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## Self-motion perception during a sequence of whole-body rotations in darkness

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**Abstract** The main aim of this study was to examine how postrotatory effects, induced by passive whole-body rotations in darkness, could alter the perception of motion and eye movements during a subsequent rotation. Perception of angle magnitude was assessed in a reproduction task: blindfolded subjects were first submitted to a passive rotation about the earth-vertical axis on a mobile robot. They were then asked to reproduce this angle by controlling the robot with a joystick. Stimulus rotations ranged from 80° to 340°. Subjects were given one of two *delay* instructions: after the stimulus, they either had to await the end of postrotatory sensations before starting reproduction (condition free delay, FD), or they had to start immediately after the end of the stimulus rotation (no delay, ND). The delay in FD was used as an incidental measure of the subjective duration of these sensations. Eye movements were recorded with an infrared measuring system (IRIS). Results showed that in both conditions subjects accurately reproduced rotation angles, though they did not reproduce the stimulus dynamics. Peak velocities reached in ND were higher than in FD. This difference suggests that postrotatory effects induced a bias in the perception of angular velocity in the ND condition.

**Key words** Self-motion perception · Vestibular system · Nystagmus · VOR · Human

### Introduction

Semicircular canals and otoliths in the vestibular apparatus detect the acceleration, angular and linear respectively, of head motion in space. The basic hypothesis is that through time integration of the vestibular signals, the

amplitude (distance and/or angle) of head displacement should also be obtained from the same sensors; the vestibular system should therefore contribute to self-orientation and localization in space. For several decades, many different teams have worked on understanding “vestibular perception,” notably during whole-body rotations, and have shown that perception of suprathreshold rotational movements is reasonably precise. To perform these studies, both early and more recent investigators asked subjects to verbally estimate angular velocity or angular displacement (Brown 1966; Parsons 1970; Clark and Stewart 1972; Mergner et al. 1996), or to judge repeatedly angular displacement during the course of a stimulus and its postrotatory sensations (Von Békézy 1955; VanEgmond et al. 1949; Collins 1964; Mittelstaedt and Mittelstaedt 1996). Other procedures involved velocity-matching tasks (Guedry et al. 1971; Ivanenko et al. 1997), goal-directed vestibulo-ocular reflex (VOR) and vestibular-memory contingent saccade tasks (Bloomberg et al. 1988; Segal and Katsarkas 1988; Israël et al. 1993).

We have recently started to investigate bidimensional path integration (Israël et al. 1996a, 1996c), defined by Mittelstaedt and Mittelstaedt (1980) as the integration of idiothetic signals generated during self-displacement (Mittelstaedt and Mittelstaedt 1973), enabling self-orientation in space. When asked to draw the trajectory of a passive motion around a square, which had been imposed in darkness, subjects actually drew curved segments instead of straight lines, for all sides of the square but the first one. Subjects had obviously been affected by the preceding 90°-angle rotation. Moreover, the successive corners were larger than 90° on the drawings. Hence, we decided to investigate quantitatively how postrotatory effects, induced by a passive whole-body rotation in darkness, could alter the perception of a subsequent rotation.

The present experimental procedure was based on a method, devised by Metcalfe and Gresty (1992), to study path integration: the self-driven return to the initial orientation after a passive angular rotation in darkness

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about the earth-vertical axis. In our experiment, instead of going back to an initial orientation, the subject was asked to reproduce in the same direction the angle he/she was first submitted to. Therefore subjects traveled two successive angles, i.e., a sequence of rotations of identical direction. A similar paradigm of "reproduction" was used in a study on linear path integration (Berthoz et al. 1995).

In our work, we investigated more specifically the effect of the presence or absence of a delay between the two successive rotations on the subjects' accuracy in the orientation task. We measured eye movements throughout the experiment because it was reasonable to think that they could be indicative of the vestibular activity, and therefore possibly of the subjects' vestibular perception (Guedry 1971, 1974; Honrubia et al. 1982). Indeed, we have previously reported a relationship between goal-directed eye-movements and vestibular motion perception (Israël et al. 1993).

Subjects were submitted to rotations that can be encountered in everyday navigation, i.e., rather small angles with respect to those used in studies devoted to postrotatory nystagmus and postrotatory sensations (Collins and Guedry 1962; Fluor and Mendel 1969; Guedry et al. 1978). In this kind of study, subjects are submitted to passive whole-body rotations of constant angular velocities, long durations and consequently large angles.

