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RESEARCH ARTICLE

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Accuracy of spatial localization depending on head posture in a perturbed gravitoinertial force field

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Abstract Spatial orientation is crucial when subjects have to accurately reach memorized visual targets. In previous studies modified gravitoinertial force fields were used to affect the accuracy of pointing movements in complete darkness without visual feedback of the moving limb. Target mislocalization was put forward as one hypothesis to explain this decrease in accuracy of pointing movements. The aim of this study was to test this hypothesis by determining the accuracy of spatial localization of memorized visual targets in a perturbed gravitoinertial force field. As head orientation is involved in localization tasks and carrying relevant sensory systems (visual, vestibular and neck muscle proprioceptive), we also tested the effect of head posture on the accuracy of localization. Subjects (n=10) were seated off-axis on a rotating platform (120° s^{-1}) in complete darkness with the head fixed (head-fixed session) or free to move (head-free session). They were required to report verbally the egocentric spatial localization of visual memorized targets. They gave the perceived target location in direction (i.e. left or right) and in amplitude (in centimeters) relative to the direction they thought to be straight ahead. Results showed that the accuracy of visual localization decreased when subjects were exposed to inertial forces. Moreover, subjects localized the memorized visual targets more to the right than their actual position, that was in the direction of the inertial forces. With further analysis, it appeared that this shift of localization was concomitant with a shift of the visual straight ahead (VSA) in the opposite direction. Thus, the modified gravitoinertial force field led to a modification in the orientation of the egocentric reference frame. Furthermore, this shift of localization increased when the head was free to move while the head was tilted in roll toward the center of rotation of the platform and turned in yaw in the same direction. It is concluded that the orientation of the egocentric reference frame was influenced by the gravitoinertial vector.

Keywords Egocentric localization · Egocentric reference frame · Head posture · Gravitoinertial · Sensory integration

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Introduction

Human sensory motor control has evolved under the omnipresent influence of the gravitational force field. Thus, gravity constitutes a highly relevant reference due to its great stability in direction and magnitude over time. However, gravity is not the only external force acting on body segments. In many everyday situations, e.g. being seated in a car taking a bend, during take-off in a plane, or simply when turning on our own feet when reaching out to grasp an object, individuals are exposed to inertial forces like centrifugal and Coriolis forces. Such inertial forces are known to be fictitious forces because of their dependence on the frame of reference in which they are observed. Coriolis force is defined as a transient inertial force that only applies to moving segments in a rotating environment. Centrifugal force, in contrast with Coriolis force, is applied to the whole body of individuals that are rotated[1]. When applied to a moving arm, such inertial forces could potentially affect the accuracy of goal-directed movements by causing their trajectory to deviate. Thus, in order to preserve movement accuracy, subjects have to take into account inertial forces before and/or during the movement, and their impacts on the moving limb. Previous studies (Dizio and Lackner 1995; Coello et al. 1996) have

[1] The Coriolis force is related to the mass of a moving segment in a rotating frame, its velocity in the rotating frame and the angular velocity of the rotating frame of reference. Centrifugal force is related to the product of the square angular velocity, the mass of the subject in rotation, and the distance of the subject relative to the center of rotation.

attempted to determine the way subjects adapt to Coriolis forces. For example, Lackner and Dizio (1994) analyzed reaching performance of subjects seated on the center of a rotating environment. Subjects were required to reach memorized visual targets as accurately as possible without visual feedback on the moving limb. Subjects initially exhibited large deviation of movement curvature and endpoint in the direction of the Coriolis force. However the subjects rapidly adapted to the Coriolis force such that their reaching movements straightened out and landed closer to the target within about ten reaches. These results provided compelling evidence that motor adaptation to movement deviations generated by Coriolis force can be achieved rapidly without vision of the moving limb. Lackner and Dizio (1994) suggested that adaptation occurred on the basis of proprioceptive information.

