Galvanic Vestibular Stimulation Modifies Vection Paths in Healthy Subjects

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The present study aimed at determining whether vestibular inputs contribute to the perception of the direction of self-motion. This question was approached by investigating the effects of binaural bipolar galvanic vestibular stimulation (GVS) on visually induced self-motion (i.e., vection) in healthy subjects. Stationary seated subjects were submitted to optokinetic stimulation inducing either forward or upward linear vection. While perceiving vection, they were administered trapezoidal GVS of different intensities and ramp durations. Subjects indicated the shape and direction of their perceived self-motion throughout the experiment by a joystick, and after each trial by the manipulation of a 3D mannequin. Results show that: 1) GVS induced alterations of the path of vection; 2) these alterations occurred more often after GVS onset than after GVS offset; 3) the occurrence of vection path alterations after GVS onset depended on the intensity of GVS but not on the steepness of the GVS variation; 4) the vection path deviated laterally according to either an oblique or a curved path; and 5) the vection path deviated toward the cathode side after GVS onset. It is the first time that vestibular information, already known to contribute to the induction of vection, is shown to modify self-motion perception during the course of vection and how vestibular information interacts with visual information in the perception of heading.

Among the sensory systems involved in the perception of heading, vision has historically received priority attention. Following the seminal hypothesis of Gibson according to which the direction of self-motion could be “picked up” from the optic flow (Gibson 1950), a strong body of research examined the contribution of vision to the determination of self-motion direction (Koenderink 1986; Lappe et al. 1999; Lee 1980). Gibson’s original view of the problem considered the “simple” case of the visual motion provided by forward rectilinear self-motion through a stable environment. In his experiments, subjects kept their head and gaze fixed in the straight-ahead direction. In these conditions, retinal images typically expand radially away from a focus of expansion that indicates the direction of self-motion (Gibson et al. 1955). Since then, it has been shown that humans can use the optical flow to reliably estimate their direction of motion (Warren et al. 1988, 1991). However, it has been proposed that other visual self-motion related signals, such as the visual egocentric localization of the goal of self-motion, participate in the perception of heading (Harris and Bonas 2002; Rushton et al. 1998). Furthermore, sensory information other than visual may contribute to this perception. It is known that specific problems arise when lateral eye rotation or combined eye–head rotation occur during forward self-motion. These rotations transform the optical flow (as originally discussed by Gibson) into a retinal flow presenting both image expansion arising from forward self-motion and image rotation arising from eye movement. Thus the retinal flow resulting from a horizontal eye, head, or even whole body rotation performed during a forward linear self-motion resembles the retinal flow resulting from a curvilinear self-motion. This ambiguity may lead subjects to confuse forward rectilinear and curvilinear self-motion (Roden 1994; Royden et al. 1994). How is the direction of self-motion extracted from a retinal flow that is affected by both body self-motion and eye rotation? This question is currently strongly debated (Lappe et al. 1999). One possibility is that the perception of heading is obtained from visual information only, the translation and the rotation components of the retinal flow having different properties (Li and Warren 2000; Stone and Perrone 1997; Warren and Hannon 1990).

INTRODUCTION

During natural locomotion, the brain is supplied with visual, vestibular, and somatosensory signals and with efferent copies of motor commands (Berthoz 1997; Schöne 1984). Under normal circumstances, these sensorimotor signals provide coherent information that allows adequate perception and control of self-motion. The perception of heading, i.e., of where we are going, is an important dimension of self-motion perception. It helps to specify the motor commands required for collision avoidance or change in the desired direction of travel. Although extensively studied during the last few decades, its sensory basis remains unclear. In particular, the relative contributions of the different sensory systems and of their interactions to this perception remain debated (Berkin and Berthoz 2004). The aim of the present study is to investigate whether...
Another possibility is that the gaze rotation component is extracted from the retinal flow using extraretinal signals such as vestibular and proprioceptive afferents and efference copy of the motor command (Banks et al. 1996; Crowell et al. 1998; Warren 1998).