To summarize, the present paper asks two main questions: (a) Do the postrotatory effects induced by a first rotation change the perception of a subsequent rotation? (b) Can eye movements give us some insight into perception of self-motion?

In order to answer these questions, subjects were passively submitted to rotations of three different angles ( $80^\circ$  up to  $340^\circ$ ), in both directions (right-left). They were asked to reproduce the stimulus angle by driving themselves the mobile robot on which they were seated. Depending on the condition, postrotatory effects induced by the first rotation could be superimposed on vestibular signals enhanced by the subsequent rotation. A preliminary account of this work has been given elsewhere (Israël and Siegler 1999).

## Materials and methods

### Experimental setup

The subject was seated on a mobile robot (Robuter, Robosoft, France) that was programmed for the present experiment to rotate about the earth-vertical axis (see Berthoz et al. 1995 for details of the experimental setup). The robot's motion could be controlled by either a remote computer via wireless modems, or by the subject himself/herself by means of a joystick. This joystick was set for the whole experiment to deliver only rotations in both directions with an angular velocity up to  $60^\circ/\text{s}$ , proportional to the joystick angular position. Robot rotation was recorded with a precision of  $0.1^\circ$  at a sampling rate of 100 Hz by means of optically encoded odometry.

Eye movements were measured throughout the experiment with an infrared system (IRIS, Skalar). The subject was seated

with the head fixed at the center of rotation by two soft cushions mounted on the robot and wore headphones delivering wideband noise to mask auditory spatial cues.

### Experimental procedure

After giving their written consent, 24 healthy volunteers, with ages ranging from 19 to 45 years and with no history of vestibular or oculomotor disorder, participated in this experiment.

In order for the subjects to gain confidence steering the robot, they were given an initial practice session. They were asked to perform, with eyes closed, four successive rightward  $90^\circ$  angles, followed by four consecutive leftward  $90^\circ$  angles, by steering the robot with the joystick. After each trial, visual feedback of the subject's performance was presented.

Thereafter, in the main experiment, the subject was first submitted to a passive whole-body rotation (stimulus) and then had to reproduce the stimulus angle by driving the robot with the joystick (response) in the dark (Fig. 1). The reproduction had to be performed in the same direction as the stimulus. We asked subjects to keep their eyes open and to direct their gaze "far away" in front of them during stimulus and response. This was to prevent them, as much as possible, from imagining a head-fixed target (which could induce VOR suppression, Barr et al. 1976). The angular velocity profile of the stimulus was triangular (i.e., with equal magnitudes of constant acceleration and deceleration at  $10^\circ/\text{s}^2$ ), in order to continuously stimulate the semicircular canals. Therefore peak stimulus velocity, which ranged from  $30^\circ/\text{s}$  to  $60^\circ/\text{s}$ , increased linearly with angle. Imposed angles were  $80^\circ$ ,  $167^\circ$  and  $340^\circ$ .

Subjects performed a total of 12 trials where the first 6 trials (3 CW and 3 CCW randomly distributed) were in a "free delay" (FD) condition and the 6 following ones were in a "no delay" (ND) condition. In the "free delay" condition, the subject was first submitted to a passive rotation, and was asked to wait until he/she felt no more postrotatory sensations (if any were experienced at all) before reproducing the stimulus rotation. The subject had previously been informed that, after the imposed rotation, a sensation of turning in the direction opposite to that of the stimulus rotation (somatogyral illusion, Benson and Burchard 1973) may be experienced. The length of delay between stimulus and reproduction was therefore self-paced and not mandatory, and was used as an incidental measure of the subjective duration of the postrotatory sensations.