There are few situations in everyday life in which subjects are exposed to high level of Coriolis force alone. Indeed, when present, Coriolis force is generally accompanied by centrifugal forces. Interestingly, Lackner and Dizio (1998) showed that no adaptation to both centrifugal and Coriolis forces occurs when vision of the moving limb is prevented. The authors hypothesized that visual feedback on reaching could be necessary to achieve a high level of accuracy when subjects are exposed to Coriolis and centrifugal forces. To test this hypothesis, Bourdin et al. (2001) studied non adaptive mechanisms of pointing movements to both centrifugal and Coriolis forces depending on the availability of vision of the moving arm. Their results confirmed that adaptation in such perturbed gravitoinertial force fields occurred when vision of the moving arm was allowed during the movement. However, these results do not enable understanding of the nature and the persistence of errors when reaching for memorized visual targets in perturbed gravitoinertial force field when no visual feedback is available. Bock et al. (1996a, 1996b) evoked some hypotheses to explain the pointing deviations they observed in the direction of the inertial forces:

1. direct mechanical effects of the inertial forces on the moving arm,
2. degradation of the information about arm position provided by proprioceptive inputs, and
3. visual mislocalization of the pointed targets.

We were particularly interested in testing the last hypothesis according to which a potential decrease of accuracy in localizing visual memorized targets in a perturbed gravitoinertial force field could lead to pointing errors.

There is a considerable amount of evidence from the literature that the visual vertical is affected by gravitoinertial stimulation (for reviews see Howard 1986, Mittelstaedt 1988, or Young 1984). Most of the previous studies dealt with the effect of inertial stimulation on geocentric coding (perception of the gravitational direction) but a few have investigated its influence on egocentric coding. It is now well established that centrifugation can induce several illusions:

1. an illusion of body pitch called "somatogravic illusion", when the subject faces towards or directly away from the rotation axis or is tilted in the saggital plane (Cohen 1977);
2. an illusion of elevation of a visual target, called "oculogravic illusion" when both amplitude and direction of the gravito-inertial vector are changed; and
3. an "elevator illusion" when amplitude only is changed (Cohen et al. 2001).

However, there is no clear evidence that centrifugation affects purely cognitive egocentric target localization tasks in addition to the perception of straight-ahead direction. Localization was often assessed by pointing tasks with the hand only (Bock et al. 1996a, 1996b) or with a joystick (Cohen et al. 2001) but necessarily involving sensory-motor loops.

The spatial location of a visual object is usually represented relative to two fundamental spatial frames of reference: egocentric and allocentric (Howard and Templeton 1966; Paillard 1991; Lacquaniti 1997). In the allocentric frame of reference objects are represented with respect to their spatial and configurational properties. In the egocentric frame of reference, in contrast, the position of an object is encoded with regard to the body of the observer, or relevant body parts. For instance, the egocentric frame might be used for cognitive target localization or for goal directed movements. Depending on the task, this egocentric frame of reference could be centered either on the head (Karn et al. 1997), on the trunk (Darling and Miller 1995), or on the shoulder (Soechting et al. 1990). The egocentric frame of reference is defined by three axes. The orientation of the first axis relies on the "idiotropic vector" which is defined by Mittelstaedt (1983) as the person's own longitudinal Z-axis. While standing, this egocentric reference is aligned with gravity. The second axis of the egocentric coordinate system corresponds to the straight-ahead direction (Jeannerod 1988), that is, the direction where an individual feels the body midline would project in front of him. Thus, the plane defined by the first and second axes would divide the extra personal space into a right and a left sector. The third axis defining the egocentric frame of reference is constrained by the two former previously defined axes. The plane defined by the first and the third axis segments the space into a front and a back sector. When coded in a head-centered frame of reference, egocentric localization of visual objects needs to take into account retinal and eye position signals. In addition, neck proprioceptive and vestibular signals (leading to head position coding) make an important contribution to target localization relative to the whole body (Blouin et al. 1995; Maurer et al. 1997; for a review see Desmurget et al. 1998). Indeed, all these previous studies have shown useful sensory interaction leading to relative accuracy in localization tasks despite vestibular and/or neck stimulation. Nevertheless, Mergner et al. (2001) showed mislocalization of the presented targets under specific conditions (low-frequency vestibular stimulation). Similarly, the accuracy of memorized visual target localization when the head is free to move decreases when the head rotations of subjects are extreme (Fookson et al. 1994). It seems that extreme head rotations induce a shift of the internal representation of the space through the visual canal. These results reveal the clear interaction between eye and head-position signals (Lewald and Ehrenstein 2000) and suggest that sensory interactions are not sufficient for accurate localization under some specific conditions.

