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## On the nature of the vestibular control of arm-reaching movements during whole-body rotations

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**Abstract** Recent studies report efficient vestibular control of goal-directed arm movements during body motion. This contribution tested whether this control relies (a) on an updating process in which vestibular signals are used to update the perceived egocentric position of surrounding objects when body orientation changes, or (b) on a sensorimotor process, i.e. a transfer function between vestibular input and the arm motor output that preserves hand trajectory in space despite body rotation. Both processes were separately and specifically adapted. We then compared the respective influences of the adapted processes on the vestibular control of arm-reaching movements. The rationale was that if a given process underlies a given behavior, any adaptive modification of this process should give rise to observable modification of the behavior. The updating adaptation adapted the matching between vestibular input and perceived body displacement in the surrounding world. The sensorimotor adaptation adapted the matching between vestibular input and the arm motor output necessary to keep the hand fixed in space during body rotation. Only the sensorimotor adaptation significantly altered the vestibular control of arm-reaching movements. Our results therefore suggest that during passive self-motion, the vestibular control of arm-reaching movements essentially derives from a sensorimotor process by which arm motor output is modified on-line to preserve hand trajectory in space despite body displacement. In contrast, the updating process maintaining up-to-date the egocentric representation of visual

space seems to contribute little to generating the required arm compensation during body rotations.

**Keywords** Reaching movement · Sensorimotor transformation · Vestibular signals · Whole-body rotation · Spatial updating

### Introduction

The study of goal-directed arm movements has provided a great deal of information about how the central nervous system controls voluntary motor behavior and responds to events imperiling the goal of the action (Desmurget et al. 1998). It has been shown that visual information related to the spatial features of the target (i.e., orientation, distance) influences movement organization, giving rise to smooth and early modulations of hand trajectory when a change in these features is detected (Blouin et al. 1995; Desmurget et al. 1998, 2001; Pélisson et al. 1986; Prablanc and Martin 1992; Sarlegna et al. 2003; Soechting and Lacquaniti 1983). In everyday life, however, changes in the spatial relationship between our body and the area of the environment that we want to reach for or where we want to stabilize the hand are more likely to result from self motion, even involuntary, than from a sudden displacement of this “goal area” (e.g. when trying to grasp the safety rail while standing in a bus that unexpectedly decelerates, or keeping a tray loaded with glasses stationary in space during accidental body motion). Therefore, the way self-motion-derived signals are implemented in the feedback loop controlling goal-directed arm movements constitutes a critical issue of sensorimotor control.

The vestibular input, which provides information about linear and angular head motion in space (Howard 1982), contributes to such a feedback loop (Adamovich et al. 2001; Bresciani et al. 2002a, b, c; Mars et al. 2003; Pigeon and Feldman 1998; Tunik et al. 2003). For instance, we recently showed that individuals passively

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rotated while reaching for a memorized earth-fixed target in the absence of any visual cue can hit the target with good accuracy for rotations as large as 40° (Bresciani et al. 2002b). In this study, the subjects modified on-line arm trajectory taking into account the vestibularly-detected body displacement. This allowed them to reach the target despite the change in the body/target spatial relationship. The mechanisms underlying this vestibular control of arm-reaching movements during body rotation are unknown yet. Two main processes could be involved:

- (1) an updating of visual space based on the perceived body displacement in space, and
- (2) a sensorimotor response of the arm motor system to body motion, this sensorimotor response being rather independent of the updating process.

Several authors have suggested that vestibular signals can be used to quantify body displacement in space and update the egocentric position of surrounding objects when body position/orientation changes (Berthoz et al. 1987; Israël et al. 1997; Nasios et al. 1999; Siegler et al. 2000). The vestibular control of arm-reaching movement could therefore be based on a central representation of target position that is updated during body rotation. In such a scenario, the on-line modifications of hand trajectory during body rotation would directly depend on the perceived body displacement, i.e. the matching between vestibular input and the perceived change in the egocentric position of the target. Bloomberg et al. (1991b) suggested that such vestibularly-derived percept of head/body displacement could underlie the control of gaze orientation during body rotation. This suggestion was based on their observation that reached gaze direction is similar when individuals are asked to provide, in the dark, an estimate of passive whole-body rotation magnitude with a saccade and when trying to maintain gaze stable in space during body rotation. Conversely, we have recently found that subjects' accuracy in reaching for a memorized target in complete darkness was greater when the movements were performed during, rather than after, passive whole-body rotations (Bresciani et al. 2002b). These results therefore suggested that the processes governing the vestibular control of arm-reaching movements differ, at least partly, from those involved in the updating of visual space.

The dynamic cues provided by the vestibular sensors are intimately related to the sensorimotor control of basic motor behavior, for example the stabilization of gaze in space during head motion (Bloomberg et al. 1991a; Angelaki 2004; Raphan and Cohen 2002; Roy and Cullen 2001) or balance control for upright standing (Day et al. 1997; Horak and Hlavacka 2002). For the control of such basic motor behavior, the vestibular signals feed on-line the actuating motor system (i.e. oculomotor system for gaze control and postural motor system for balance control) and trigger short latency responses to detected head motion. For instance, the vestibular control of gaze orientation mainly relies on a

sensorimotor arc, the vestibulo-ocular reflex (VOR). This reflex produces a slow-phase eye rotation in the direction opposite to the vestibularly-detected head movement and with a similar amplitude (Bloomberg et al. 1991a; Angelaki 2004; Raphan and Cohen 2002; Roy and Cullen 2001). The vestibular control of arm-reaching movements, as it contributes to keep the hand trajectory stationary in space when involuntary body rotations occur during goal-directed arm movements (Bresciani et al. 2002b), is reminiscent of such vestibularly-driven motor responses. Moreover, vestibular signals can trigger short-latency arm motor responses (about 40 ms, Britton et al. 1993). Therefore, arm control during body motion could rely on a sensorimotor transformation between vestibular input and the arm motor commands. In this scenario, on-line modifications of hand trajectory during body rotation would be quite independent of the updated representation of target position with respect to the body. These modifications would, rather, depend on the sensorimotor matching between vestibular input and the motor output necessary to preserve the ongoing hand trajectory in space despite body motion.

