment had not revealed any leftward/rightward differences). In the visuo-vestibular trials, the subject was subjected to an impulse of forward linear physical motion.

2. *Outward semicircles* (the conditions **semicircle outward)** were presented with radius R=1.5m and R=5m. For these conditions, clockwise and counter-clockwise rotations were presented. In the visuo-vestibular trials, subjects were subjected to an impulse of pure yaw motion in the appropriate direction.

3. Linear, forward movement with counter-clockwise 180° yaw (the conditions **linear half-turn**) were presented with path lengths of 4.71m and 7.85m. In the visuo-vestibular trials, subjects were subjected to an impulse of linear, forward motion.

All stimuli lasted a total of 12s: 2s with stationary dotscape, then 8s of simulated manoeuvre, and then again 2s of stationarity.

2.5 Experimental protocol.

The experiment was performed in a darkened room, to prevent light from entering the HMD from behind. Subjects sat on the Robuter throughout the session, wearing the HMD. The stimuli were presented in pseudo-randomised order. After each trial, the subjects shut off the walkman; the signal for this was the appearance of the "reproduction screen". In order to remove doubts about the intended response, we asked them to briefly describe exactly what they had just "drawn" after they had made the reproduction of the perceived manoeuvre. We also asked some additional questions. When the reproduced manoeuvre represented a (more or less) circular movement, subjects were asked to qualitatively estimate the radius (small, medium, large, etc.), either by comparison with the previous stimulus, or directly. All subjects reliably detected the presence or absence of robot movement; nevertheless, we questioned systematically whether or not the robot had moved and, if so, how. In certain cases, more detailed questions were asked to relate specific particularities of the reproduced manoeuvre (e.g. a transition from linear to curvilinear movement) to the robot's movement. Finally, we asked whether or not a visuo-vestibular combination had been perceived as conflicting, or as "OK". Notes were taken, and the discussions were recorded for off-line processing and analyses of the reproductions.

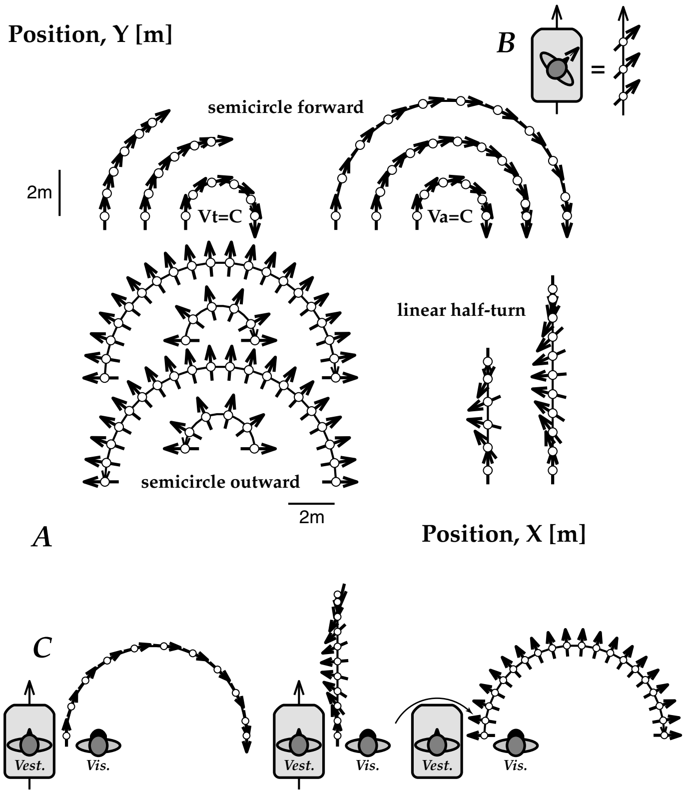

Figure 4: Top-down view of the presented (simulated) manoeuvres.

a) Arrows represent the observer's orientation at the indicated positions along the trajectory as explained by the icon inset (b); the direction of translation is indicated by the large arrowhead at the end of each trajectory. (The **semicircle forward** stimuli were all in clockwise direction.)

c) The visuo-vestibular stimulus combinations that were presented.

Subjects were thoroughly instructed about this demanding protocol. It was stressed that they should principally concentrate on the visual stimulus, and that they should reproduce the manoeuvre that they had "perceived visually" (the radius estimation task was intended to help improve the focus on the visual stimulus). They were furthermore asked to indicate themselves when a noticeable delay had occurred between the onset of the vestibular and visual stimuli, and when they had sensed a strong conflict. Ample time was given to get comfortable with the model vehicle and reproduction task; during this training, comprehension of the possibly unyoked nature of path and orientation (yaw) was verified. Subjects were asked to draw their reproductions on as large a scale as possible.