The contribution of vestibular information to the perception of heading is suggested by two lines of argument. First, experiments on vestibular stimulation in healthy subjects performing arm-pointing movements in the sitting or standing position have shown that vestibular information participates in the perception of the straight-ahead direction. Thus, subjects requested to point straight ahead deviated their arm movements toward the stimulated side when exposed to unilateral ice caloric vestibular stimulation (Bottini et al. 1994; Karnath et al. 1994). Similarly, subjects pointing in complete darkness at memorized visual targets exhibited deviations of their arm movements toward the anode side when receiving binaural bipolar galvanic stimulation (Bresciani et al. 2002). The second line of argument stems from data on vestibular imbalance during self-motion, whether active or passive. Vestibularly impaired patients are known to suffer from misperception of self-motion, in particular regarding their path or trajectory, and have been reported to have difficulties in staying in the lane while driving (Cohen et al. 2003). Menière’s patients examined after unilateral vestibular neurotomy have been reported to exhibit trajectory deviations while walking eyes open toward a currently perceived target or eyes closed toward a memorized target. The direction and magnitude of the deviations depended on the availability of vision: subjects exhibited small deviations toward the intact side while walking eyes open, and large deviations toward the operated side while walking in the dark (Borel et al. 2004). The vestibular origin of the precession trajectory deviations is supported by experiments on vestibular stimulation in healthy subjects required to walk straight ahead in the dark toward a memorized target. These experiments showed that subjects deviated their path toward the anode side during binaural galvanic vestibular stimulation (Bent et al. 2000; Fitzpatrick et al. 1999).

To assess the possible involvement of the vestibular inputs in the perception of heading during self-motion, we studied the effects of artificially induced vestibular imbalance in healthy subjects on the perception of the direction of visually induced illusory self-motion (or vection). Vection is an illusory perception of self-motion felt by a stationary observer exposed to the motion of visual surroundings. As any body motion through space, vection kinematics are conventionally described with respect to the fore–aft or sagittal x-axis, the left–right or lateral y-axis, and the head–foot (up–down) or spinal z-axis (Hixson et al. 1966; Holly and McCollum 1996a,b).Canonical linear vections are illusions of translation along one of these three axes. Canonical circular vections are illusions of rotation around one of these axes (roll, pitch, and yaw around the x-, y-, and z-axes, respectively).

The vestibular imbalance was produced by binaural bipolar galvanic vestibular stimulation (GVS). This GVS consists in applying moderate DC between the mastoid processes. It modulates the spontaneous firing rate of vestibular afferents by enhancing the vestibular nerve discharge on the cathode side and decreasing it on the anode side (Goldberg et al. 1984). At the sensorimotor level, the onset of GVS induces the perception of a self-tilt toward the cathode side that provokes compensatory postural (Britton et al. 1993; Day et al. 1997; Severac Cauquil et al. 1997, 2000) and locomotor (Bent et al. 2000; Fitzpatrick et al. 1999) deviation toward the anode side. Results obtained on a subject with complete loss of somatosensory afferents below the neck indicate that these compensatory reactions are regulated by somatosensory information. When this subject was exposed to transmastoid GVS while sitting, he displayed a continuous lateral tilt of the head and trunk that persisted for the whole duration of the stimulus, instead of the temporary lateral tilt usually associated with GVS onset (Day and Cole 2002). At the perceptual level, the GVS onset induces an illusory lateral tilt of the visual scene toward the cathode side (Zink et al. 1997, 1998) and consequently deviates the subjective visual vertical toward the anode side (Mars et al. 2001; Tardy-Gervet and Severac-Cauquil 1998). Compared with the GVS onset, the GVS offset induces directionally opposite sensorimotor and perceptual responses (Severac Cauquil et al. 1997, 2000). However, it is not clear whether GVS induces only the perception of an illusory lateral tilt through an action on the otolithic afferents, or whether it also produces a signal of rotation through an action on the canal afferents. Such an action of GVS on the semicircular canals is suggested by Fitzpatrick et al. (2002): healthy subjects exposed to transmastoid GVS while lying supine on a rotatory platform reported a greater or a lesser spin depending on whether the GVS was congruent or incongruent with the actual rotation.