In this experiment we tested whether the vestibular control of arm-reaching movements relies on an updating process (i.e. updated representation of the visual space), or on a sensorimotor process.

To disentangle these alternatives, we separately adapted each process and then compared the respective influences of the adapted processes on the vestibular control of arm-reaching movements. Our rationale for using adaptive procedures was that if a given process underlies a given behavior, any adaptive modification of this process should give rise to an observable modification of the behavior—the behavior here being reaching movements during whole-body rotations. The adaptation of the updating process (hereafter called “updating adaptation”) changed the matching between vestibular input and the corresponding perceived body rotation. More specifically, the updating adaptation was designed to make the subjects perceive the amplitude of rotations smaller than they actually were, i.e. to induce a systematic underestimation of body rotation in space. If the vestibular control of arm-reaching movement relies on an updating process based on the perceived body displacement, then we expected the “updating adaptation” to evoke systematic directional undershoots when reaching for the target during body rotations (namely under compensation for body rotations). On the other hand, inspired by methods used to adapt the VOR (e.g. Gauthier and Robinson 1975; Miles and Fuller 1974), the adaptation of the sensorimotor process (hereafter called “sensorimotor adaptation”) changed the matching between vestibular input and the arm motor output necessary to keep the hand fixed in space during body rotation. To keep the hand fixed in space during body rotation, one has to produce a hand displacement in the direction opposite to and of same amplitude as body rotation. The sensorimotor adaptation was designed to

make the subjects under-compensate for body rotation with the arm, i.e. to produce hand displacements in the direction opposite to but of smaller amplitude than body rotations. If the vestibular control of arm-reaching movement relies on a sensorimotor process, then we expected the “sensorimotor adaptation” to evoke systematic directional undershoots when reaching for the target during body rotations.

## Materials and methods

### Subjects

Twenty-four subjects participated to the experiments. They were right-handed volunteers aged from 18 years to 37 years (mean 29). None of the subjects had a history of vestibular disorder and all had normal or corrected to normal visual acuity. All subjects gave written informed consent for participating in the experiment, which was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

### Set-up

Subjects were seated facing a large horizontal semi-circular table, the surface of which was 67 cm high, at mid-trunk level (Fig. 1A). The chair was fixed on the rotation axis of a motorized revolving platform (1.5 m in diameter), which was independent of the earth-fixed table. The subjects' heads were firmly kept in alignment with the trunk by an adjustable headrest so that the vertical axis of the head and trunk coincided with platform rotation-axis. The experiment was run in darkness and the subjects wore earphones diffusing white noise to remove any spatial reference of acoustic origin. A chair-fixed red light-emitting diode (LED), located 7 cm above table level and in the subjects' egocentric mid-sagittal plane, was used as central fixation light to minimize eye movements during rotations. A green LED fixed on the right index fingertip (finger LED) was used to provide visual feedback about hand position before the onset of

reaching movements. Hand movements were recorded using a magnetic tracking device (Polhemus Fastrak, sampling rate of 120 Hz), the sensor of which being fixed on the right index fingertip. A circular plastic disk (5 mm in diameter) placed on subjects' xiphoid process (sternum) was used as the forefinger starting position for reaching movements. Because the disk location was very close to platform's rotation axis, finger-starting position was independent of subject orientation at reaching movement onset.

### Rotational stimuli

The platform was rotated by a servo-motor whose speed was controlled by a Smart Motor Control Card (Baldor SMCC). The platform angular position was returned to the computer by the axis control card (sampling rate of 120 Hz). The rotation amplitudes used in the different experimental conditions were 20, 30 or 40°. Their duration (and peak velocity) was, respectively, 730 ( $48^\circ \text{ s}^{-1}$ ), 855 ( $62^\circ \text{ s}^{-1}$ ), and 980 ms ( $72^\circ \text{ s}^{-1}$ ). The velocity profile of platform rotation was Gaussian (Howard 1982) to simulate natural head movements and thereby preserve the ecological validity of the findings.

## Design

We used a classical adaptation paradigm with a pre-test to measure subjects' baseline performance, an adaptive exposure (i.e. training trials in which subjects received modified vestibularly derived feedback), and a post-test to measure the effect of the adaptation. The experimental design is presented in Fig. 2. The experiment was composed of four sessions. Two sessions were run to verify that both the updating and the sensorimotor adaptation efficiently adapted the updating and the sensorimotor process, respectively (validation sessions). Two other sessions were run to test the effect of both types of adaptation on reaching movements performed during whole-body rotations. Six different subjects were tested in each session (we used different groups of

**Fig. 1** A Schematic representation of the experimental setup. B Galvanometer-based device used to modify the position of the red laser dot during body rotations (arm adaptive procedure)

