

On-line versus off-line vestibular-evoked control of goal-directed arm movements

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The present study tested whether vestibular input can be processed on-line to control goal-directed arm movements towards memorized visual targets when the whole body is passively rotated during movement execution. Subjects succeeded in compensating for current body rotation by regulating ongoing arm movements. This performance was compared to the accuracy with which subjects reached for the target when the rotation occurred before the movement. Subjects were less accurate in updating the

internal representation of visual space through vestibular signals than in monitoring on-line body orientation to control arm movement. These results demonstrate that vestibular signals contribute to motor control of voluntary arm movements and suggest that the processes underlying on-line regulation of goal-directed movements are different from those underlying navigation-like behaviors. *NeuroReport* 13:1563–1566 © 2002 Lippincott Williams & Wilkins.

Key words: Arm movement; Body orientation; Human; Memorized target; Motor control; Spatial updating; Vestibular signals; Whole-body rotation

INTRODUCTION

Goal-directed arm movements are initiated on the basis of both perceived object position and sensed initial state of motor apparatus. Once the movement is triggered, continuous processing of arm- and target-related signals allows the CNS to compare the predicted end-point of the ongoing movement with actual goal location and on-line regulation of the motor command optimizes movement accuracy [1]. Such on-line control is particularly suitable to overcome external perturbations likely to impair movement accuracy.

One of the most extensively used methods of probing the on-line responses of the CNS to external perturbations consists of changing the spatial goal of the movement during its execution. Visual detection of a change in target position usually induces amendment of hand trajectory to reach the new target location [2–4]. However, in many situations, such as walking, required movement regulation is related to body displacement rather than to a change in target position. In line with this, we recently tested subjects' responses to vestibularly-detected body motion when performing goal-directed arm movements [5]. In this study, head-fixed subjects were instructed to reach for memorized visual targets in complete darkness and their vestibular afferent pattern was modified at movement onset by applying a bipolar electric current to the mastoid processes (galvanic vestibular stimulation). The vestibular stimulation elicited significant deviations of hand path towards the anode side. These were interpreted as on-line regulations of arm movement resulting from sensed body displacement towards the cathode side. Although highlighting vestibular

participation in on-line control of arm movements, these directional deviations of hand path remained nevertheless uninformative about subjects' ability to process vestibular signal to preserve reaching accuracy. Indeed, no effective body displacement occurred and head movement sensation artificially evoked by galvanic vestibular stimulation is difficult to quantify precisely.

In the present study, the ability to control on-line goal-directed arm movements through vestibular input was assessed by submitting human subjects to passive whole-body rotations during reaching movement execution. Reaching movement control during body motion could either be based on a sensorimotor compensation of sensed body rotation or on an updating of the internal representation of target position. To determine which of these alternatives was most likely to underlie arm movement regulation, subjects' accuracy in reaching for a memorized visual target was compared across two different conditions: rotation occurring during movement and rotation occurring before movement. Arm movements initiated after rotation completion were designed to assess the degree to which the control of reaching movements could rely on a vestibularly updated internal representation of target position during body motion.

MATERIALS AND METHODS

Six right handed volunteers aged 22–27 (mean 25) years participated in the experiment, which was approved by the

local ethics committee. None of these subjects had a history of vestibular disorder and all had normal vision.

The experimental setup is schematically represented in Fig. 1a. Subjects were comfortably seated, facing a horizontal semi-circular table, the surface of which was 67 cm high (at mid-trunk level). The chair was fixed on the rotation axis of a motorized revolving platform (1.5 m diameter) which was independent of the earth-fixed table. Subjects' head was 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 a white noise to remove any spatial reference of acoustic origin. A 3 mm diameter red light emitting diode (LED) incorporated into the table was used as the earth-fixed target. The target was 57 cm distant from subjects and located twenty degrees to the right with respect to the initial (allocentric) straight-ahead orientation. A translucent surface covering the black table prevented tactile cues about target position. Another red LED, located in front of the subject at table level (subject's egocentric mid-sagittal plane), rotated with the chair and was used as central fixation LED (CFL) to minimize eye movements during rotations. Hand movements were recorded using a magnetic tracking device (Polhemus Fastrack), the sensor of which was fixed on the right index fingertip. A circular plastic disk (5 mm 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 subjects orientation at movement onset.