With regard to vection, an extensive literature, ranging from behavioral studies (Dichgans and Brandt 1978; Wertheim 1994) to recent neuroimaging studies (Brandt et al. 1998; Deutschlander et al. 2004; Kleinschmidt et al. 2002; Wiest et al. 2001) demonstrated that both vestibular and visual information interact at the brain stem and cortical levels during vection and that both of these sensory inputs are likely to participate in this perception. In spite of this, major characteristics of vection such as the shape of the perceived path of self-motion (e.g., linear, curvilinear, circular) and its direction are still defined with respect to visual input only, as if they were independent from vestibular input. Thus circular vections are usually presented as induced by rotating optokinetic stimulation (e.g., the optokinetic drum triggering yaw vection). Similarly, linear vections are said to be induced by translatory optokinetic stimulation. It is generally accepted that the vection path follows the same direction and the way opposite to that of the optokinetic stimulus.

However, one may wonder whether the vection path depends on visual input only or whether it also depends on vestibular afferents. To answer this question, stationary healthy subjects sitting with their head kept vertical and their gaze oriented straight ahead were exposed to optokinetic stimulation known to induce forward and upward linear vections. Soon after the beginning of the perception of an illusory self-motion (vection onset), subjects were (experimental trials) or were not (control trials) administered binaural bipolar GVS and required to code their vection path. It was hypothesized that a contribution of the vestibular afferents to the heading perception would lead to different illusory movement perceptions in control and experimental trials. It was expected that subjects would perceive canonical linear vection in control trials because of their state of left–right vestibular balance, whereas they would experience vection path deviations during the
experimental trials because of the left–right vestibular imbalance induced by GVS. As stated earlier, there is some indication that GVS may act not only through otolithic afferents but also through canal afferents (Fitzpatrick et al. 2002). Therefore fusion of the linear upward or forward self-motion perception induced by vection and of the lateral tilt (otolithic effect) or rotation (canal effect) perception induced by the GVS was expected to deviate the vection path respectively obliquely or curvilinearly toward the cathode side. Zink et al. (1998) showed that GVS at low-current intensities excites the otolithic afferents, whereas at high intensities it stimulates in addition the canal afferents. Therefore a second aim of the experiment was to compare the effects of several GVS parameters, such as its current intensity, the steepness of the current increase and decrease, and the onset or offset of stimulation, on vection paths. To achieve this aim, trapezoidal GVS of varied ramp duration and/or plateau magnitude were used.

**METHODS**

**Subjects**

Twelve healthy volunteers, seven females and five males, ages between 18 and 35 yr (mean age = 23.4 yr), were included in the study approved by the Ethics Committee of the Saint Louis Hospital in Paris (N° DGS 2002/0417). The subjects signed an informed consent form before their participation in the study. In presenting the experiment, care was taken to keep them naive as to the perceptual effects of GVS and to the specific goals of the study. All subjects were free of known neurological problems and had normal or near-normal vision. To assess that their vestibular function was normal, subjects underwent a structured clinical interview, the Sensory Organization Test of the computerized dynamic posturography system of the EquiTest, and a measure of their eye movement during a caloric vestibular test. The subjects’ tolerance to GVS was assessed by having them to four GVSs of increasing intensity (0.5, 1, 1.5, and 2 mA). The GVSs were trapezoidal. Their increasing ramp, plateau, and decreasing ramp lasted 3 s each. During the stimulation, subjects kept their eyes open and performed a distractive task (counting down 3 × 3 starting from 100). After each GVS, the subjects rated their sensations on a three-level scale (“no problem”; “acceptable”; “not acceptable”). Only the subjects who rated the 2-mA GVS as “acceptable” or better participated in the experiment.

**Optokinetic stimulation**

The visual stimulation device consisted of two 17-in. LCD flat-screen monitors placed on each side of the subject’s head and facing each other. The monitors were placed 25 cm apart and displayed identical images 34 cm wide and 27.3 cm high. With respect to a point located midway between the monitors on a line joining the centers of the screens, the images’ angular size was 107° × 95°. The monitors were positioned so that the rear edges of the images were at the level of the subjects’ ears and the midheight of the images was at eye level. The images consisted of black and white vertical or horizontal stripe patterns of constant spatial frequency (0.05 cpd). The patterns translated and thus produced lamellar optokinetic stimulation (Andersen and Braunstein 1985), which is known to induce linear vections (Giannopulo and Lepecq 1998; Lepecq et al. 1999). Forward vection was induced by backward movement of the vertical stripes in a direction parallel to the x-axis, and upward vection by a downward movement of the horizontal stripes in a direction parallel to the z-axis (see Fig. 2). The velocity of these movements was constant and was the same for both monitors and for both vertical and horizontal stimulation (linear velocity = 7.04 cm/s; angular velocity = 31°/s). The experimental setup was in a small experimental chamber made of black opaque fabric. When the monitors were switched off, the inside of the chamber was completely dark.