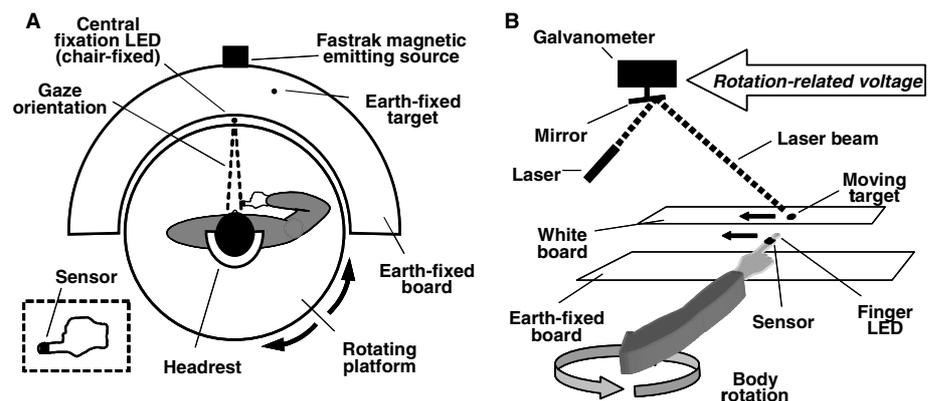


Fig. 2 Experimental design

Session	TIME		
	Pre test blocks	Exposure blocks	Post test blocks
Validation of updating adaptation	Reaching memorized target <u>after</u> body rotation	Updating adaptation	Reaching memorized target <u>after</u> body rotation
Updating contribution to vestibular control of reaching movements	Reaching memorized target <u>during</u> body rotation	Updating adaptation	Reaching memorized target <u>during</u> body rotation
Validation of sensorimotor adaptation	Maintaining extended arm stationary in space <u>during</u> body rotation	Sensorimotor adaptation	Maintaining extended arm stationary in space <u>during</u> body rotation
Sensorimotor contribution to vestibular control of reaching movements	Reaching memorized target <u>during</u> body rotation	Sensorimotor adaptation	Reaching memorized target <u>during</u> body rotation

subjects to avoid possible noise related to multiple adaptive exposures). Each pre and post block of the two validation sessions consisted of 30 trials, i.e. ten trials per rotation amplitude. Each exposure block consisted of 120 trials, i.e. 40 trials per rotation amplitude. Finally, each block where reaching movements were performed during body rotation (pre and post) consisted of 40 trials, i.e. ten trials per rotation amplitude and ten control trials without body rotation. Within each block, the order of the presented trials was always randomized, and the time interval between two successive trials was 30 s to allow the vestibular system to return to its normal resting state. On the whole, each of the two validation sessions consisted of 180 trials (i.e., 30 pre, 120 exposure, 30 post) for a total duration of 120–130 min. On the other hand, each of the two sessions testing the respective effects of the updating and sensorimotor adaptation on reaching movements performed during body rotation consisted of 200 trials (i.e. 40 pre, 120 exposures, 40 post) for a total duration of 130–150 min.

### Adaptive procedures

The adaptive exposures used to adapt the updating process and the sensorimotor process are shown in Fig. 3. Figure 4A presents the spatio-temporal organization of the exposure trials for both the updating and sensorimotor adaptation. Figure 4B presents the spatio-temporal organization of pre/post trials in the validation sessions.

#### Updating adaptation

This exposure was designed to modify the matching between vestibular input and the perceived amplitude of body rotation in the surrounding space. More specifically, the updating adaptation aimed at making the subjects underestimate the amplitude of body rotation in space. A red LED incorporated into the semi-circular table was used as the earth-fixed target. The target was

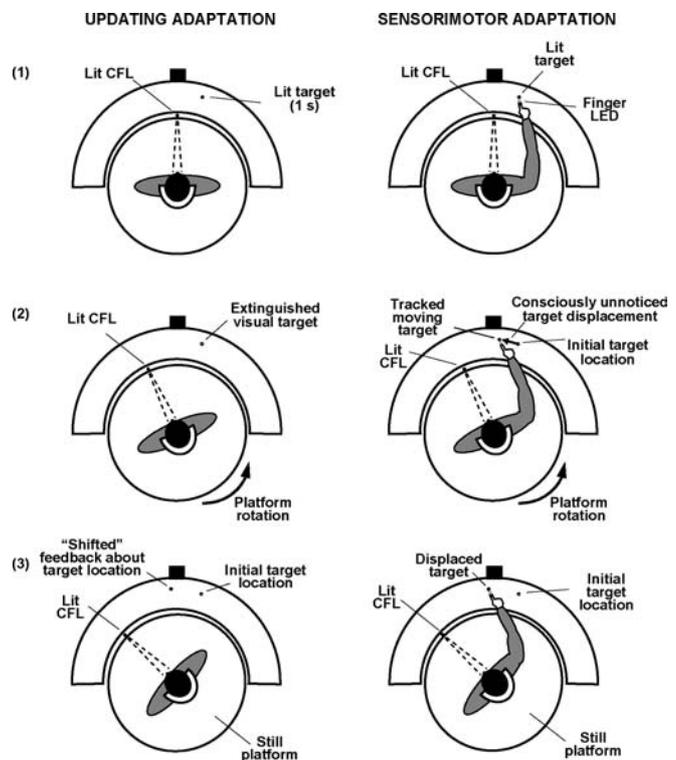
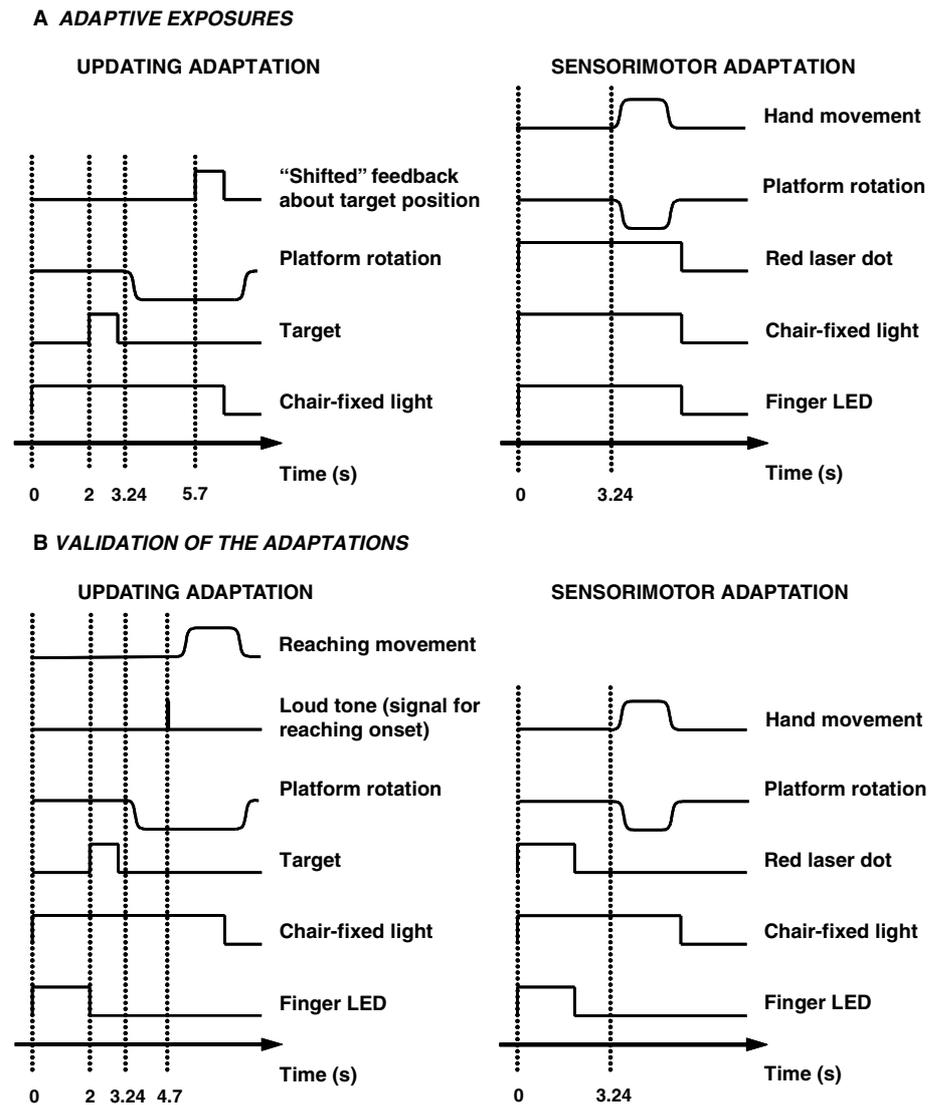