The experiment lasted between 1 and 2 hours, depending on the duration of briefing and questioning, and the number of trials that had to be restarted.

2.6 Data analysis.

Artefacts in the reproductions were suppressed based on the verbal descriptions given, filtered with a lowpass filter and resampled to 20 points as described in (Bertin, Israël *et al.*, 2000). The responses to visuo-vestibular trials were then classified according to the nature of the interaction (*none*, *visuo-vestibular*, *vesti-*

bulo-visual, *mutual*), the nature of the perceived vestibular movement (including "*none*" and "*don't know*"), and the perceived nature of the interaction (*OK*, *conflict*, *dual/transparent*).

Responses were analysed using two different measures. The first measure describes each response in terms of three angles[2]: the reproduced yaw (Ψo), rotation of the path (Ψp) and the average orientation relative to the path (<Φr>); figure 5. This measure allows us to describe observer rotation (yaw) independently from the eventual curvedness of the trajectory over which this observer is displaced (rotation of the path). The average path-relative orientation links these two angles to obtain a generalised but quantitative measure of the reproduced manoeuvre. Thus, a **semicircle forward** manoeuvre is described as {Ψp; Ψo; <Φr>} = {-180°; -180°; 0°}. This measure is only fully defined for responses that are not rotations in place (RIP; for RIPs, only yaw is defined).

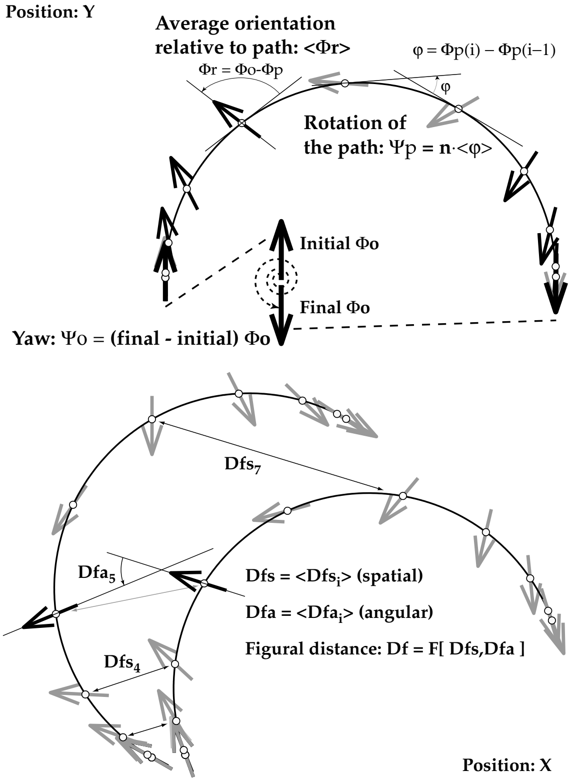

Figure 5: Explanation of the indices used in the quantitative analyses. See text (Methods) for details. In this example (clockwise semicircle with counterclockwise yaw; not used in the experiments), yaw Ψo=180°, path-rotation Ψp=-180° and path-relative orientation (gaze) <Φr>=179.7°±109.8°; figural distance Df=4.857 with spatial figural distance Dfs=4.689 and angular figural distance Dfa=1.264.

The second measure is a *figural distance* measure, adapted from (Conditt, Gandolfo *et al.*, 1997). This measure quantifies the overlap (or rather: the error in the overlap) between a reproduction and the corresponding stimulus manoeuvre. It is a function of the *spatial figural distance* (Dfs: the average distance between the individual corresponding points on the trajectories) and the *angular figural distance* (Dfa: the average difference in orientation at these points, normalised with respect to Dfs). Here, we use $Df=\sqrt{Dfs^2+Dfa^2}$. Thus, a perfect response would give a value of 0 (perfect overlap) according to this measure. To obtain sensible comparisons among the stimulus/response differences, all responses were first shifted, rotated and/or scaled so as to obtain a maximum overlap with the corresponding stimulus (this was done by minimising the figural distance using a Simplex downhill method). This operation was possible because position, scale and orientation of the reproductions are not informative in our protocol: initial position and orientation were not defined, and absolute distance (scale) is not conveyed by the optic flow. The individual Dfs and Dfa values were then normalised to the maximum respective values encountered. The advantage of this figural distance measure over the other measures is that it can be applied to all responses (RIP or not), and that it captures other aspects as well: e.g. three orthogonal linear segments can correspond to a 180° path rotation, while never being equal to a semicircle.

---

[2] NB: we use Ψ to refer to rotation and Φ to refer to orientation. Thus, Φo represents the observer's orientation at a given point, and Ψo the amount of change in this orientation ("yaw") relative to the starting point.

3— Results.