Subjects were instructed to look at the CFL, which was switched on at the beginning of each trial and left on until the end of the trial. One second after CFL illumination, the target LED was switched on for 1 s and subjects had to localize it in peripheral vision. At 240 ms after target extinction, while the subjects were still fixating the CFL, the platform was rotated either clockwise (CW) or counter-clockwise (CCW) around the vertical axis. Four rotation amplitudes were used on either side (10°, 20°, 30° and 40°). The rotations lasted from 418 ms for a 10° amplitude to 705 ms for a 40° amplitude. To simulate natural head movements, the velocity profile of the platform rotation was gaussian (Fig. 1b).

Two reaching conditions were used. In the on-line condition, subjects initiated their movement at the extinction of the earth-fixed target. Because rotation onset started 240 ms after target extinction, reaching movement was initiated near the beginning of the rotation. Therefore, accurate reaching implied on-line regulation of arm movement trajectory taking into account body rotation. In the off-line condition, subjects had to wait for rotation completion to initiate their reaching movement. Thus, subject orientation in space remained constant during movement execution and reaching movement was performed according to the updated internal representation of target position with respect to the body.

After reaching movement completion, the CFL was switched off and subjects put their index finger back on the starting position (xiphoid process). Then, the platform was rotated back to its initial orientation. Trials without rotation (control trials) were also performed in each

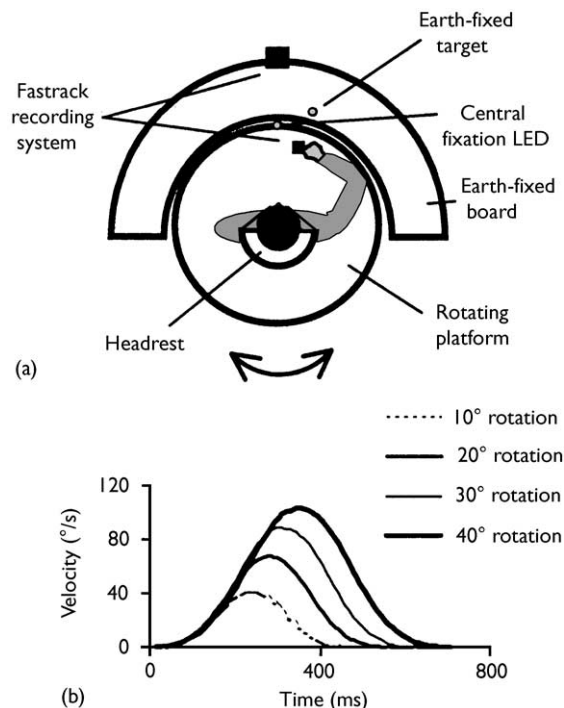


Fig. 1. Experimental set-up (a) and velocity profiles of chair rotation for the different rotation amplitudes (b).

condition to assess subjects' accuracy in localizing and reaching a previously presented (memorized) peripheral visual target. Visual feedback about hand position was never available during the experiment.

All subjects participated in both experimental conditions. In each condition, eight trials per amplitude/direction rotation combination were performed in a random order to avoid any predictability about the forthcoming rotation. Finger direction at the end of reaching movements was used to assess subjects' accuracy in both conditions. Finger direction was defined as the angle between the vector from starting position to end position and the vector from starting position to allocentric straight-ahead. For both conditions and for all subjects, reaching errors were computed by subtracting mean finger direction for control trials from finger direction measured for each trial with rotation. Leftward and rightward deviations with respect to control trials were respectively assigned negative and positive values. Four separate $2 \times 2 \times 4$ (condition (on-line, off-line) \times rotation direction (CCW, CW) \times rotation amplitude (10°, 20°, 30°, 40°)) ANOVAs were performed, one for each of the four dependent variables measured: signed errors, intra-subject variability, absolute errors and movement time.

RESULTS

Figure 2 shows mean hand trajectories produced by one subject for control (no rotation), 40° CCW and 40° CW rotations in the on-line condition. Hand trajectory in space remained almost unaffected by the ongoing body rotation (Fig. 2a). Since subject was rotating during reaching movement execution, preserved spatial constancy in hand trajectory resulted from egocentric hand paths that were