Fig. 3 Diagrams showing the procedures used for updating (*left panel*) and sensorimotor (*right panel*) adaptations at three different times: before (1), during (2) and after (3) body rotations

57 cm distant from subjects and located  $10^\circ$  to the right with respect to their initial straight-ahead orientation. Each trial started with the illumination of the chair-fixed light, subjects being instructed to keep fixating it. Two seconds later, the target was presented for 1 s. About 240 ms after target extinction, subjects were rotated counter-clockwise about the vertical axis. During and after body rotation, subjects were required to concentrate on the spatial location of the extinguished target. About 2.7 s after target extinction (that is 1.48 s after the offset of the rotation having the greatest magnitude), while still fixating the chair-fixed light, subjects were

**Fig. 4** Spatio-temporal organization of **A** exposure trials for the updating and sensorimotor adaptation and **B** pre- and post-trials for the validation of the adaptations



presented with a “shifted” visual feedback about target position for 1 s (i.e. other LEDs incorporated into the table were lit). The shifts were always in the direction of the platform rotation (i.e., counter-clockwise), and their amplitude depended on platform rotation amplitude. They were 0.26 times the amplitude of the rotation, i.e.  $5.2^\circ$ ,  $7.8^\circ$ , and  $10.4^\circ$  for the  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations, respectively.

#### Validation of the updating adaptation

This session verified that the updating adaptation really adapted the vestibular updating of visual space (this was necessary because, to our knowledge, it was the first time that such an adaptive procedure had been used to adapt the vestibular updating of visual space). For pre and post blocks, the subjects’ task was to reach for a memorized visual target after body rotation. At the beginning of each trial, subjects had their right hand lying on their right thigh. Then, the chair-fixed light and the finger

LED were simultaneously switched on. Subjects were instructed to look at the chair-fixed light (until the end of the trial) and to place their index finger at the starting position of the reaching movements (xiphoid process). Two seconds later the finger LED was switched off and the target LED (seen in peripheral vision) switched on for 1 s. Some 240 ms after target extinction, the platform was rotated counter-clockwise about the vertical axis. About 1.7 s after target extinction (rotation was then completed and the body still), a loud tone (50 ms) indicated to the subjects that they should initiate their reaching movement for the memorized target. The loudspeaker was fixed under the rotating chair such that the tone, which was loud enough to be heard over the white noise diffused in the earphones, could not be used as a spatial reference to determine body orientation after rotation. Subjects were instructed to tap the target with their index fingertip and then lift the finger slightly above the table. A translucent surface covering the table prevented tactile cues about target position. After the reaching movements, the chair-fixed light was switched

off and subjects put their hand back on their right thigh. Then, the platform was rotated back to its initial orientation.