When purely visual stimuli were presented, subjects performed much like the subjects in our earlier, visual experiments (Bertin, Israël, and Lappe, 2000; Bertin and Israël, 2002). That is, we observed many RIP responses in the conditions with the smallest radius. The perceived rotation of the subject (yaw) and of the path undershot the presented angles when the stimulus simulated a movement along a semicircle with tangential orientation (the **semicircle forward** conditions). The **linear half-turn** conditions were in general perceived as tangential, curvilinear manoeuvres. Subjects did not have particular difficulties with the complicated protocol itself. although many judged that reproducing a perceived manoeuvre with the model vehicle was not easy.

As expected by our working hypothesis, we observed modifications of the *final reconstruction* caused by an effect of the vestibular stimulus on the *initial percept* (see below). Several kinds of sensory interactions and different perceptions of the visual and vestibular stimuli could be observed underlying these results. Surprisingly, many subjects had a clear percept of two separate manoeuvres – the "visual movement" and the robot's movement. These percepts were sometimes (both) correct, sometimes quite different from each other, but generally without inducing a feeling of conflict (reports of conflict occurred at between 0% and 44% of the presentations). Figure 6 shows all subjects' responses to one particular stimulus (**semicircle forward**, R=1.5m).

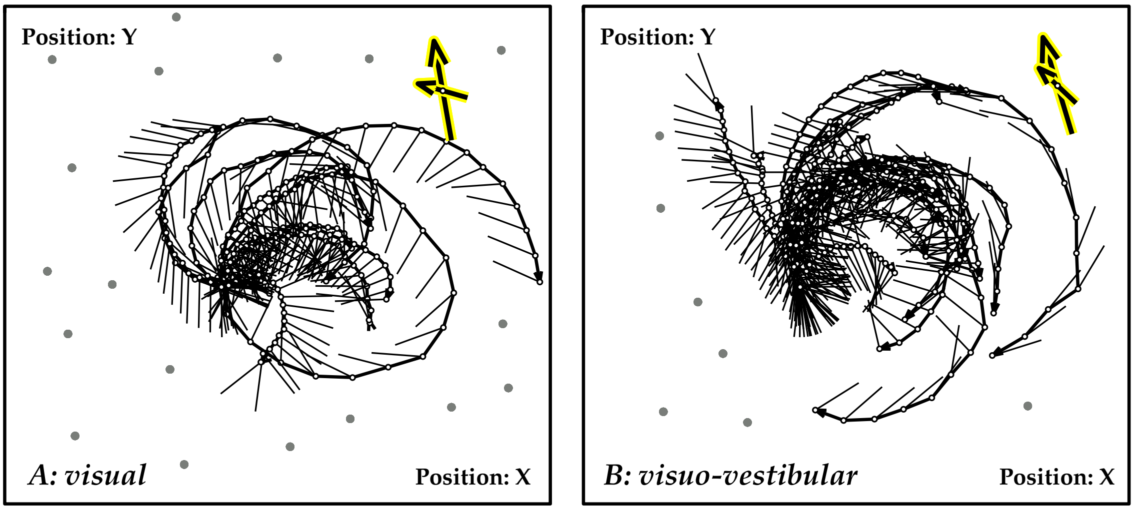

Figure 6: all responses to the small conditions **semicircle forward**, without (A) and with (B) vestibular stimulation. The reproduced manoeuvres are displayed as in figure 4, except that for clarity, the orientation at each point is shown by thin streamlines defining the subject's rear. The large grey dots are rotation in place (RIP) responses, for which orientation is not shown. All responses were normalised to the longest response (thus no scale is shown), shifted to start in the origin, and rotated such that the average direction of the first segment (the average departure direction) is at 90° (along the positive Y axis). RIP responses were not altered, but displaced to the periphery. The two large, outlined arrows indicate the original average departure direction (the larger arrow) and the original average initial orientation (at the starting point; the smaller arrow); the angle between these arrows gives the average initial path-relative orientation (Φr). A clear effect of the vestibular stimulus on the number of RIP responses can be seen (cf. figure 7a), as well as on the average initial path-relative orientation (the panels are on identical scale).