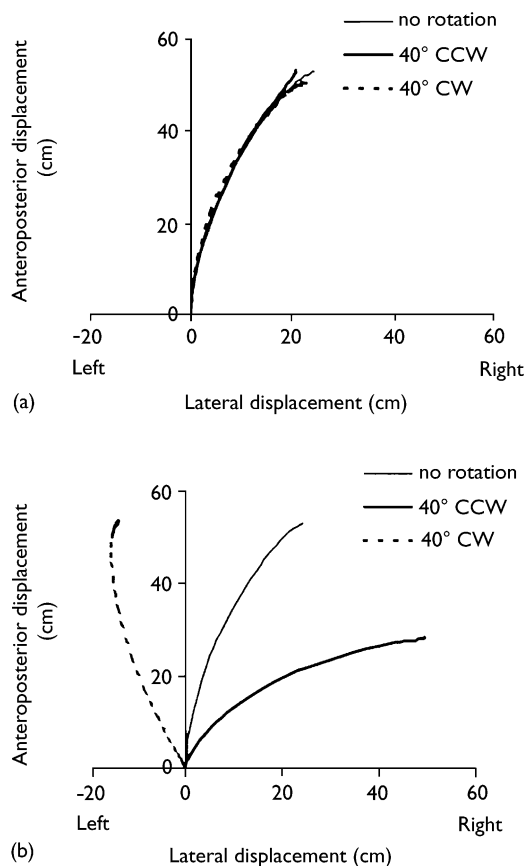


Fig. 2. Mean hand trajectories produced by a subject in the control condition (where no rotation of the chair occurred), and for 40° clockwise and counterclockwise rotations. Mean trajectories have been computed after temporal normalization. The same trajectories are represented in an earth-fixed reference frame (a) and in subject's reference frame (b). Trajectories in the subject's reference frame have been computed using the formula: $X' = (X \times \cos\alpha) - (Y \times \sin\alpha)$, $Y' = (X \times \sin\alpha) + (Y \times \cos\alpha)$, with α varying for each sample in accordance with the chair position profile. The subject regulated his hand trajectory taking into account ongoing body rotation (a), so that hand path in space remained almost unaffected (b).

markedly different depending on rotation direction and magnitude (Fig. 2b). As evidenced by the figure, hand trajectory regulation was smooth and continuous all along the movement.

For control trials in the on-line and off-line conditions, subjects' finger direction was on average 19.40° and 19.62°, respectively. Body rotations had little effect on subjects' accuracy when occurring during the reaching movements (Fig. 3a). In the on-line condition, subjects pointed on average $0.85 \pm 1.76^\circ$ leftward with respect to control trials. The errors were larger when the rotations took place before the arm movement, since in the off-line condition, subjects pointed on average $2.35 \pm 1.97^\circ$ leftward with respect to control trials. The ANOVA revealed that this main effect of condition on signed errors was significant ($F(1,5) = 6.72$, $p < 0.05$). Neither the amplitude nor the direction of the rotation significantly affected signed errors, but the interaction between these two factors turned out to be significant ($F(3,15) = 15.27$, $p < 0.0001$). Newman-Keul's tests indicated

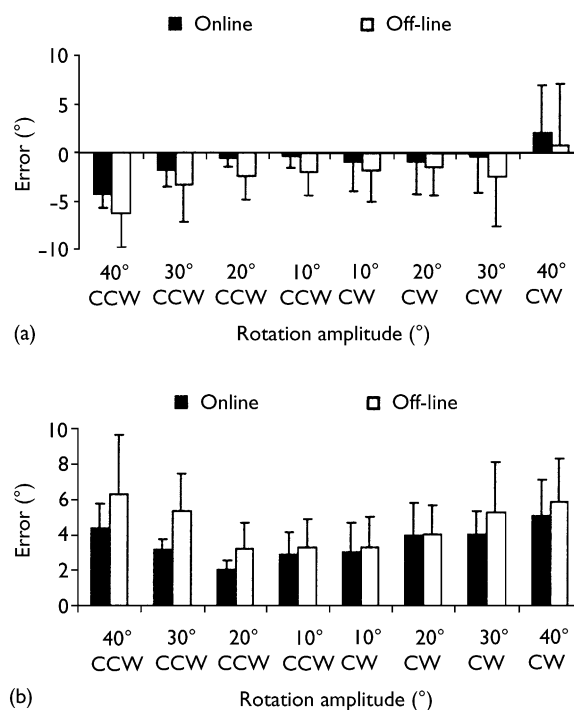


Fig. 3. Mean signed (a) and absolute (b) reaching errors measured at movement offset for each condition and each rotation amplitude.

that large leftward errors committed for 40° CCW rotation and rightward errors induced by 40° CW rotation significantly differed from each other as well as from errors evoked by smaller rotation amplitudes ($p < 0.05$). None of the factors had a significant effect on finger direction variability (intra-subject s.d. for signed errors). On average, finger direction variability was $3.26 \pm 0.53^\circ$ and $3.71 \pm 0.85^\circ$ in the on-line and off-line conditions, respectively. Absolute errors (Fig. 3b) were also significantly smaller in the on-line condition ($3.60 \pm 0.98^\circ$) than in the off-line condition ($4.63 \pm 1.26^\circ$; $F(1,5) = 7.27$, $p < 0.05$). Absolute errors were affected by rotation amplitude ($F(3,15) = 10.86$, $p < 0.0005$), being significantly greater for 30° and 40° rotations than for 10° and 20° rotations (Newman-Keul's tests, $p < 0.05$).