Thus, as the head is exposed to inertial forces (Coriolis and centrifugal forces), one may ask whether changes in head position (or in the perception of head position) could affect the accuracy of egocentric localization of visual objects in a perturbed gravitoinertial force field. The aim of this study was first to investigate the accuracy of egocentric localization of memorized visual targets in a perturbed gravitoinertial force field and, second, to test the specific role of head position on localization accuracy, because of its possible influence on the orientation of the egocentric frame of reference. Finally, this study investigated whether errors in pointing when exposed to gravitoinertial forces were, at least partly, attributable to localization errors.

Materials and methods

Subjects

Ten subjects (four women and six men; age range 18–35 years) gave informed consent to participate in this study, which was pre-approved by the local ethics committee. Subjects showed no apparent vestibular deficiency and reported no known sensory-motor disease.

Experimental set-up

Figure 1 schematically represents the experimental set-up. Subjects were tangentially seated on a rotating platform at 70 cm from the center of rotation. The platform was brought to a counter clockwise rotation with constant angular velocity of 120° s^{-1}. This angular velocity was reached in 110 s. The mean angular acceleration magnitude was 0.9° s^{-2}, linearly decreasing from 1.96° s^{-2} at t=0 to 0° s^{-2} at t=110. This value is above all the vestibular canal threshold values found in the literature (for example, see Bringoux et al. 2002). At this speed, the direction of the gravitoinertial vector (Gi) was significantly changed (17.38°) but not the amplitude (1.05 G). A four-points safety belt was used to prevent any movement of the body relative to the chair during rotation.

Fifteen red light-emitting diodes (LED) were arranged horizontally along the arc of a circle at eye-level in front of the subject (at 70 cm). One LED (central diode) was centered on the cyclopean eye of the seated subject, seven LEDs were positioned at equal intervals on either side of this central LED. The LEDs were separated from each

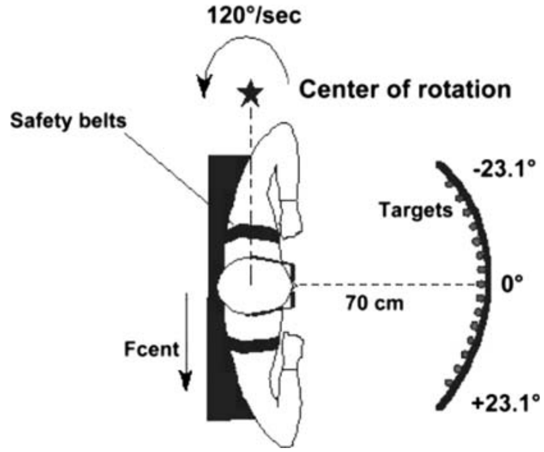

Fig. 1 Schematic representation (top view) of the experimental setup with *Fcent* corresponding to the direction of the centrifugal force during the rotation of the platform

other by 4 cm (3.3° from the subject's view point). There were no instructions about eye position before or during the trials.

The experiment was performed in complete darkness. In addition, subjects wore filtering glasses to be sure that no visual information (except the flashed targets) was available.