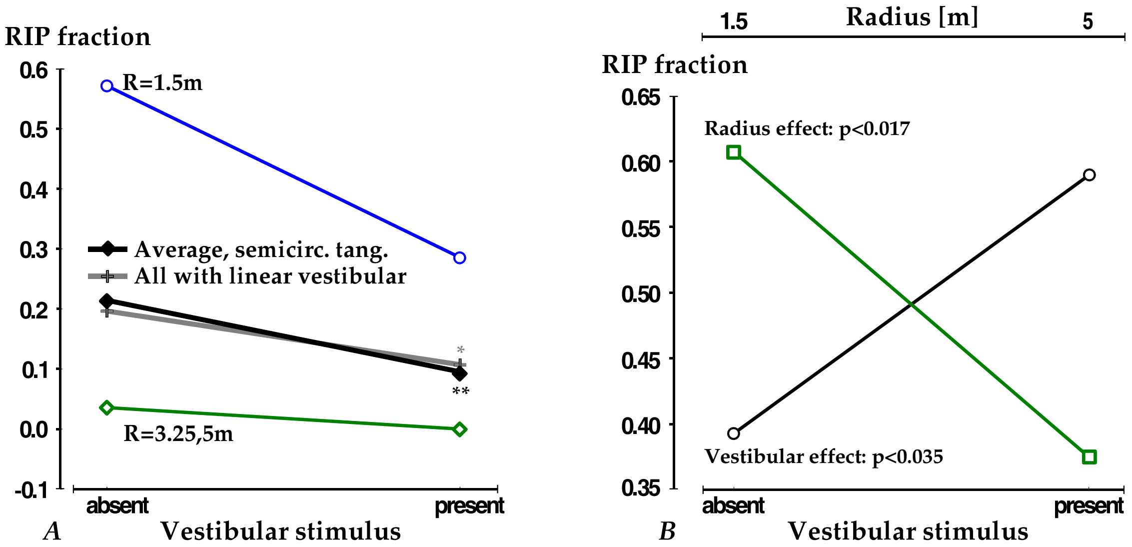

Figure 7: effect of vestibular stimulation on the fraction of the subjects that erroneously reported a rotation in place (RIP fraction).

a) Effect of a linear displacement on the RIP fraction in the **semicircle forward** conditions. The effect is a significant reduction (**"average, semicirc. tangential"**; F(1,13)=10.48; $p< 0.006$; **), and is due mainly to the smallest radius (R=1.5m; 2-way F(2,26)=4.79; $p< 0.017$ radius X vestibular; cf. figure 6). The effect remains when the responses to all conditions with linear robot movement are taken into account (**semicircle forward** and **linear half-turn**; **"All with linear vestibular"**; F(1,13)=7.22; $p< 0.019$; *).

b) Effect of a linear displacement on the RIP fraction in the **semicircle outward** conditions. The effect is a significant *increase* in the number of erroneously reported rotations in place (F(1,13)=5.52; $p< 0.035$). In these conditions there is also a significant *reduction* in the RIP fraction when the radius increases (upper X-axis; F(1,13)=7.50; $p< 0.017$). Note the high baseline number of RIP responses in these conditions (panels A and B are not on the same scale).

3.1 Improvement of visual perception by a vestibular stimulus (conditions semicircle forward)

Linear physical displacements were imposed at the onset of visual stimuli simulating a displacement along a semicircular tangential path. We observed several positive effects of this vestibular stimulus on the perception of the visual stimulus. A striking effect was a 50% reduction in the number of erroneous rotation in place perceptions in response to the smallest radius condition (ANOVA, F(1,13)=10.48; $p<0.006$). This is visible in figure 6 (the number of grey dots is less in ***B*** than in ***A***) and quantified in figure 7a. The reduction was due mainly to the smallest radius condition (R=1.5m; 2-way ANOVA, F(2,26)=4.79; $p< 0.017$ radius × vestibular), but remained significant when the responses to all conditions with linear robot movement were taken into account (**semicircle forward** and **linear half-turn**; ANOVA, F(1,13)=7.22; $p< 0.019$). This was the result that we had expected.

The initial vestibular stimulus thus improved the perception of the translation simulated in the visual stimulus. But it also improved the veracity of the perceived manoeuvres from a quantitative point of view. This was not due to the decrease in the number of RIP responses: RIP responses were excluded from quantitative analyses since too many of the measures were non-defined.

Without the vestibular stimulus, the reproduced yaw tended to be around 22% smaller than the presented yaw (undershoot). The vestibular stimulus (a linear displacement!) reduced these errors: we observed 10% undershoot for the **Vt=C** conditions and 10% overshoot for the **Va=C** conditions (a reduction of the absolute error) (ANOVA, F(1,13)=7.31; $p< 0.018$; figure 8a).

Without a vestibular stimulus, the perceived rotation of the path also undershot the simulated values: 70% for the **Vt=C** conditions, 33% for the **Va=C** conditions. With the vestibular stimulus the undershot was reduced to 50% for the **Vt=C** conditions and 5% for the **Va=C** conditions (ANOVA, F(1,11)=4.59; p≈ 0.055; figure 8b).