### Sensorimotor adaptation

This exposure was designed to modify the matching between vestibular input and the arm motor commands necessary to keep the arm stable in space despite body rotation. More specifically, the sensorimotor adaptation aimed at reducing the gain of the transfer function between vestibular input and arm motor output. A galvanometer driven by a voltage related to platform rotation was positioned 1 m above the earth-fixed table (Fig. 1B). A mirror fixed on this galvanometer was used to reflect a laser beam on to the white surface of a recessed earth-fixed table located 12 cm above the larger one. At the beginning of each trial, the chair-fixed light, the finger LED, and a red dot (laser reflection), which was located 57 cm from subjects and  $10^\circ$  rightward with respect to body midline, were simultaneously switched on. Subjects were instructed to gaze at the chair-fixed light and to stretch their arm under the recessed table to place their index finger just beneath the laser dot. The task was to keep the finger in alignment with the laser dot throughout the trial. Three seconds after the beginning of the trial, the platform was rotated counter-clockwise and then remained still for 1 s before returning back to its initial orientation. The chair-fixed light, the finger LED and the laser dot were extinguished after the return rotation. The laser dot position/motion depended on platform orientation/motion. Therefore, platform rotation smoothly displaced the laser dot in the same direction and by a rotation-related amplitude (0.26 times the amplitude of platform rotation). At the end of the rotation, the laser dot was shifted by  $5.2^\circ$ ,  $7.8^\circ$ , and  $10.4^\circ$  for  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations, respectively (the shifts were therefore of the same magnitude as the target shifts in the updating adaptation). Thus, to keep the index finger aligned with the laser dot during body rotations, subjects had to move the arm in the direction opposite to the body but with a smaller magnitude. For instance, for a  $40^\circ$  counter-clockwise rotation, subjects only had to produce a  $29.6^\circ$  clockwise arm motor compensation.

### Validation of the sensorimotor adaptation

Because this adaptive procedure has never been used before, a specific session tested that the sensorimotor adaptation really adapted the sensorimotor transformation between vestibular signals and arm motor commands. For pre and post blocks, the subjects' task was to keep the extended arm stationary in space during body rotation. At the beginning of the trials, the central fixation light, the finger LED and the red laser dot were simultaneously switched on. As for exposure trials,

subjects were instructed to fixate the chair-fixed light and to stretch their arm to place their index finger just beneath the red laser dot located  $10^\circ$  to their right. Two seconds after the beginning of the trial, the finger LED and the laser dot were switched off. One second later, the platform was rotated counter-clockwise before remaining still for 1 s and returning back to its initial orientation. For the entire duration of each trial, subjects had to fixate the chair-fixed light and their task was to keep the unseen hand still in space at the position initially indicated by the red laser dot.

### Reaching movements performed during passive whole-body rotations (pre and post blocks of the main experimental condition)

The effects of the updating and sensorimotor adaptations on arm-reaching movements performed during body rotation were tested in separate sessions. The pre and post blocks of both sessions were similar to the pre and post blocks used to validate the updating adaptation (see Fig. 5). The only difference relied on the fact that subjects were here instructed to initiate their reaching movement at target extinction (rather than after the rotation as in the updating adaptation trials). Because rotation onset started 240 ms after target extinction, reaching movements were actually initiated near the beginning of the rotation (results showed that reaching movements, which lasted on average 744 ms, started on average 95 ms after rotation onset). Consequently, reaching accuracy could only be preserved through on-line control of arm movement trajectory taking into account body rotation. Subjects were asked to briefly touch the memorized location of the target before lifting their finger slightly above the table. This procedure was

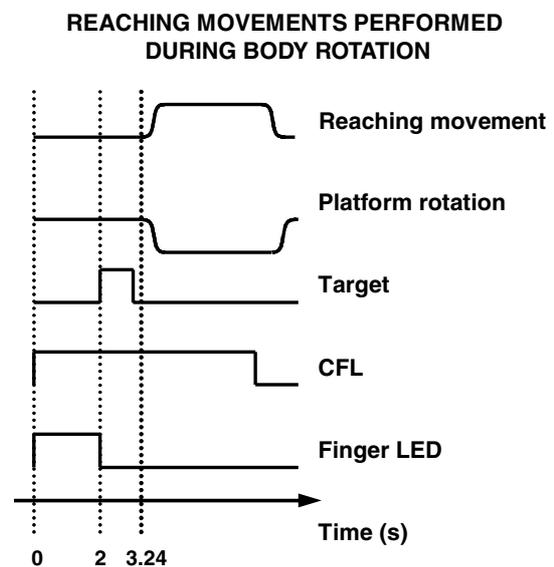


Fig. 5 Spatio-temporal organization of the trials where subjects performed reaching movements during body rotation

used to avoid any prolonged contact between the finger and the table if subjects reached the table before the end of the rotation. After the reaching movements, the chair-fixed light was switched off and subjects put their hand back on their right thigh. The platform was then rotated back to its initial orientation. Control trials without body rotation were also performed to assess subjects' accuracy in localizing and reaching for a previously presented peripheral visual target.

### Data analysis and statistics

Reaching movements (performed either during or after whole-body rotations)

For each trial, subjects' reaching performance was assessed by measuring finger direction at the end of the movements (when the index fingertip first touched the table, i.e. when finger velocity in the vertical dimension dropped under  $1^\circ \text{ s}^{-1}$ ). Finger direction was defined as the angle between the vector from starting position to end position and the mid-sagittal plane.

For each block and for all subjects normalized direction errors were computed by subtracting mean finger direction obtained in the trials without rotation from finger direction measured for each trial with rotation. This procedure bypassed the constant errors that each subject was likely to produce when reaching for a memorized peripheral target without visual feedback of the hand.

For each session, the effect of the adaptation was assessed comparing the mean finger direction recorded in the pre block and the mean finger direction recorded in the post block. The statistical significance of this difference was tested using in each case a  $2 \times 3$  [block (pre, post)  $\times$  rotation amplitude ( $20^\circ$ ,  $30^\circ$ ,  $40^\circ$ )] repeated measures ANOVA. Because adaptive exposures were designed to affect vestibular-evoked processes, trials without rotation were not taken into account (these trials were only used to compute the normalized errors as described above).