In one session, head position on trunk was recorded along the three axes of rotation using a magnetic position tracker system (Polhemus Fastrak) which had been previously tested in situ in order to check for possible distortion induced by metal. The calibration procedure showed no distortion of the working space. The Fastrak sensor was fixed on the subject's head at 50 cm from the emitting source (sampling frequency 120 Hz) which was fixed on the rotating platform. Yaw angle corresponds to rotation along the head longitudinal axis relative to the body sagittal plane. Negative values represent head rotation toward the left (i.e. toward the center of rotation). Roll angle corresponds to rotation along the head antero-posterior axis relative to sagittal plane. Negative values correspond to left-ear-down rotation (i.e. toward the center of rotation). Pitch angle corresponds to rotation along the head sagittal axis relative to the horizontal plane. Negative values are given to forward tilt. Preliminary inspection of the data showed that rotation of the platform did not induce a shift of head position in pitch (confirmed by Sarès et al. 2002). Therefore, pitch angles were not included in the body of the results or in the discussion section. Moreover, after the completion of the experiment subjects reported systematically head roll rotation but not systematically any head yaw rotation and clearly no head pitch rotation.

Procedure

Subjects were required to report verbally the spatial egocentric localization of visual targets flashed for 200 ms. Responses consisted in giving both the direction of the flashed target (that is by saying central, to the left or to the right relative to the subjective straight ahead direction) and the eccentricity of the presented target (that is the distance in centimeters separating the target from the subjective visual straight ahead). Subjects began the trials by mean of a small trigger, such that no time limit was imposed for the response. In general, subjects were able to complete the task in less than 5 s.

Two experimental sessions (called head-fixed and head-free) were conducted on different days. Each session was preceded by a training session (composed of 30 trials), which allowed subjects to be familiar with the localization task without any rotation of the platform. During the training session, the experimenter gave a feed-back on the results of every second trial (that is the exact position of the presented target). At the end of the training session, all subjects were able to determine the spatial localization of the presented targets with great accuracy.

The head-fixed session was performed with the head kept aligned with the trunk. The back of the head was leaned on a head-rest. The subject's head was stabilized against this head-rest by means of two screws, the end of which was covered with hard rubber cap, which pressed firmly against the forehead.

The head-free session was performed with the head unrestrained so that the direction of head and trunk could be dissociated. No specific head position was imposed on the subjects. The only recommendations given to the subjects were that they should have a comfortable head position and should limit rapid head movements during platform rotation to prevent any motion sickness provoked by Coriolis cross-coupling stimulation (e.g. Woodman and Griffin 1997).

The order of presentation of the experimental sessions (head-fixed or head-free) was counterbalanced across the subjects. Each experimental session was performed under three conditions of rotation of the platform: before rotation (PRE-), during rotation (PER-), and after rotation (POST-) of the platform. In the PER-rotation condition subjects were required to start the first trial 1 min after the platform reached constant velocity in order to eliminate undesirable effects of vestibular nystagmus. Indeed, the time constant of the semi-circular canal nerve afferents in response to constant speed rotation is 2 to 6 s (see Goldberg and Fernandez 1984 for references). Therefore, nystagmus has been found to decay with a time constant of 15–20 s for the horizontal canals (see Young 1984 for references), hence one minute of rest at constant velocity should be sufficient to ensure the disappearance of the vestibulo-ocular reflex. Moreover, after one minute of rest the subjects were asked whether either eye and/or body motion was perceived to ensure a static illusory situation. For similar reasons, the POST-rotation condition was started 1 min after the end of the rotation. Each target was presented five times for a total of 75 trials per condition of rotation and 225 trials per experimental session. The order of presentation of the target was randomly selected.

Data analysis

Before any further analysis, data in centimeters were transformed into degrees. The main variable computed to determine the influence of the inertial forces and head position on target spatial localization was the error in localizing the position of the presented target. To compute error, the actual position of the presented target was subtracted from the reported position of the target. Positive values correspond to a shift of the perceived position to the right (in the direction of the centrifugal force) and negative values correspond to a shift of the perceived position to the left (toward the axis of rotation). Moreover, standard deviations (*SD*) of the mean responses were computed in order to analyze variability of the responses according to the different rotation and head position conditions.