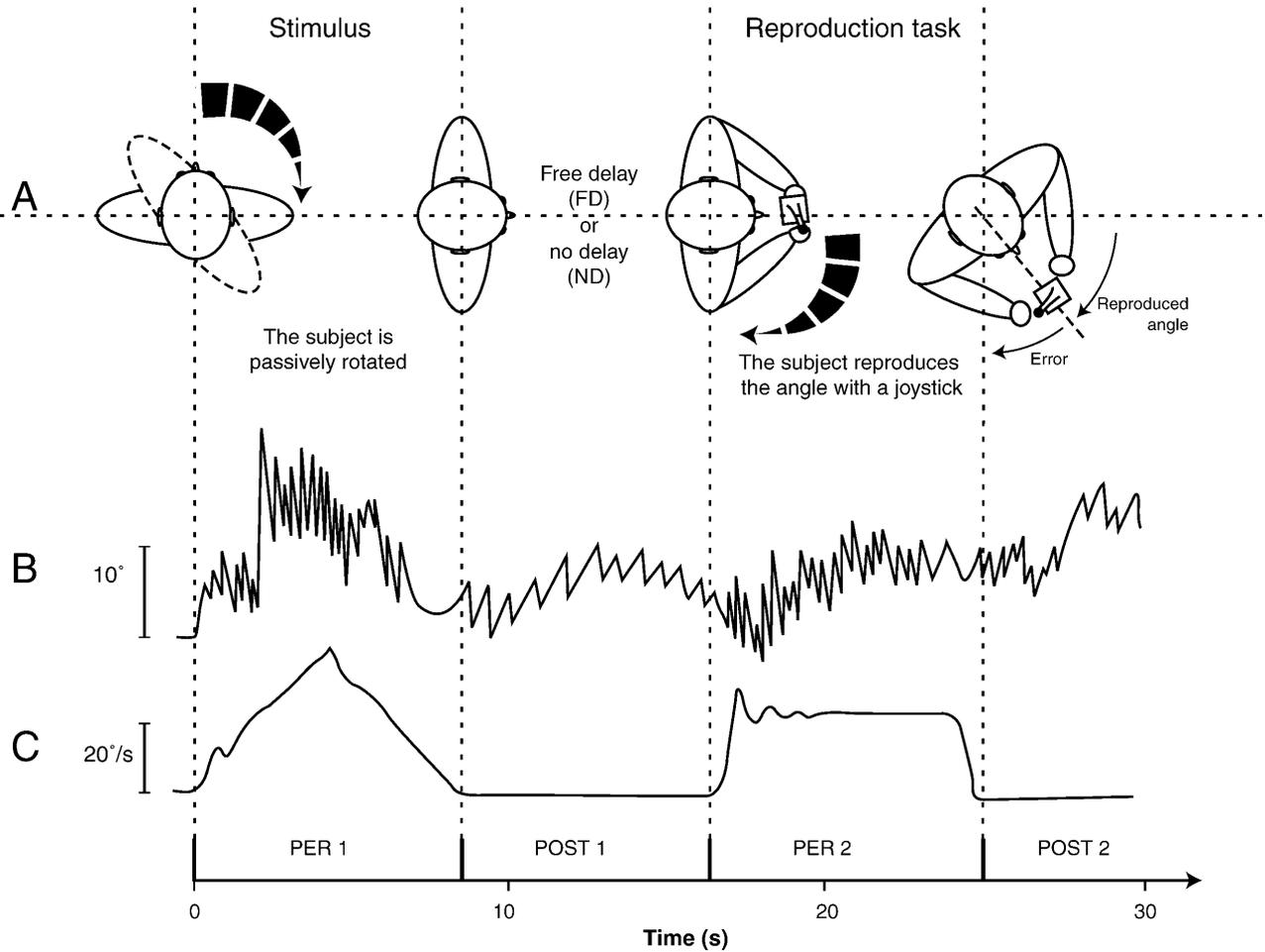
The second condition, the "no delay" condition, required subjects to start reproduction as soon as the stimulus rotation was terminated. In this condition vestibular primary afferents were still indicating a rotation in the other direction when reproduction started, which could therefore induce a modification of the perception of self-motion during the reproduction task. The FD condition was tested first in the experiments (i.e., before ND) so that subjects could gently become familiar with the possible sensations. In doing so they would also not be biased by the task of starting the reproduction quickly after the end of stimulus.

### Movement analysis

The statistical analysis of the reproduction task was carried out by a three-factor repeated-measures ANOVA (condition  $\times$  angle  $\times$  direction of movement) on performance (reproduced angle/stimulus angle), velocity and duration of reproduction.