In the on-line condition, subjects initiated their reaching movement on average 31 ± 61 ms after rotation onset. The average movement duration was shorter in the on-line (673 ± 193 ms) than in the off-line (833 ± 121 ms) condition, as if subjects tried to reach for the target earlier and minimize the perturbing effects of rotation. The difference in movement duration between the on-line and off-line conditions was significant ($F(1,5) = 10.01$, $p < 0.05$), whereas neither the side nor the amplitude of rotation had a significant effect.

DISCUSSION

Passively rotated when reaching for a memorized target, subjects regulated on-line arm trajectory to compensate for the change in body orientation. This regulation of arm movement allowed them to preserve a fairly good reaching accuracy. For instance, body rotations as large as 40° only modified movement endpoint by about 4°. Because subjects

did not have visual feedback about target location during rotations, these results show that subjects process vestibular signals to control goal-directed arm movements. Furthermore, signed and absolute reaching errors were smaller when rotations occurred during movement execution than when subjects initiated the movement after rotation completion. Thus, CNS processing of vestibular information was more efficient in monitoring on-line body orientation to control the movement than in updating the internal representation of visual space. This may suggest that arm movement regulation during body rotation was not based on a vestibularly updated internal representation of target egocentric location. Controlling an ongoing arm movement during body rotation essentially necessitates sensorimotor transformations of vestibularly sensed rotation. Therefore, the smooth corrections of the hand path could reflect a mere counteraction to the detected body rotation where subjects integrate the extent of self-motion and perform a continuous cancellation of rotation-induced effects on motor output. On the other hand, updating the internal representation of visual space requires access to vestibular signals by systems specialized in object localization. In this case, subjects have not only to compute the change in body orientation, but this change has to be incorporated into the internal map of the surrounding space. As suggested by previous studies dealing with spatially oriented behaviors, such incorporation would remain fairly coarse. Indeed, whereas subjects are quite accurate in using vestibular signals to determine the magnitude of passive whole-body rotations in darkness [6–8], they usually exhibit sizeable errors when required to use the same input to update the internal representation of visual space [6,9,10]. In line with this, our results suggest that processes underlying arm trajectory regulation during rotation are different from those underlying the updating of the internal representation of space.

The reason why subjects underestimated the amplitude of CCW rotations but overestimated the amplitude of CW rotations (except for 40° clockwise rotation) remains unclear. As the target was located 20° rightward from initial straight-ahead, CCW rotations always turned subjects away from the target so that the angular distance between subject orientation and target position increased with rotation amplitude. On the other hand, CW rotations brought subjects' egocentric straight-ahead closer to the target. One possibility is that the asymmetry observed in signed error patterns results from a range-like effect [11], this effect corresponding to the tendency to undershoot more distant targets and overshoot closer ones.

In the on-line condition, inertial perturbations, although relatively weak considering the acceleration/velocity used in the experiment, could have affected the reaching arm

during rotation by adding external forces to natural hand motion. For instance, Coriolis forces acting perpendicularly to the radial displacement of the moving limb could have induced rightward reaching errors when rotating CCW and leftward reaching errors when rotating CW. However, leftward signed errors produced when rotating CW were always larger in the off-line than in the on-line condition and, in the on-line condition, 30° and 40° CCW rotations gave rise to greater leftward deviations than identical CW rotation amplitudes. Therefore, if passive forces effectively perturbed movement execution, evoked errors were only of small amplitude. The possible contribution of these forces to improving arm control by providing inertial kinesthetic information during the movement is also very unlikely since kinesthetic cues alone have been evidenced not to allow on-line corrections of the directional component of movements unfolding in modified force field [12,13].

CONCLUSION

The present experiment demonstrated that the CNS can use vestibular input to control on-line goal-directed arm movement and preserve a fairly good reaching accuracy when the whole-body is passively displaced during movement execution. Since subjects were less accurate in using vestibular signals to update the internal representation of surrounding space, our results suggest that arm movement regulation during whole-body rotations relies on a continuous sensorimotor counteraction to rotation-induced effects rather than on an updated internal representation of visual space.

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