We also directly compared the effect of the updating and sensorimotor adaptation on arm-reaching movements performed during body rotation using a  $2 \times 3$  [adaptation (updating, sensorimotor)  $\times$  rotation amplitude ( $20^\circ$ ,  $30^\circ$ ,  $40^\circ$ )] between subjects ANOVA.

Hand/arm stabilization in space during whole-body rotations (pre- and post-blocks of the validation of the sensorimotor adaptation)

For each trial, subjects' performance in stabilizing their hand in space during whole-body rotation was assessed by comparing finger direction 50 ms before rotation onset and at the offset of the outwards rotation. This difference was defined as the rotation-induced error.

For this session, the exposure-induced effect was measured by comparing, for each rotation amplitude, the

mean rotation-induced error recorded in the pre block and the mean rotation-induced error recorded in the post block. The statistical significance of this difference was tested using a  $2 \times 3$  [block (pre, post)  $\times$  rotation amplitude ( $20^\circ$ ,  $30^\circ$ ,  $40^\circ$ )] repeated measures ANOVA.

## Results

Subjective reports of the subjects

After each session, the subjects were asked whether they noticed any target displacement during adaptive exposure, i.e. when the visual feedback was shifted (updating adaptation) or when the laser was smoothly displaced (sensorimotor adaptation). None of the subjects reported having perceived any target displacement.

Validation of the updating adaptation

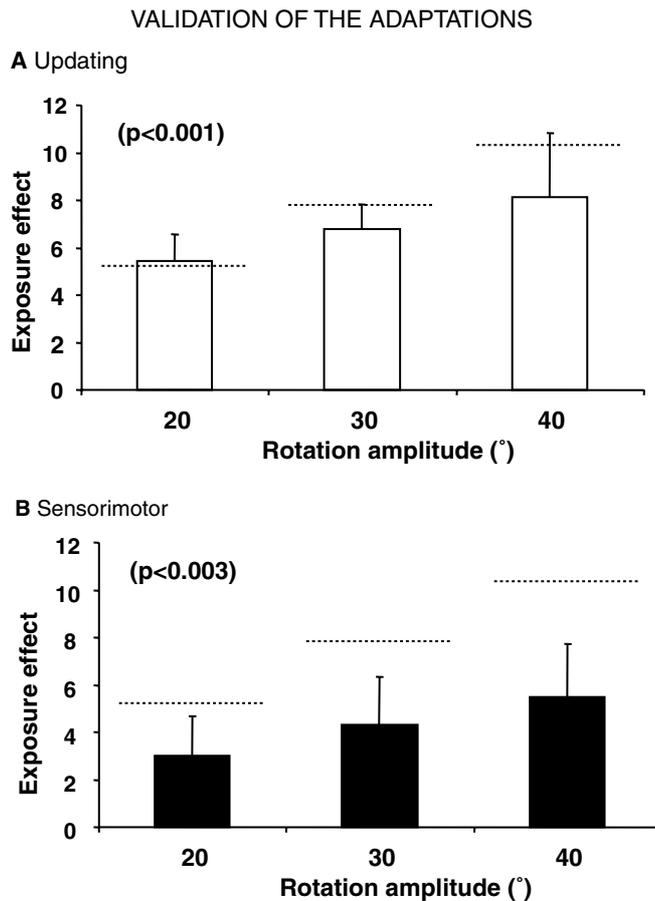
The validation session confirmed the efficacy of the updating adaptation in modifying the vestibular updating of surrounding space during body rotations (Fig. 6A). On average, in the post block, subjects undershot the target with respect to the pre block performance by  $5.44^\circ$  ( $\pm 1.10^\circ$ ),  $6.78^\circ$  ( $\pm 1.03^\circ$ ), and  $8.14^\circ$  ( $\pm 2.68^\circ$ ) for the  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations, respectively. This adaptation-evoked average undershoot was statistically significant ( $F_{(1,5)} = 251.30$ ,  $P < 0.001$ ). However, this effect did not significantly depend on rotation amplitude.

Validation of the sensorimotor adaptation

The sensorimotor adaptation successfully adapted the sensorimotor transformation between vestibular signals and arm motor commands (Fig. 6B). On average, in the post block, hand position in space after counter-clockwise body rotation was shifted counter-clockwise with respect to the pre-exposure block by  $3.02^\circ$  ( $\pm 1.67^\circ$ ),  $4.33^\circ$  ( $\pm 2.02^\circ$ ), and  $5.48^\circ$  ( $\pm 2.24^\circ$ ) for the  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations, respectively. This adaptation-evoked under-compensation of body rotation was significant ( $F_{(1,5)} = 29.892$ ,  $P < 0.003$ ). The effect of rotation amplitude was also significant ( $F_{(1,5)} = 12.167$ ,  $P < 0.008$ ).

Reaching performance during body rotation in the pre-test trials

On average, reaching movements' duration was 744 ms. Subjects' reaching accuracy was almost unaltered by the rotations. Indeed, body rotations evoked only minor reaching errors compared with the reaching movements performed without rotation. The fingertip overshot the target by only  $0.93^\circ$  ( $\pm 1.66^\circ$ ),  $2.20^\circ$  ( $\pm 1.68^\circ$ ), and  $3.42^\circ$  ( $\pm 2.01^\circ$ ) for the  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  rotations, respectively.