In this experiment one of our aims was to study the characteristics of induced eye movements, especially VOR gain, which we thought could help us gain some new insights into the subjects' perception of rotation and their performance in this kind of reproduction task. We also measured the shift of the beating field of vestibular nystagmus, which is the subject of two other papers (Siegler et al. 1998; Viaud-Delmon et al. 2000). An example of an eye movement recording with the concurrent robot angular velocity is shown in Fig. 1.

The gain of the vestibulo-ocular reflex (VOR) was computed by a specially designed program as follows: for each slow phase,



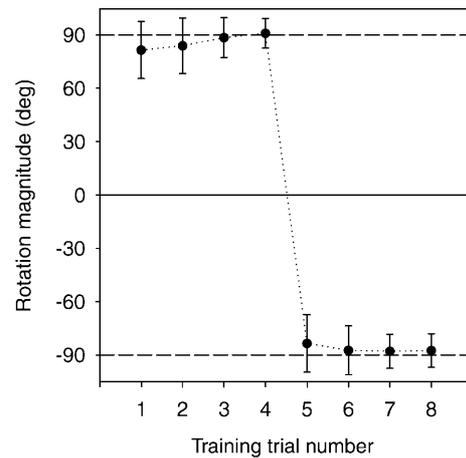
**Fig. 1** **A** Scheme of the experimental paradigm. **B** Eye position. **C** Robot angular velocity. **A–C** are divided into four time periods: PER1 during the stimulus rotation, POST1 between the two rotations, PER2 during the reproduction rotation, and POST2 after the second rotation

regression polynomials of degree 3 were fitted to the recorded data of both eye and robot angular position. Eye and robot angular velocities were calculated from these polynomials and their ratio gave the estimate of VOR gain. The VOR gain values of the slow phases were finally averaged to obtain a mean VOR gain for each trial.

## Results

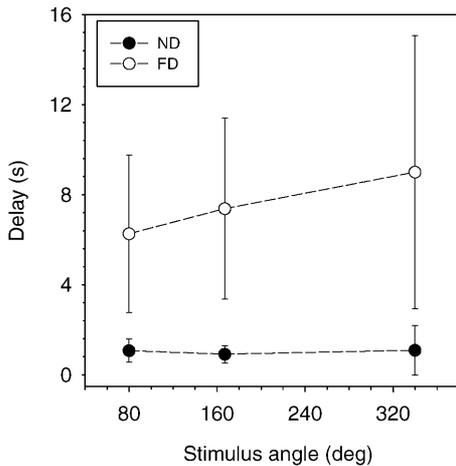
### Practice session

The average traveled angle of the very first trial of the practice session was  $81.6^\circ$  instead of the  $90^\circ$  expected angle, and intersubject variability (SD) was  $16.0^\circ$  (Fig. 2). The performed angles were much closer to  $90^\circ$  at the fourth trial ( $91.0 \pm 8.3^\circ$ ) in the same direction. A *t*-test for dependent samples showed a significant difference between the mean angle amplitude at the first trial and at the fourth one ( $N=24$ ,  $t=-2.41$ ,  $P=0.02$ ). When subjects changed direction, it is as if they had lost some



**Fig. 2** Performance (mean reproduction amplitude  $\pm$  SD) during the eight-trial training session. Subjects were asked to execute four successive  $90^\circ$  angles to the right (trials 1–4) and four to the left (trials 5–8)

of the benefit of the training: they undershot again the first  $90^\circ$  angle they made in that direction ( $83.5 \pm 16.2^\circ$ ). However, subjects improved their performance significantly in the subsequent trials and interindividual differences decreased.



**Fig. 3** Delays (means  $\pm$  SD) between stimulus and reproduction in conditions FD and ND

### Delay

The mean delay that subjects waited was computed for each angle in both conditions (FD and ND) (Fig. 3). In FD, the delay increased with the imposed angle: it was  $6.3 \pm 3.5$  s (mean  $\pm$  SD),  $7.4 \pm 4.0$  s and  $9.0 \pm 6.0$  s at  $80^\circ$ ,  $167^\circ$  and  $340^\circ$ , respectively. Although the variability (SD) was large, an ANOVA showed that the influence of stimulus angle amplitude on the delay was significant [ $F_{(2,46)}=5.2$ ,  $P=0.009$ ]. Individual mean delay values (across all angles) ranged from 2.0 s to 18.3 s in FD, which reflected a large intersubject variability. In ND, the mean delay remained approximately equal to 1 s for all angles. At each stimulus angle magnitude, the delay in ND was significantly shorter than the corresponding value in FD [ $F_{(1,23)}=64$ ,  $P<0.0001$ ], as expected.