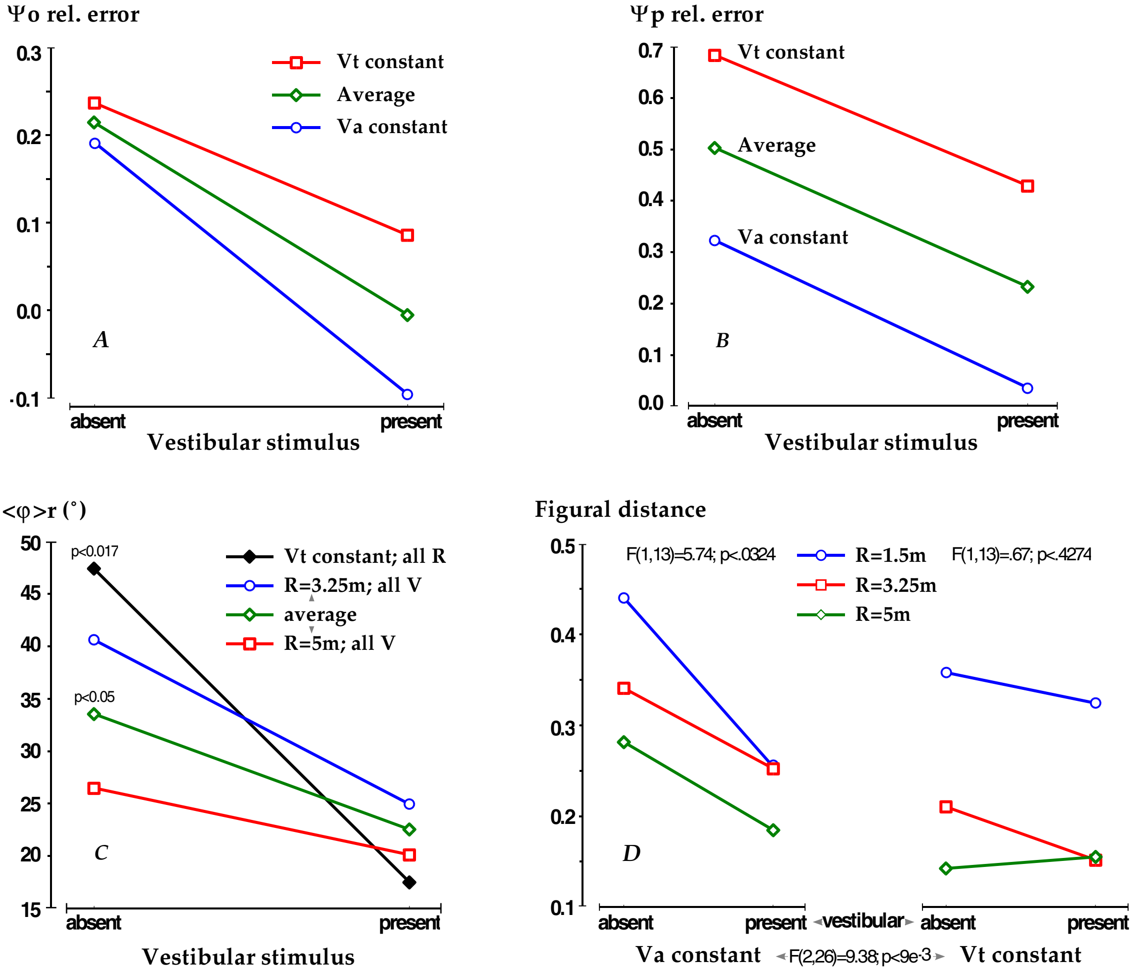

Figure 8: quantitative effects of vestibular stimulation on the perception of the **semicircle forward** stimuli.

a) Effect on the perceived yaw, all radii (relative error). There is a significant reduction of the error to close to 0 over all conditions when a vestibular stimulus is presented (**"average"**). There is no difference between the conditions with constant tangential velocity (**Vt constant**) and constant angular velocity (**Va constant**).

b) Effect on the perceived rotation of the path (relative error), radius R=3.25m and R=5m (there were too many RIP responses in the smallest radius). There is again no significant difference between the **Va constant** and **Vt constant** conditions; the decrease in error with vestibular stimulation is marginally significant (**"average"**; F(1,11)=4.59; p≈ 0.055).

c) Effect on the perceived path-relative orientation, for radii R=3.25m and R=5m (all V) and for all radii for the **Vt constant** conditions. Presence of a vestibular stimulus causes the perceived path-relative orientation to be more veridical in all cases (**"average"**; all R=3.25,5m: F(1,11)=4.93; p< 0.049; all **Vt constant**: F(1,6)=10.77; p< 0.017).

d) Effect on the figural distance measure. According to this measure, there is a highly significant difference between the effects of the vestibular stimulus on the **Va constant** and the **Vt constant** conditions (2-way ANOVA, F(2,26)=9.38; p< 0.009). There is a significant increase in stimulus/response resemblance for the **Va constant** conditions (F(1,13)=5.74; p< 0.033), with again the strongest effect and the largest error for the smallest radius condition.