**Fig. 6** **A** Validation of the updating adaptation, i.e. efficacy of the updating adaptation in modifying the vestibular updating of surrounding space during body rotation. **B** Validation of the sensorimotor adaptation, i.e. efficacy of the sensorimotor adaptation in modifying the sensorimotor transformation between vestibular signals and arm motor commands. For both graphics, the *error bars* represent between-subjects standard deviations and the *dotted lines*, the magnitude of the target shift for each rotation amplitude

#### Effect of updating adaptation on reaching movements performed during whole-body rotations

The updating adaptation failed to affect reaching movements performed during whole-body rotations. Reaching accuracy after the updating adaptation (post block) was not significantly different from that for pre block ( $P > 0.05$ ). On the other hand, rotation amplitude had a significant effect on normalized direction errors, larger rotation amplitudes inducing larger errors ( $F_{(1,5)} = 247.78$ ,  $P < 0.001$ ).

#### Effect of sensorimotor adaptation on reaching movements performed during whole-body rotations

The sensorimotor adaptation strongly affected reaching movements performed during whole-body rotations. On average, after sensorimotor adaptation (post block), subjects undershot the target with respect to the pre-exposure block by  $3.48^\circ (\pm 0.95^\circ)$ ,  $4.61^\circ (\pm 1.15^\circ)$  and

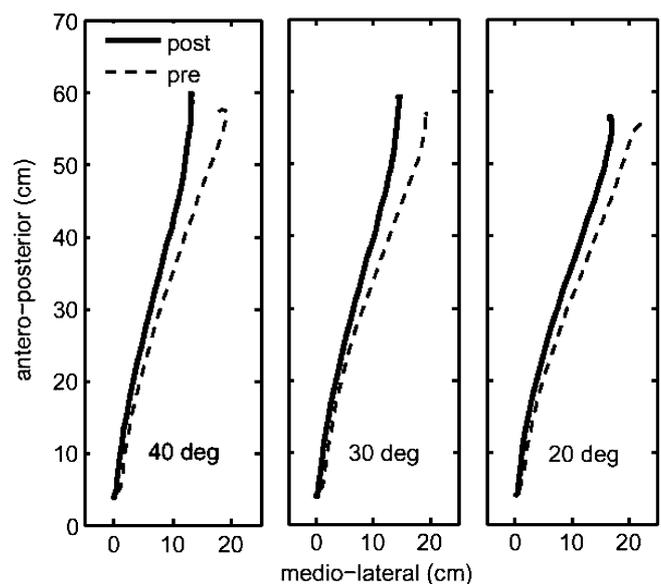
$5.04^\circ (\pm 0.85^\circ)$  during the  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations, respectively. This adaptation-induced effect was significant ( $F_{(1,5)} = 143.04$ ,  $P < 0.001$ ). Rotation amplitude also had a significant effect, the normalized direction errors increasing with rotation amplitudes ( $F_{(1,5)} = 38.34$ ,  $P < 0.001$ ). The effect of sensorimotor adaptation on reaching movements performed during body motion is shown in Fig. 7, which shows the mean hand trajectories produced by a representative subject during  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations in the pre and post blocks of the sensorimotor adaptation condition.

Direct comparison of the respective effects induced by the two adaptive exposures on reaching movements performed during whole-body rotation

As shown in Fig. 8, the sensorimotor adaptation had a stronger effect on reaching movements performed during body rotation than did the updating adaptation. This difference was significant ( $F_{(1,10)} = 9.15$ ,  $P < 0.05$ ).

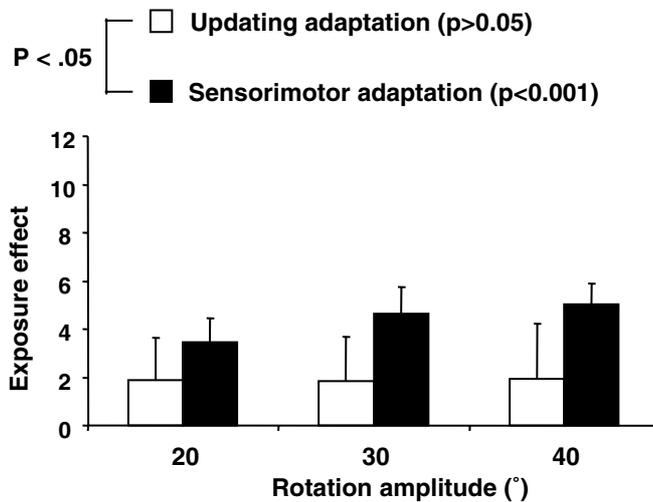
## Discussion

The results of this experiment confirm previous results showing that the vestibular signals can be used on-line to control the trajectory of arm-reaching movements during passive whole-body rotations, and thereby preserve reaching accuracy despite body displacement (Bresciani et al. 2002b). More interestingly, the results provide, for the first time, some hints about the mechanisms that likely underlie this vestibular control of arm-reaching movements. Our working hypothesis was that if a given process underlies a given behavior, any adaptive modi-



**Fig. 7** Mean hand trajectories produced by a subject during  $20^\circ$ ,  $30^\circ$ , and  $40^\circ$  body rotations in the pre and post blocks of the sensorimotor adaptation condition

## Effect of adaptation on the vestibular control of reaching movements



**Fig. 8** Effect of updating and sensorimotor adaptations on reaching movements performed during whole-body rotation. The error bars represent between-subjects standard deviations

fication of this process should give rise to an observable modification of the behavior. Adapting the updating process that associates every change in vestibular input to a perceived body displacement failed to alter the vestibular control of arm-reaching movements. Indeed, whereas reaching movements performed after body rotations were highly sensitive to adaptation of the updating process (see validation of updating adaptation), reaching movements performed during body rotation was not significantly affected by the updating adaptation. This suggests that the updating process that maintains the egocentric representation of visual space up to date during body rotations makes little contribution to generating the required arm movement compensation during such motion. On the other hand, adapting the vestibularly-driven sensorimotor process allowing the arm to remain immobile in space, despite body rotation, markedly affected the vestibular control of arm-reaching movements. The sensorimotor adaptation reduced the gain of the transfer function between vestibular input and arm motor output. When adapted, the subjects consistently and significantly undershot target position. Interestingly, the amplitude of this adaptation-evoked undershoot (on average  $4.38^\circ$ ) was similar to the adaptation-evoked deviation of arm position recorded for the validation of the sensorimotor adaptation (on average  $4.28^\circ$ ). These results therefore suggest that the vestibular control of arm-reaching movements during self-motion (Adamovich et al. 2001; Bresciani et al. 2002b; Pigeon and Feldman 1998; Tunik et al. 2003) essentially derives from a sensorimotor process by which arm motor output is modified on-line to preserve the desired hand trajectory in space during body displacement.