### Reproduction characteristics

#### Performance

For each subject, a stimulus-response angle regression line was first calculated separately for each direction

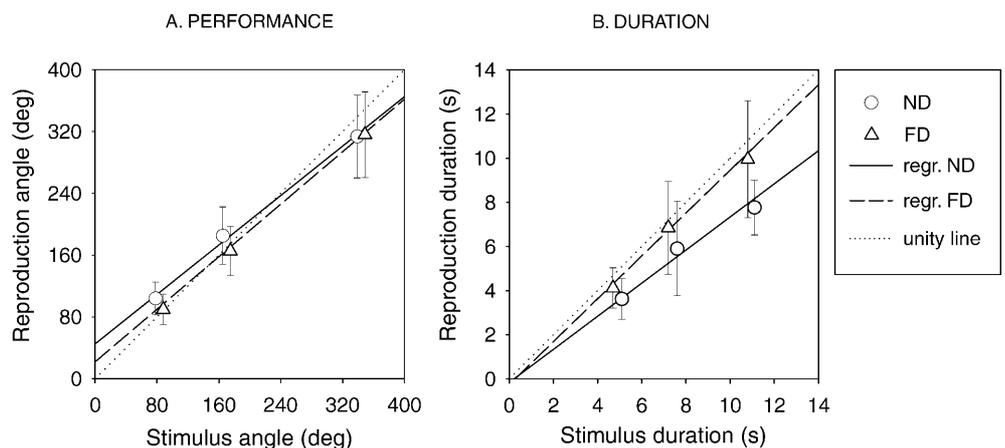
(L, R) in each condition ND and FD ( $N=3$ ). As no significant difference was found between left and right, regression lines of unsigned values were recalculated with both directions pooled ( $N=6$ ). All the correlation coefficients of the regression lines were significantly different from zero ( $P<0.01$ ), except for one subject in ND. The average slope was  $0.85 \pm 0.19$  in FD and  $0.81 \pm 0.18$  in ND (Fig. 4A). Mean correlation coefficients ( $r$ ) were 0.95 and 0.96 in FD and ND, respectively.

In order to examine performance more extensively, we computed the amplitude ratio (AR) of the reproduction angle to stimulus angle. Overall mean values of AR were  $1.00 \pm 0.22$  in FD and  $1.11 \pm 0.26$  in ND. AR was not constant across the different angles but diminished with increasing angle. At  $80^\circ$ , mean AR was above unity in both conditions ( $1.11 \pm 0.26$  in FD;  $1.29 \pm 0.26$  in ND). In other words, subjects tended to overshoot this stimulus angle. At  $167^\circ$  in ND, the average ratio was still above 1 ( $1.11 \pm 0.22$ ), whereas in FD the average ratio was approximately equal to 1 ( $0.99 \pm 0.19$ ). At  $340^\circ$  in both conditions subjects undershot the angle they were expected to reproduce with surprisingly identical ratios (FD  $0.92 \pm 0.16$ ; ND  $0.92 \pm 0.16$ ). A three-factor repeated-measures ANOVA indicated, as suggested by mean values above, that the decrease in AR with increasing angle was significant [ $F_{(2,46)}=37$ ,  $P<0.0001$ ]. In addition, AR was significantly higher in ND than in FD [ $F_{(1,23)}=23$ ,  $P<0.0001$ ]. Furthermore there was an interaction between angle and delay condition [ $F_{(2,46)}=5$ ,  $P=0.01$ ]. Indeed, it could be observed that the difference in AR between the two conditions decreased when the angle increased: at  $80^\circ$  subjects made reproductions of larger amplitude in ND than in FD and this difference between FD and ND was clearly significant ( $P<0.001$ ). At  $167^\circ$ , the difference remained significant ( $P=0.04$ ). Finally, at  $340^\circ$  there was no significant difference between FD and ND. Small angles were therefore more influenced by the delay than large angles.