The subjective visual straight-ahead (VSA) constitutes a relevant psychophysical variable for measuring perception of spatial orientation (Jeannerod 1988). A shift of straight ahead direction leads inevitably to localization errors but not reciprocally. Indeed, localization errors might in certain cases not be due to a change in VSA. They could be due do a decrease in accuracy, or to a remapping (imagine you wearing magnifying lenses: straight-ahead is not affected while lateral object localization is). For instance, studies on the egocentric reference frame in neglect patients (Farne et al. 1998; Cusack et al. 2001) clearly report no systematic change of subjective midline in these patients, yet they committed errors in target localization. Consequently, a mathematical analysis was performed on the localization data in order to deduce the subjective straight ahead direction used by the subjects as a reference for their responses. For such analysis, a score of 0 was attributed to the target perceived on the left, a score of 0.5 for the target perceived on center and a score of 1 for the target perceived on the right. The mean probability for each target to be perceived to the right (P=1) was pooled depending on each condition of rotation and each session. A non-linear regression function (Probit function) was then used to match the probability 0.5 to a subjective target which represents the subjective straight-ahead direction (C_0). The psychometric function was expressed as Eq. (1)[2]:

$$P_i = 1/\left(1 + \left(C_{(i,j)}/C_0\right)^n\right) \tag{1}$$

Localization errors, SD and VSA were submitted to three conditions (PRE, PER, POST-rotation)×two sessions (head-fixed, head-free) univariate analyses of variance (ANOVA) with repeated measures on all factors. Specific effects were tested with post-hoc tests (Newman Keuls, P<0.05). Head position data were submitted to three conditions (PRE, PER, POST-rotation) analyses of variance (ANOVA) with repeated measures on all factors.

[2] Equation 1 is the Probit function used to evaluate the VSA. Variables: P_i=probability for the ith target to be perceived to the right, i=target number, j=trial number; Parameters: C_0=target for P=0.5, n=power of the effect

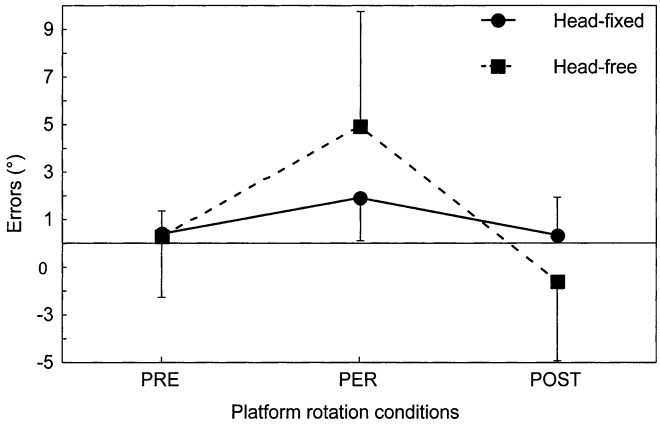

Fig. 2 Mean errors and *SD* in the localization task in both sessions (head-fixed and head-free) during each rotation condition (PRE-, PER-, and POST-rotation), with positive values corresponding to deviations to the right and negative values corresponding to deviations to the left

Results

Errors in localizing targets

The ANOVA yielded a significant interaction (rotation×session) on the errors in localizing the presented targets ($F_{(2,18)}=10.42$, $P<0.001$; Fig. 2). Post-hoc test revealed a significant shift of localization to the right (that is in the direction of the inertial forces) during the rotation of the platform for both head-fixed and head-free sessions compared with the PRE and POST-rotation conditions. This shift was greater during the head-free session than in the head-fixed session (on average 4.91° and 1.92°, respectively). On the other hand, subjects showed a similar high level of accuracy in determining target position during PRE and POST-rotation conditions (on average −0.13°).