**Galvanic vestibular stimulation (GVS)**

Binaural bipolar GVS (anode left–cathode right or vice versa) were delivered by 9-cm² rectangular Ag–AgCl pregelled disposable electrodes placed over each mastoid. The electrodes were secured with adhesive tape and an elastic bandage wrapped around the head. The GVSs were computer controlled and delivered by a battery-isolated constant-current generator. The GVSs were trapezoidal: the current intensity linearly increased from 0 up to either 1 or 2 mA in either 3 or 6 s, and symmetrically decreased down to 0 mA after a plateau of 10 s (Fig. 1). Thus the GVS lasted 16 s (3-s ascending ramp + 10-s plateau + 3-s descending ramp) or 22 s (6-s ramp + 10-s plateau + 6-s ramp). The minimal intensity of 1 mA was reputed to be above threshold (Bent et al. 2000). The maximal intensity of 2 mA was chosen after a pilot investigation had demonstrated that it was easily tolerated. A 2 × 2 × 2 factorial design with two polarities (anode left or right), two current intensities (1 or 2 mA), and two ramp durations (3 or 6 s) gave rise to eight different GVS stimulation profiles.
Subjects’ placement

The subjects were seated in an armchair with their head vertical. They leaned the back of their head on a medical headrest equipped with two separate convex surfaces of contact, on which they were attached by the means of a large Velcro strap pressed on the forehead. Thus their head was kept in a fixed position and orientation during the experiment, and any head tilt induced by GVS was prevented. The subjects gazed straight ahead at a fixation point located 32 cm from their eyes in the sagittal plane and at eye level. The subjects’ gaze direction was monitored on-line by the experimenter. The few trials in which it deviated from straight ahead were rejected and repeated. The subjects wore earphones through which white noise was delivered to mask external stimuli. They held in their preferred hand a joystick equipped with a trigger. The joystick could be tilted in pitch and roll, and rotated in yaw (Fig. 2).

Procedure

The experiment was divided into two sessions, each concerned with either forward or upward vection and lasting about 1 h. The order of the sessions was randomized between subjects and a rest period was inserted between the two. Each session consisted of two phases: a first phase during which optokinetic stimulation was delivered alone and a second phase during which optokinetic and galvanic stimulations were combined.

PHASE WITH OPTOKINETIC STIMULATION ALONE. First, the subject’s susceptibility to vection was investigated using optokinetic stimulation alone for a maximum of five trials. Each trial started with 3 s of motionless images followed by 60 s of moving images. The subject had to press the joystick trigger as soon as and as long as vection was perceived, and to release it as soon as vection vanished. If vection was felt during these 60 s, optokinetic stimulation was continued for 20 s after the first press on the trigger. After each trial inducing vection, the subject verbally reported the direction of the perceived self-motion. Once the subject had given two consecutive correct reports (e.g., forward vection during a backward optokinetic stimulation or upward vection during a downward optokinetic stimulation), the subject’s susceptibility to vection was considered good enough to continue.

The vection trajectory was then assessed in two complementary trials during which the optokinetic stimulation lasted 38 s after vection onset. This assessment was made both during vection perception by the manipulation of the joystick and immediately after each trial by manipulation of a small three-dimensional (3D) mannequin. To indicate the vection trajectory by the joystick, the subject was instructed to obey the following rules (Fig. 2): if the vection followed a rectilinear path along either the sagittal body axis (like in a train) or the spinal body axis (like in an elevator), the subject had only to press the trigger and left the joystick in its rest position; if the vection followed a rectilinear path that deviated obliquely either leftward or rightward, the joystick should be tilted respectively toward the left or the right; if the vection followed a leftward or rightward curved path, the joystick should be rotated respectively counterclockwise or clockwise.