#### Velocity profile of reproduction

In order to understand the differences in performance between FD and ND, the velocity profiles of reproduction

**Fig. 4** Angle reproduction (A) and duration of reproduction (B) in both delay conditions (FD/ND). In each graph, means  $\pm$  SD and regression lines (of the means) corresponding to the two delay conditions are shown. Dotted line corresponds to the perfect reproduction of the stimulus angle (A) and stimulus duration (B), respectively



**Table 1** Peak velocity imposed during stimulus, and plateau velocity during reproduction in FD and ND

Angle (°)	Peak velocity in stimulus (°/s)	Plateau velocity in FD (°/s)	Plateau velocity in ND (°/s)
80	31	26.5±7.9	39.3±7.8
167	43	30.9±7.3	43.2±6.5
340	61	38.4±8.1	47.6±6.2

rotations were examined: their shape, magnitude and duration. All stimuli had a triangular velocity profile. However, subjects tended to perform the reproduction task using mostly trapezoidal velocity profiles with very short acceleration and deceleration phases (Fig. 1), rather than triangular velocity profiles. From these trapezoidal profiles, the mean plateau velocity (PV) and the response duration were measured.

ANOVA revealed a significant increase in PV with the angle [ $F_{(2,46)}=98$ ,  $P<0.0001$ ], which resembles the linearly increasing peak velocity of stimulus as a function of angle (Table 1). A surprising result was the higher PV in ND than in FD [ $F_{(1,23)}=158$ ,  $P<0.0001$ ]. ANOVA on PV also showed an interaction between stimulus angle amplitude and condition (FD, ND) [ $F_{(2,46)}=6.0$ ,  $P=0.005$ ]. This interaction meant that the difference between the two conditions was decreasingly significant with increasing angle magnitude.

### Reproduction duration

Since all the imposed rotations were traveled with a triangular velocity profile with the same acceleration and deceleration values, stimulus duration and stimulus angle were interdependent. Therefore, stimulus duration could have provided some additional information which could have assisted the subject in the reproduction task. We analyzed to what extent stimulus duration was reproduced.

Mean duration ratios (ratio of reproduction duration to stimulus duration) were computed for each angle and each delay condition. In the FD condition, they remained approximately constant across angles and close to unity (between 0.94 and 0.96). In the ND condition, the mean duration ratios were much smaller than in the FD condition, but also remained almost constant across the different angles (between 0.74 and 0.79). This difference in duration ratio between FD and ND was strongly significant [ $F_{(1,23)}=57$ ,  $P<0.001$ ].

These results can lead to the conclusion that the duration of motion helped subjects to reproduce angles, though differently in both conditions. However, the reproduction of duration could also be a simple consequence of the reproduction of angle magnitude. In order to better understand these results, a control experiment was carried out on eight volunteers. They were first subjected to the FD condition, with exactly the same stimuli of variable duration as in the main experiment (variable duration, VD). Then they had to execute another set of

trials in the FD condition, but with other stimuli. The stimulus angular velocity profiles were again triangular, but were chosen so that they all had the same duration of 9 s (constant duration, CD).

Mean amplitude ratios were  $1.02\pm 0.28$  in VD and  $0.93\pm 0.29$  in CD. A three-factor repeated measures ANOVA (CD vs VD  $\times$  angle  $\times$  direction) showed that this difference between the two conditions was significant [ $F_{(1,7)}=11$ ,  $P=0.01$ ]. Duration ratios were also analyzed: no significant difference was found between the two conditions ( $0.80\pm 0.17$  in VD,  $0.87\pm 0.21$  in CD). In other words, subjects had a similar tendency to reproduce duration in both conditions.

### Eye movements

There were a large number of trials during which no nystagmus occurred. The percentage of trials for which VOR gain could be computed with respect to the total number of trials depended on the angle magnitude. Indeed in only 45% of  $80^\circ$  trials could perrotatory nystagmus be observed during both stimulus and reproduction. This percentage reached 69% in  $167^\circ$  trials, and 71% in  $340^\circ$  trials.

Variations of the VOR gain were observed from subject to subject and from trial to trial. Individual mean values of VOR gain ranged from 0.20 to 0.85. We wondered whether differences in the VOR gain could be observed between the two delay conditions, as differences were observed in response velocities. Contrary to our expectations, no significant difference was found in the VOR gain between FD and ND during the reproduction rotation.