The perceived orientation relative to the path was also improved by the vestibular stimulus, that is, it was more tangential (figure 8c). Without a vestibular stimulus, the error ranged between 25% and 48% overshoot; with a vestibular stimulus between 17% and 25% overshoot (ANOVAs, all R=3.25,5m: F(1,11)=4.93; p< 0.049; all **Vt=C**: F(1,6)=10.77; p< 0.017).

The figural distance measure confirmed these positive effects: there was less difference between stimulus and reproduction when the vestibular stimulus was present (ANOVA, F(1,13)=5.74; p<0.032; figure 8d). According to this measure, the improvement existed only for the **Va=C** conditions (ANOVA, F(2,26)=9.38; p< 0.009, condition × vestibular).

3.2 Adverse effect of a vestibular stimulus on visual perception (conditions semicircle outward)

We also imposed a pure physical rotation in place at the onset of visual stimuli that simulated a displacement along a semicircular path with outward orientation. Without the vestibular stimulus, these visual stimuli were often perceived as lateral linear translations when the large radius version was presented (resulting in a significant 50% undershoot of the path-rotation; t-test, p<0.002). The small radius version was again often perceived as a rotation in place. We had hoped to observe more curvilinear reproductions for the large radius with the vestibular stimulus than without. However, adding the vestibular stimulus increased the number of rotation in place responses from 40% to 60% (all radii; ANOVA, F(1,13)=5.52; p< 0.035: figure 7b), thus deteriorating perception instead of making it more veridical.

3.3 Absence of effect of the vestibular stimulus (conditions linear half-turn)

Finally, we presented a linear vestibular stimulus with visual stimuli simulating a linear displacement with 180° degree of yaw (full-body rotation). In this case, the perception of the visual stimulus was not more veridical with the vestibular stimulus than without. We had hoped to observe the perceived path-rotation to be closer to 0° when an initial vestibular stimulus had been presented. Without vestibular stimulus, the average perceived path-rotation was 118° for the short and 221° for the long version: the subjects perceived curvilinear paths as expected. With the vestibular stimulus, these figures are 155° for the short and 296° for the long trajectories (all highly significantly different from 0°). Thus, the reproduced manoeuvres remained predominantly curvilinear instead of linear, despite the vestibular stimulus.

4— Discussion

We have studied the reconstruction of passively travelled manoeuvres from optic flow, and the influence of vestibular stimulation on this task. Optic flow is one of the important visual sources of information concerning ego-motion in space. It is however prone to misinterpretation when information is missing, underrepresented or ambiguous. Thus, illusions can occur. It has been shown for heading perception that these illusions can be reduced by adding additional visual information to the optic flow (a structured environment; Li and Warren, Jr. (2000), but also by adding non-visual information: eye- or head movements (Crowell, Banks, Shenoy, and Andersen, 1998) and even whole-body tilt (Sibigtroth and Banks, 2001). Previous experiments suggested that the final reconstruction of passively travelled manoeuvres might well be governed by the initial percept obtained from the optic flow stimulus. In the present paper, we addressed this idea, by studying the effect on the final reconstruction of vestibular information provided at the visual stimulus' onset. We show that our hypothesis is confirmed. We also show that an initial vestibular stimulus can *improve* the perception of the visual stimulus in a limited number of conditions. This is (to our knowledge) the first time that such effects of a vestibular stimulus on the perception of a visual stimulus have been reported.

When we presented a linear vestibular stimulus with a visual stimulus that simulated movement along a circular arc with tangential orientation (**semicircle forward**), perception of the visual stimulus improved. We predicted that the vestibular stimulus would decrease the number of erroneous rotation in place (RIP) responses by increasing the saliency of the translation component of the simulated manoeuvre. This is indeed what we found: there were 50% less RIP responses in the small radius condition with vestibular stimulus than without vestibular stimulus. But, surprisingly, the simulated manoeuvres were also better perceived according to quantitative measures: the error in the perception of yaw decreased by almost 50%, the error in the perception of the path-rotation somewhat less.

There are several possible explanations for this improvement. The high number of RIP responses in the vision-only conditions can most likely be explained by the limited field of view (FOV) that we used. We presented the visual stimuli in an HMD; thus, the field of view (FOV) was approximately 40° horizontally. When the FOV is decreased, radial components in the optic flow (corresponding to forward ego-translation) become less salient. Thus, for a small radius curvilinear tangential manoeuvre, the translation component of the simulated ego-motion may become undetectable against the rotation component: a RIP response will be the result. The first and most appealing explanation for the observed improvement would then be that an initial physical, forward translation increases the saliency of the underrepresented components: "visual translation" supported by "vestibular translation". A second explanation might be that although a linear physical displacement may cause some (initial) confusion, it lacks the (lasting) disorienting effect of a rotation. As such, it could help or force the subject to concentrate on the interpretation of the visual stimulus (this would also explain the observed quantitative improvement). Finally, a strong sense of conflict would arguably have resulted when a visually induced percept of a RIP were combined with a percept of linear or curvilinear physical ego-motion.