The subject was told that the amplitude of the joystick manipulations was not supposed to represent the amplitude of the trajectory deviations. Immediately after each trial, the subject reproduced the trajectory of the vection using the small 3D mannequin. The two types of responses were discussed between the experimenter and the subject to make the vection perception as clear as possible in terms of direction and shape. In the very rare cases of disagreement between these two types of responses, the trial was repeated.

PHASE WITH COMBINED OPTOKINETIC AND GALVANIC STIMULATIONS. To assess the effects of vestibular information on vection, the optokinetic and the galvanic stimulations were combined (Fig. 1). In this phase, each trial consisted of three parts during which the vection direction and shape were assessed continuously by joystick manipulation. In the first part, the optokinetic stimulation was delivered alone. If neither vection interruption nor alteration occurred for 6 s after the beginning of self-motion perception, the second part was undertaken; otherwise, the trial was repeated. In the second part, the GVS was added to the optokinetic stimulation. In the third part, the optokinetic stimulation was continued alone for 10 s after GVS offset. This sequential organization of the optokinetic and galvanic stimulations was intended to allow both the analysis of the effects of the presence of GVS and the comparison of the effects of the increasing and the decreasing galvanic ramps.

In each forward or upward vection session, the subject was given 11 trials: eight with GVS and three without GVS. The eight trials with GVS resulted from the complete factorial design of two polarities (anode left or right) × two current intensities (1 or 2 mA) × two ramp durations (3 or 6 s). The order of the eight trials with GVS was randomized for each subject. The three trials without GVS were aimed at checking that vection induced by vision alone remained unaltered throughout the session. A trial without GVS consisted of optokinetic stimulation alone and lasted 38 s after vection onset. This duration corresponded to the maximal duration of acquisition time during trials with GVS. The three trials without GVS were presented at trials 1, 6, and 11 (i.e., before, during, and after GVS trials). For each trial (with or without GVS), the presence of absence of vection was signaled by pressing or releasing the trigger and the subject had to indicate the vection trajectory “on-line” by the joystick manipulation and “off-line” by the mannequin. A minimum of 4 min separated the end of a trial from the beginning of the next.
**Data acquisition**

Throughout the experiment, the timings of stimulation (optokineti
cal galvanic), of the joystick trigger (press and release), and of the
joystick tilts (in roll) and rotations (in yaw) were sampled at 20 Hz
and stored for further analysis.

**Data analysis**

Vection path alterations collectively referred to any path deviation
from the canonical straight forward or straight upward paths. They
corresponded to deviations ascertained by both the joystick manipu-
lations and the mime production. For each “with GVS” trial, vection
path alterations were analyzed separately for two time windows: one
constituting the GVS increasing slope and the plateau (period A, Fig.
1), and the other constituting the GVS decreasing slope and the 10
following seconds (period B, Fig. 1).

**RESULTS**

GVS induces modifications of the self-motion perception
caused by visual stimulation. The occurrence of path alter-
ations in the different experimental conditions is considered
first, then the shape (oblique or curved) of these path alter-
ations, and finally their direction (toward the cathode or toward
the anode).

**Occurrence of vection path alterations**

The first result is that the GVS modifies the perceived
self-motion induced by vection. Indeed, vection path alter-
ations were observed only after GVS during the experimental
trials, and never during the control trials or during the 6 s of
optokinetic stimulation alone preceding the vestibular stimula-
tion in the experimental trials.

Data from all subjects were pooled together after Fisher’s
exact probability tests showed that there was no order effect of
the two sessions (upward vection or forward vection) on the
occurrence of vection path alterations (all tests, \( n_1 = 6, n_2 =
6, P > 0.05 \)). The effects of GVS polarity, duration, and
intensity were then assessed using McNemar’s binomial tests.
These tests indicated no effect of GVS polarity (all binomial
tests, \( n = 12, P > 0.05 \)) or GVS duration (all binomial tests,
\( n = 12, P > 0.05 \)) but showed some effects of GVS intensity
(some binomial tests, \( n = 12, P < 0.05 \)). Consequently, the
analysis was focused on GVS intensity, after pooling together
data obtained in the different GVS polarity and duration
conditions.