The main purpose of studying postrotatory nystagmus between stimulus and reproduction rotations was to see if there was any relationship between the characteristics of the possible postrotatory nystagmus and delay in FD. However, many subjects did not exhibit postrotatory nystagmus after angles of smallest amplitude ( $80^\circ$ ) or even after angles of largest amplitude ( $340^\circ$ ). Among trials for which subjects exhibited perrotatory nystagmus during both rotations, only 68% exhibited postrotatory nystagmus (or only the beginning of it) after the first rotation and 81% after the second one. Because of this variability in nystagmus occurrence, it was impossible to safely correlate perception of postrotatory effects with concurrent eye movements.

## Discussion

Subjects were asked to reproduce, in the dark, the angle of a rotation they were previously submitted to, by driving a mobile robot with a joystick. The key question was whether postrotatory effects induced by a first rotation could change the perception of a subsequent one. In one of the two experimental conditions (free delay FD), subjects were asked to wait until they no longer felt postro-

tatory sensations before performing the reproduction task. This delay was hence an incidental measure of the postrotatory sensation duration. A discrepancy was observed between FD and ND (no delay) in the characteristics of the reproduction rotation: subjects reached higher angular velocities in the ND condition than in the FD condition. The hypothesis we discuss in this section is that the perception of angular velocity during reproduction was different in the two delay conditions. The reproduction experiment was preceded by a practice session that is discussed before the main findings are addressed.

### Practice session

At the first trial of the practice session, subjects performed on average too small a rotation as already reported by previous experiments (Blouin et al. 1994; Ivanenko et al. 1997). After very few trials in the same direction with visual feedback, subjects became more accurate at performing the required 90° angle and the interindividual variability was reduced. However, when subjects changed direction, their first performance (trial 5) was no better than that of the very first trial in the initial direction (trial 1). It is as if the training in one direction did not apply for the other direction. Nevertheless, subjects succeeded in improving their performance in that direction too, after very few trials. We conclude that we obtained a homogeneous population after the practice session.

### Delay

Longer stimulations were correlated with a longer post-rotatory delay, which is in agreement with the integration of an acceleration signal taking place in the vestibular system. However, signaling when a vestibular perception terminates involves a difficult decision. The large variability observed in the delay is probably due to the idiosyncratic differences in judgments of gradually decaying signals (Reason and Benson 1968; Guedry 1974).

### Performance in FD

Before commenting on the difference in performance between the two delay conditions – a key point in the study– we will briefly comment on results obtained in FD only, allowing us to compare them with other results.

### *Angle reproduction and angular velocity*

The subjects' capacity to reproduce the stimulus angles was good. Performance was first characterized by the slopes of regression lines through paired values of reproduced and stimulus angular displacement, for each subject, under each delay condition. Mean slope was 0.81 in

FD, which is larger than the one found in a previous experiment on a homing task (0.66 in condition NOT in Israël et al. 1996b). However, mean amplitude ratios were very much alike. Indeed, in the former experiment, the overall mean amplitude ratio was 1.04; we found it equal to 1.00 in the FD condition. It is also interesting to note the similarity between the subjects' mean performance in the present experiment when stimulus magnitude was 340° (AR=0.92) and the results from Guedry's experiment (Guedry et al. 1971), where subjects were asked to make a retrospective judgment of a 375° angular displacement (AR=0.93).

In a previous experiment on this same mobile robot, but with linear motion (Berthoz et al. 1995; Israël et al. 1997), it was found that motion dynamics were stored during the passive displacement and played back during the reproduction phase. We therefore expected that subjects would likewise reproduce the triangular waveform of stimulus velocity profiles. However, subjects performed angular velocity profiles in the form of trapezoids. The same observation has been reported in similar experiments but with sinusoidal stimuli (Metcalf and Gresty 1992; Israël et al. 1996b). Linear and angular motions stimulate predominantly otoliths and semicircular canals respectively, which do not bear the same frequency response characteristics; otoliths are thought to be more sensitive to higher derivatives of motion dynamics (i.e., acceleration, jerk) than semicircular canals (Fernandez and Goldberg 1976; Guedry 1974; Benson 1990), which could enable a more precise perception and restitution of motion velocity. Neck and trunk proprioception might also be more involved in the perception of motion dynamics during linear than angular motion, which could also explain the discrepancy between the experiments. For example, the head, with its point of suspension at the neck several centimeters below the center of mass, may serve as a linear accelerometer (Young 1984).