Additional support for our hypothesis, and for the first explication above, comes from a stimulus combination in which the visual stimulus simulated a semicircular movement with outward orientation and the vestibular stimulus was a RIP. We predicted that this would increase the perception of the path's rotation in the large radius conditions. Instead, we found that the number of RIP responses *increased*, even for the large radius stimuli. Thus, a rotational vestibular stimulus increases the saliency of the rotational component in the visually simulated manoeuvre. This result supports the effect discussed above. However, in this case the perception of the visual stimulus is *worse* with than without vestibular stimulus: the translational component is often suppressed. It is known that a strong vestibular stimulus can cause the temporary perceptual freezing of a moving visual pattern (Pavard and Berthoz, 1977; Buizza, Leger, Droulez, Berthoz, and Schmid, 1980), and recent studies found physiological evidence for reciprocal cross-modal inhibition (Wenzel, Bartenstein *et al.*, 1996; Brandt, Bartenstein *et al.*, 1998). Also, the vestibular stimulus we imposed can temporarily decrease the *retinal flow* by inducing a VOR eye movement in the same direction as the optic flow in the visual stimulus: this will strongly modify the retinal flow. The suppression of the translation component may be explained by a combination of central suppression and peripheral modification of the visual input.

Finally, we found that a vestibular stimulus that does not provide additional, helpful information has little or no effect. We imposed a linear vestibular stimulus at the onset of visual stimuli simulating a linear translation combined with a large (180°) yaw rotation, predicting that this would increase the linearity of the reproductions. (Remember: alone, this visual stimulus usually results in reproductions of curvilinear, tangential manoeuvres.) This effect did not occur. We can understand this given the results from the **semicircle forward** conditions. When a **semicircle forward** visual stimulus is correctly perceived as a tangential curvilinear manoeuvre, adding a linear physical forward displacement does not qualitatively alter that perception. The physical displacement may itself be perceived as slightly curvilinear, or it may slightly reduce the curvedness of the visually perceived movement, but it is not (perceived as) incompatible with that visual percept. Thus, when optic flow can be perceived as either a tangential curvilinear manoeuvre (illusion) or as a linear translation with yaw (correct), a linear vestibular stimulus does not help in choosing between these two alternatives because it is compatible with both percepts. In other words, it cannot disambiguate that particular optic flow. This finding is in agreement with the study by Crowell *et al.* (Crowell, Banks, Shenoy, and Andersen, 1998) who found that a physical, passive whole-body rotation cannot disambiguate a similar optic flow. The information that this vestibular stimulus gives ("the body turns") is also in agreement with both interpretations.

Summarising, we have shown for the first time that a short-lasting vestibular stimulus given at the onset of a longer-lasting visual stimulus can influence the perception of the latter in a navigation/orientation task that involves more than instantaneously indicating the direction of heading. Our results suggest that cross-modal congruence is essential: a linear vestibular stimulus can improve the perception of translation in the visual stimulus, and a rotational vestibular stimulus can improve the perception of the rotational component in the visual stimulus. The resulting effect on visual perception can be positive (perception of a displacement together with rotation, instead of only rotation) but also negative (perception of only rotation, instead of a displacement together with rotation…). These findings can be of relevance to the development of low-cost driving simulators, especially those making use of HMDs for visual display. Our results suggest that physical rotation for augmenting realism may improve perception of rotation (e.g. reduce the underestimation of turning), but may well have to be used with some caution.

5— References

Bakker NH, Werkhoven PJ, Passenier PO (1999) The effects of proprioceptive and visual feedback on geographical orientation in virtual environments. Presence 8: 36-53

Bertin RJV, Israël I, Lappe M (2000) Perception of two-dimensional, simulated ego-motion trajectories from optic flow. Vision Res. 40: 2951-2971

Bertin RJV, Israël I (2002) Optic flow based perception of two-dimensional trajectories: the effects of a single landmark. Submitted for publication in Vision Research

Brandt T, Bartenstein P, Janek A, Dieterich M (1998) Reciprocal inhibitory visual-vestibular interaction. Visual motion stimulation deactivates the parieto-insular vestibular cortex. Brain 121 (Pt 9): 1749-1758

Buizza A, Leger A, Droulez J, Berthoz A, Schmid R (1980) Influence of otolithic stimulation by horizontal linear acceleration on optokinetic nystagmus and visual motion perception. Exp.Brain Res. 39: 165-176