The occurrence of vection path alterations as a function of
GVS intensity and vection direction is presented in Fig. 3. The propor-
tion of vection path alterations occurring during the
increasing GVS ramp and the GVS plateau (period A) was
considerably higher than that occurring during the decreasing
GVS ramp and the following 10 s (period B). The difference
was significant for upward vection at both GVS intensities
(Wilcoxon signed-rank test, 1 mA: \( n = 12, Z = 2.80, P < 0.006 \))
and for forward vection in the 2-mA condition (\( Z = 2.80, P < 0.006 \)).
It did not reach statistical significance for forward vection in the 1-mA
condition (\( Z = 1.40, P > 0.05 \)). All conditions pooled together,
vection path alterations occurred during period A in 57% of the
experimental trials (110 of 192 trials) and during period B in
10% of the trials (20 of 192 trials). Of the 20 trials in which an
effect of GVS offset (period B) occurred, 14 also presented an
effect of GVS onset (period A) and six presented no effect of
GVS onset. Therefore the effects for GVS offset seldom
occurred when there had been no previous effect of GVS onset
in the same trial. Because of the small number of vection path
alterations during period B, further analysis was focused on the
vection path alterations associated with period A, so the fol-
lowing results concern only these path alterations.

The occurrence of vection path alterations varied with GVS
intensity. The proportion of trials during which these alter-
ations occurred was significantly larger with 2- than with 1-mA
GVS, in the upward vection (Wilcoxon signed-rank test, \( n =
12, Z = 2.80, P < 0.006 \) as in the forward vection conditions
\( Z = 2.24, P < 0.03 \)).

Upward and forward vections were not equivalent in their
susceptibility to the effects of GVS, as shown by the higher propor-
tion of vection path alterations observed in the upward
than in the forward vection condition. However, the difference
was significant only in the 2-mA condition (Wilcoxon signed-
rank test, \( n = 12, Z = 2.36, P < 0.02 \)). The median vection
onset times (2.81 vs. 2.46 s for the upward vs. forward
vections) did not differ between the two vection conditions
(Wilcoxon signed-rank test, \( n = 12, Z = 1.02, P > 0.05 \)).

**Shape of vection path alterations**

The canonical linear vection shape is either straight upward
or straight forward. The vection shape alterations were of two
types: oblique or curved. In the first case, the subject perceived
him/herself as moving along a rectilinear trajectory whose
direction was deviated leftward or rightward relative to straight
upward or straight forward (see Fig. 2). In the second case, the
subject perceived him/herself as moving along a curvilinear
trajectory, as if following a leftward or rightward turn about a
vertical axis of rotation in the case of forward vection or about
a horizontal axis in the case of upward vection (see Fig. 2). For
forward vection, for example, a curved shape looks like taking
a large bend while driving a car. For upward vection, the
subjects would perceive a clockwise or counterclockwise cur-
vature with respect to the forward axis.
The proportions of oblique and curved shapes reported during period A are presented in Fig. 4. At low GVS intensity, the proportion of path alterations perceived as curved was significantly smaller than the proportion of path alterations perceived as oblique in the upward vection condition (Wilcoxon signed-rank test, \( n = 12 \), \( Z = 2.17, P < 0.03 \)). The proportion of path alterations perceived as curved increased with GVS intensity. This increase was statistically significant in the upward vection condition (\( Z = 2.01, P < 0.05 \)) and marginally significant in the forward vection condition (\( Z = 1.82, P < 0.07 \)).

**Direction of vection path alterations**

Vection alteration can also be characterized by its direction. The proportions of deviations toward the cathode side and the anode side during period A are presented in Fig. 5. During this period, significantly more vections were reported toward the cathode side than toward the anode side, whatever the condition (Wilcoxon signed-rank test, upward vection, 1 mA: \( n = 12, Z = 2.80, P < 0.003 \); 2 mA: \( Z = 2.80, P < 0.003 \); forward vection, 1 mA: \( Z = 1.82, P < 0.04 \); 2 mA: \( Z = 2.67, P < 0.004 \)).

**Discussion**

The present study aimed at determining whether vestibular inputs contribute to the perceived self-motion path. This question was approached by investigating the effects of binaural bipolar GVS on linear vection. Results show that 1) GVS induces alterations of the path of vection; 2) vection path alterations occur more often after GVS onset than after GVS offset; 3) the occurrence of vection path alterations after GVS onset depends on the intensity of GVS but not on the steepness of the GVS variation; 4) the vection path deviates laterally according to either an oblique or a curved path; and 5) the vection path deviates toward the cathode side after GVS onset.