Updating the egocentric representation of visual space is a process underlying our navigation behavior, e.g. trying to reach the exit of a building (Golledge 1999). For the vestibular input to contribute to this updating process, the labyrinths' primary dynamic signals have first to be integrated to provide position signals. Then, the perceptual systems underlying the representations of visual space must refer these body position signals to the memorized landmarks located in the surrounding environment. This was confirmed in the present experiment by the observation that reaching movements performed after body rotation—validation of updating adaptation—were highly sensitive to adaptive modification of the matching between vestibular input and the perceived body position in space. However, online movement control consists in using the different sensory channels to monitor the ongoing movement and “correct” in real-time any detected discrepancy between the desired and the actual movements. The mental processes underlying the updating of the internal representation of the visual space could be much too time-consuming (see Yardley et al. 1999) to be compatible with the temporal constraints of optimum on-line control of goal-directed arm movements. This could be the reason why, in this study, the updating process did not affect the vestibular control of arm trajectory during passive body rotation.

Our results suggest that the vestibular control of goal-directed arm movements is based on a sensorimotor process. This makes sense if one considers that, in everyday life, the dynamic signals provided by the vestibular sensors are mainly processed automatically to control basic motor behavior, for example keeping the eyes stationary in space during head movements—vestibulo-ocular reflex—(Angelaki 2004; Bloomberg et al. 1991a; Raphan and Cohen 2002; Roy and Cullen 2001) or maintaining balance during upright standing—vestibulo-spinal reflex—(Day et al. 1997; Horak and Hlavacka 2002). Common to such motor behavior is the fact that vestibular signals enable individuals to preserve the spatial goal of their action when their body is moving, voluntarily or not. This also applies to the vestibular control of arm-reaching movement (Adamovich et al. 2001; Bresciani et al. 2002a, b; Mars et al. 2003; Pigeon and Feldman 1998; Tunik et al. 2003; Britton et al. 1993). For example, the present results and those obtained in a previous study (Bresciani et al. 2002b) showed that vestibular signals trigger on-line modifications of arm trajectory that enable preservation of reaching accuracy during body motion. The neural pathways conveying the vestibular information to the arm motor neurons could include both the vestibulospinal and reticulospinal tracks. Indeed, these tracks are known to receive input from the vestibular nuclei (Ladpli and Brodal 1968; Peterson and Abzug 1975) and they both have direct projections to cervical motoneurons (Brodal 1981).

Previous experiments compared subjects' ability to retrieve the memorized position of a target after body

rotations with their performance in tracking (finger pursuit of a moving target) or pointing at the target during these rotations (Guedry et al. 1971; Ivanenko et al. 1997; Bresciani et al. 2002b). It was found that subjects are more accurate when the vestibular signals are processed to control the motor output than when they are used to update the internal representation of visual space. These performance differences could be explained by the results of the present experiment. Indeed, if the mechanisms underlying the vestibular control of arm-reaching movements are independent of the updating of visual space, one can expect to observe performance differences at behavioral level.

Difference between vestibular updating and vestibular control could also reflect differences between vestibular signal processing for motor planning and online motor control. Studying the visual control of reaching and grasping movements, Glover and Dixon (2001a, b, 2002) showed that the planning of goal-directed movements is sensitive to visual illusions, whereas the execution is not. For instance, in Glover and Dixon (2002), subjects were instructed to grasp a disk, the apparent size of which was manipulated by surrounding the target with circles that were either larger or smaller than the disk. The size-contrast illusion resulting from this manipulation (known as the Ebbinghaus illusion) affected the grip aperture at the beginning of the grasping movement. However, the grip aperture was no more affected by the illusion at the end of the movements, even when they were performed without vision of the hand. Similar results were observed for hand orientation (Glover and Dixon 2001a, b). The authors concluded that visual information could be processed differently for planning and for controlling arm-reaching movements. If one admits that similar principles can be applied to both visual and vestibular inputs, our results can be viewed in parallel with theirs. Indeed, they suggest that vestibular signals are also processed differently for planning and for controlling goal-directed arm movements.

## Conclusion

This experiment corroborated previous results showing that the CNS can use vestibular inputs to control on-line goal-directed arm movements and preserve reaching accuracy when the whole-body is passively rotated during movement execution. Moreover, our results showed that this vestibular control of arm-reaching movements does not rely on an updated representation of visual space but rather on a sensorimotor process. Finally, the present experiment demonstrated for the first time that the vestibulo-manual relationship is under adaptive control. This provides further evidence of the tight link between vestibular and arm motor systems to control hand position and movements in space during body motion. Further experiments are needed to determine whether the vestibular control of arm movements

depends on automatic-like processes, with low cognitive loads and low attentional demands, as with vestibular control of eye and body movements. These experiments could also compare the contribution of vestibular signals to the control of arm movements that are directed towards either a body-fixed target (e.g. reaching for a worn hat) or an earth-fixed target during body motion, or that are performed in synergy with body motion (e.g. reaching for object located outside the prehensile space).

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