Conditt MA, Gandolfo F, Mussa-Ivaldi FA (1997) The Motor System Does Not Learn the Dynamics of the Arm by Rote Memorization of Past Experience. J.Neurophysiol. 78: 554-560

Crowell JA, Banks MS, Shenoy KV, Andersen RA (1998) Visual self-motion perception during head turns. Nature neuroscience 1: 732-737

Ehrlich SM, Beck DM, Crowell JA, Freeman TC, Banks MS (1998) Depth information and perceived self-motion during simulated gaze rotations. Vision Res 38: 3129-3145

Gibson JJ (1950) The perception of the visual world. Houghton Mifflin, Boston

Groen EL, Valenti Clari MSV, Hosman RJAW (2000) Psychophysical thresholds associated with the simulation of linear acceleration. AIAA 4294-4302

Harris LR, Jenkin M, Zikovitz DC (2000) Visual and non-visual cues in the perception of linear self motion. Exp.Brain Res. 135: 12-21

Hlavacka F, Mergner T, Bolha B (1996) Human self-motion perception during translatory vestibular and proprioceptive stimulation. Neurosci Lett 210: 83-86

Jürgens R, Bob T, Becker W (1999) Estimation of self-turning in the dark: comparison between active and passive rotation. Exp.Brain Res. 128: 491-504

Kim NG, Turvey MT (1998) Visually perceiving heading on circular and elliptical paths. J Exp Psychol Hum Percept Perform 24: 1690-1704

Koenderink JJ (1986) Optic Flow. Vision Res 26: 161-180

Lambrey, S., Viaud-Delmon, I., Berthoz, A. (in press) Influence of a sensorimotor conflict on the memorisation of a path travelled in virtual reality. Brain Res special issue on multisensory integration.

Lappe M, Bremmer F, van den Berg AV (1999) Perception of self-motion from visual flow [Review]. Trends in Gognitive Sciences 3: 329-336

Li L, Warren WH, Jr. (2000) Perception of heading during rotation: sufficiency of dense motion parallax and reference objects. Vision Res. 40: 3873-3894

Loose R, Ayan T, Probst T (1999) Visual motion direction evoked potentials are direction specifically influenced by concurrent vestibular stimulation. Clinical Neurophysiology 110: 192-199

Mergner T, Becker W (1990) Perception of horizontal self-rotation : multisensory and cognitive aspects. In: Warren R, Wertheim AH (eds) Perception and control of self-motion. Lawrence Erlbaum Ass., Hillsdale, pp 219-263

Mergner T, Schweigart G, Müller M, Hlavacka F, Becker W (2000) Visual contributions to human self-motion perception during horizontal body rotation. Arch Ital Biol 138: 139-166

Mesland, B. S. About horizontal self-motion perception... 1998. PhD thesis, Utrecht University, the Netherlands.

Pavard B, Berthoz A (1977) Linear acceleration modifies the perceived velocity of a moving visual scene. Perception 6: 529-540

Probst T, Loose R, King SK, Stott JR, Wist ER, Wright R (1996) Perception of direction of visual motion. II. Influence of linear body acceleration. Behav Brain Res 81: 147-154

Probst T, Loose R, Niedeggen M, Wist ER (1995) Processing of visual motion direction in the fronto-parallel plane in the stationary or moving observer. Behav Brain Res 70: 133-144

Redlick FP, Jenkin M, Harris LR (2001) Humans can use optic flow to estimate distance of travel. Vision Res. 41: 213-219

Royden CS, Crowell JA, Banks MS (1994) Estimating heading during eye movements. Vision Res 34: 3197-3214

Rushton SK, Harris JM, Lloyd MR, Wann JP (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow. Curr Biol 8: 1191-1194

Sibigtroth, M. P. and Banks, M. S. Vestibular Stimulation in Heading Estimation. Presentation at VSS, 2001.

von der Heyde, M., Riecke, B. E., Cunningham, D. W., and Bülthoff, H. Visual-vestibular sensor integration follows a Max-Rule: Results from psychophysical experiments in Virtual Reality. Poster at the Tübinger Wahrnehmungskonferenz (TWK) 2001

Wann, JP, Schwapp, DK (2000) Why you should look where you steer. Nature neuroscience 3: 647-648

Wann JP, Swapp D, Rushton SK (2000) Heading perception and the allocation of attention. Vision Res. 40: 2533-2543

Wenzel R, Bartenstein P, Dieterich M, Danek A, Weindl A, Minoshima S, Ziegler S, Schwaiger M, Brandt T (1996) Deactivation of human visual cortex during involuntary ocular oscillations - A PET activation study. Brain 119: 101-110