**Occurrence of vection path alterations**

GVS induces vection path alterations. This is shown by the fact that vection paths are always perceived as straight forward or straight upward in the absence of GVS, and as oblique or curved only after GVS administration. Because the subjects’ head position was fixed throughout the experiment, the vection path alterations cannot be attributed to GVS-induced head movements, but can be attributed to a direct effect of the vestibular imbalance generated by the GVS. The distortion of vection paths by GVS suggests that they do not depend on visual afferents only, but rather on the conjunction of visual and vestibular afferents. Thus the classical notion according to which vection paths are fully determined by the way and the direction of the inducing optokinetic stimulus appears to be valid only in cases of vestibular balance. Concerning the perception of heading, our results suggest that, as one would expect, it integrates a vestibular contribution and does not rely exclusively on visual afferents.

Vection path alterations occur more often after GVS onset than after GVS offset. Because the GVS onset and offset were symmetrical and are known to evoke illusory self-motion in opposite directions (Severac Cauquil et al. 2000), the larger effect of GVS onset may arise from a sequential effect of the vestibular stimulation. Indeed, very few vection path alterations were observed after GVS offset, and most of these occurred when there had been a vection path alteration produced by GVS onset in the same trial. The occurrence of vection path alterations depends on the GVS intensity. Vection path deviations were more frequent in the 2- than in the 1-mA condition. This result is in agreement with previous studies showing that GVS-induced illusory self-motion is greater for higher GVS magnitudes (Bent et al. 2000). There was no significant effect of the GVS ramp duration on the occurrence of vection deviations. Because the effects of GVS are mediated through modulation of the firing rate of the vestibular afferents (Goldberg et al. 1984), these results suggest that this firing rate is affected by the magnitude of the GVS and not by the rate at which it reaches peak magnitude.

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**Fig. 4.** Proportions of oblique and curved alterations of the vection path during period A (increasing GVS ramp + plateau) for each experimental condition (upward and forward vection; 1- and 2-mA GVS).

**Fig. 5.** Proportions of deviations of the vection path toward the cathodal or the anodal side during period A (increasing GVS ramp + plateau) for each experimental condition (upward and forward vection; 1- and 2-mA GVS).
Shapes of vection path alterations

The subjects described two basic shapes of vection paths: oblique and curved. This dichotomy does not result from a constraint imposed on the subjects’ responses by the set of rules used for the coding of vection path with the joystick. This set of rules was established after a pilot study showing that practically all path alterations fell into one of these two categories. Furthermore, coding through the manipulation of a mannequin followed coding with the joystick. In this case, the subjects’ responses were not constrained at all and the two methods for coding gave the same results. However, the perception of an oblique path is puzzling. During natural walking, people normally walk straight forward or on a curved path; they seldom translate diagonally. An explanation may stem from our results concerning the effect of GVS intensity on the shape of the vection paths. These results show that the proportion of curved vection is higher in the 2- than in the 1-mA condition. They raise the possibility that the GVS always induces curved shape alterations, which curvature increases with GVS intensity. At lower GVS intensity, the curvature is small and tangentially perceived as an oblique. At higher GVS intensity, the curvature is large and thus perceived as a true curve. Another possibility is that canal afferents are excited at a higher current intensity than otolithic afferents (Zink et al. 1998).

Direction of vection path alterations

The GVS onset unambiguously provokes deviations of the vection path toward the cathode side. This direction of the vection path alteration is in agreement with previous work using GVS but no visual stimulation inducing an optic flow, and reporting illusory self-motion toward the cathode side by immobilized standing subjects strapped to an upright support (Wardman et al. 2003). Similarly, seated subjects with the head immobilized also perceive illusory movements toward the cathode side after GVS onset or increments in intensity (Watson et al. 1998). Postural and locomotor deviations toward the anode side have been repeatedly found after the GVS onset (Bent et al. 2000; Severac Cauquil et al. 2000) and interpreted as compensations for self-motion or self-tilt toward the cathode side induced by the GVS (Fitzpatrick et al. 1994; Wardman et al. 2003). In the present study, GVS is applied during vection induced by an optical flow, demonstrating for the first time that the direction of the vection path results from the combination of both the visually and the vestibularly induced self-motion perceptions.