### *Reproduction duration*

Subjects did not precisely reproduce stimulus duration: mean duration ratios stayed below unity. However, reproduction duration was strongly related to stimulus duration since duration ratios stayed approximately constant across angles. Is it a consequence of angle reproduction, or did the subjects try to reproduce duration per se? To tackle this question, a control experiment was carried out, where all the stimuli had the same duration. Subjects performed the reproduction task better when the duration of stimulus was variable and related to the angle magnitude: they took advantage of the duration of motion when it was possible. Therefore, duration could be considered as a message delivered during self-motion, which is probably one of the different signals integrated (Berthoz 1997) to yield a perception of self-motion in darkness.

## A change in performance in ND vs FD?

In ND, when subjects started reproduction, on average 1 s after the end of stimulus, canal cells were still discharging at a level indicating a rotation in the opposite direction to that of the stimulus. Did this induce a change in the subjects' perception of rotation and thus diminish their ability to reproduce stimulus angle?

We believe it did have a certain influence on the way subjects reproduced stimulus angles. The difference in angle reproduction between both conditions was significant: subjects reproduced larger angles in ND than in FD. However, there was an interaction between angle and delay condition. It has to be underlined that postrotatory effects could interact with vestibular signals induced by the reproduction motion, only at the beginning of the reproduction task, for a very brief period of time. Indeed, the angular acceleration of the reproduction motion rapidly forced vestibular afferents to indicate the correct direction of motion (the same one as stimulus direction). Therefore the time period during which posteffects interacted with motion-induced signals was much more important in proportion in a short-duration motion than in a long-duration one. This could explain the fact that the disturbance due to postrotatory signals was more noticeable at small angles. It could also be argued that subjects had time to unconsciously compensate for those effects when motion lasted long enough, i.e., during large-amplitude rotations.

When reproduction in ND was compared with that in FD, the most striking result was the large difference in plateau velocity. The subjects who had postrotatory sensations may have been turning at a high velocity to rapidly overcome these sensations and perceive the motion direction correctly. Another hypothesis was that postrotatory effects induced a misperception of angular velocity during the second rotation. Indeed, if subjects used the same motion dynamics during the reproduction rotation in the two conditions, the firing rate of the primary afferents would indicate a lower angular velocity in ND than in FD because of the initial discrepancy in the firing rate at the onset of the rotation. In that case and if subjects tried to reproduce the angular velocity of stimulus similarly in both conditions, they would have to use a higher angular velocity in ND than in FD.

Although angular velocity was possibly ill perceived, velocity signals coded by the canal cell firing rate may have been well integrated to yield a correct perception of head position in space. This probably explains why duration ratios were smaller in ND than in FD. Indeed, since plateau velocities were much higher in ND than in FD, rotations had to be of shorter duration in this first condition in order to avoid overshoot.

## Eye movements

Before performing the experiment, we had suspected that the angles and the velocity profiles used would not

enhance strong per- and postrotatory nystagmus, but we had not expected such a strong intersubject and intertrial variability. Collins and Guedry (1962) showed that the arousal level of the subjects could have an influence on their nystagmus. Drowsiness and sleep modify the nystagmus pattern, but in our experiment subjects were alerted before each trial, which, in addition, never lasted more than 12 s. It could also be speculated that some cortical inhibition took place among the subjects who exhibited very little vestibular nystagmus (Goebel et al. 1983, with eyes closed), but such possible cortex inhibition is difficult to account for.

No difference was found in the VOR gain during the reproduction rotation between FD and ND. This was unexpected because of the difference in the canal cell firing rate during reproduction between the two conditions, which we thought would induce a lower VOR gain in ND than in FD. We can wonder whether this difference in VOR gain was not hidden by the large variability. Finally, we had thought that the observation of postrotatory nystagmus could help us understand the relationship between the cupula dynamics and the delay (i.e., duration of postrotatory sensations). There again, the stimuli did not induce sufficiently consistent nystagmus to be able to draw any conclusion from the eye movement study.

However, differences at the perception level appeared between the two experimental conditions. We did find an influence of postrotatory effects induced by a first rotation on a subsequent rotation, which should be taken care of when studying sequential whole-body motions.

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