To compare the level of constancy of the responses in the different conditions, within-subject variability was analyzed. The ANOVA yielded also a main effect of rotation on the variability of the localization task ($F_{(2,18)}=7.76$, $P<0.01$, Fig. 3a). Post-hoc test revealed that the variability of the responses was higher during PER-rotation (on average ±4.26°) than during PRE (on average ±3.32°). In addition, results showed that the variability was greater in the head-free session (on average ±4.25°) than in the head-fixed session (on average ±3.49°) ($F_{(1,9)}=7.59$, $P<0.05$).

Head position during the head-free session

Subjects perceived the targets as being shifted to a greater extent in the direction of the inertial forces when their head was free to move than when it was kept aligned with the trunk. The different level of accuracy in the head-fixed and head-free sessions could be due to head rotation when the platform was rotating. As mentioned in the experimental set-up section, results of pitch angle are not presented.

Head yaw angle

The ANOVA showed a main effect of rotation on head tilt in yaw ($F_{(2,18)}=18.63$, $P<0.001$). Subjects turned their head to the left (toward the center of rotation) during PER-rotation (on average −7.2°), whereas, they kept it quite straight during PRE and POST-rotation conditions (on average −0.72°). Post-hoc analysis showed that head yaw position was similar in both conditions performed without platform rotation ($P>0.05$).

Head roll angle

The ANOVA showed a main effect of rotation on head tilt in roll ($F_{(2,18)}=7.3$, $P<0.05$). Left-ear-down rotation of the head during platform rotation was significantly greater

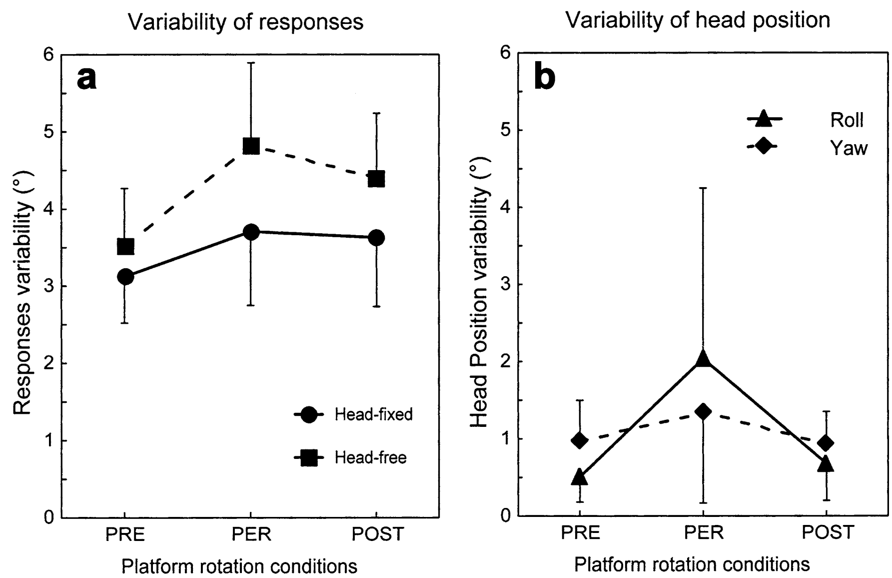

Fig. 3 **a** Within-subjects variability of the responses in the localization task during each rotation condition (PRE-, PER-, and POST-rotation). **b** Within-subjects variability of the head position in yaw and roll during each rotation condition (PRE-, PER-, and POST-rotation)