GVS has been shown to activate the primary vestibular afferents innervating all vestibular sensory regions in a uniform fashion (Kim and Curthoys 2004). Thus it is very likely that both the canal and the utricular first-order vestibular neurons were activated by GVS in our experimental conditions. However, our experiment leads to a surprising result: it seems that only part of the information conveyed by the vestibular afferents was used in a given situation. For example, when forward vection and GVS were combined the subject perceived him/herself as moving along a curved or an oblique path deviated leftward or rightward with respect to the straight forward direction. This suggests that in this case information resulting from the activation of the anterior and posterior canal afferents was not taken into consideration. In a similar way, when upward vection and GVS were combined, the subject perceived him/herself as moving along a path deviated with respect to the straight upward direction. This suggests that, in this case, information resulting from the activation of the horizontal canal afferents was neglected. It is known that visual–vestibular interaction may result in a selection among inputs from different sensory modalities. Thus visual motion stimulation has been shown to deactivate the parietoinsular vestibular cortex in humans (Brandt et al. 1998).

Our results suggest that there is in addition a selection among inputs within a same sensory modality because different vestibular inputs appear to be selected depending on the optokinetic stimulus. Crowell et al. (1998) showed that the response to simultaneous vestibular and neck-proprioceptive stimulation was generally greater than the sum of the responses to separate vestibular stimulation and neck proprioception. Thus as in the present study, integration of vestibular information with that arising from other sensory systems was not simply additive. This is in agreement with the demonstration by Ivenenko et al. (1997) that reconstructing a trajectory in space does not imply a mathematically perfect transformation of the linear and angular motion-related inputs into a Cartesian or polar two-dimensional representation. These results open the question of the neuronal mechanisms at play (for reviews see Angelaki et al. 2004; Greenlee 2000; Miles 1998; Sherk and Fowler 2001).

At the cortical level, integration of visual and vestibular information could take place in several areas. Single-unit studies on monkeys have shown that 63% of the neurons in the parietoinsular vestibular cortex (PIVC), the main vestibular cortex in monkeys (Grüsser et al. 1990), respond to both vestibular and visual stimuli (Guldin et al. 1996). They also indicate that MST (V5a) is a site of optic-flow extraction and that this information can be used to guide pursuit eye movements and to estimate heading. This area receives both visual and vestibular canal signals (Britten and van Wezel 1998; Duffy and Wurtz 1995; Kawano and Sasaki 1984; Kawano et al. 1984). In humans, several other cortical areas are involved in the processing of vestibular information (Baudonière et al. 1996; Bottini et al. 1994, 1995; Bucher et al. 1998; De Waele et al. 2001; Friberg et al. 1985; Lobel et al. 1998; Vitte et al. 1996). This multiplicity may be explained by the increased need for balance control associated with bipedal. This hypothesis is corroborated by the participation of the frontal and prefrontal cortex, which are thought to be involved in planning motor strategies to counteract loss of equilibrium, to the processing of vestibular information (De Waele et al. 2001).

Apart from a direct action on the firing rate of vestibular afferents, GVS might induce vection path alterations by other mechanisms that are likely to be a complex combination of various effects. Vection path alterations may be affected by the GVS-induced lateral tilt of the visual scene (Zink et al. 1998), by the GVS-induced torsional eye movements (Severac Cauquil et al. 2003; Zink et al. 1998), and/or by the GVS-induced self-tilt or rotation in roll percepts (Fitzpatrick et al. 2002). Complementary studies are needed to disentangle among these effects of GVS and determine their precise contribution to vection path alterations.

Finally, the present research points out a visual–vestibular mechanism that may be responsible for common complaints concerning spatial perception and spatial orientation in vestibular and visual sensory systems.
ular patients. After unilateral labyrinthectomy, there is an asymmetry of the resting discharge of the two vestibular nuclei. This pathological condition therefore mimics galvanic stimulation. Accordingly, one would expect deviation of the vection path in these patients during the acute period after the vestibular lesion. We show in a paper now in preparation that this is indeed the case.

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