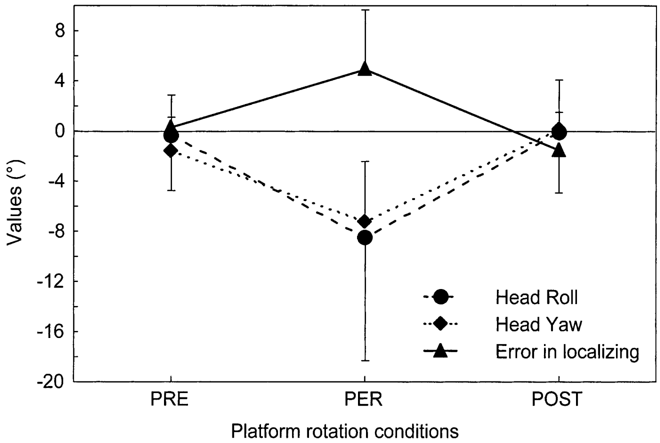

Fig. 4 Mean head positions and *SD* in yaw and roll with respect to the perceived target location for all three rotation conditions. The positive values correspond to deviations to the right and negative values correspond to deviations to the left

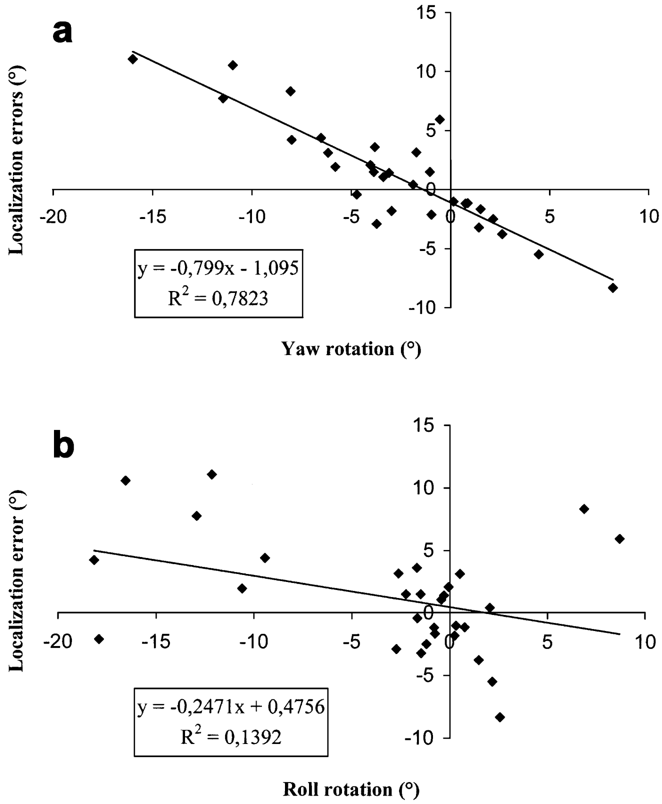

Fig. 5 Head rotation in yaw (**a**) and roll (**b**) as a function of the mean error of localization during the head-free session for PRE-, PER-, and POST-rotation conditions for all subjects

(on average, −8.5°) than during PRE and POST-rotation (on average, −0.21°; $P<0.05$). The post-hoc test showed no significant difference between the two conditions performed without rotation of the platform ($P>0.05$).

Thus, the data from the head-free session showed that subjects actively moved their head in order to partly align the head axis with the gravitoinertial vector.

Figure 4 represents the mean head position (yaw and roll) and the mean errors in localizing the targets when subjects provided their verbal estimates of target position as a function of the platform rotation. Visual inspection of the results reveals a strong inverse relationship between errors in the localization task and head rotation in roll and yaw. Indeed, while the head was actively tilted (−8.5°) and turned to the left during platform rotation (−7.2°), subjects made target localization errors to the right (4.91°), which is in the opposite direction of head rotation. This corresponds to an increase of the error by 2.99° relative to the head-fixed session, which is roughly a third of the head angle relative to the target plane. Furthermore, when rotation of the platform stopped, the head was re-aligned with the trunk (roll: −0.08° and yaw: 0.14°) and subjects achieved a high accuracy level in localizing the targets (POST-rotation: 0.35° similar to the level of the PRE-rotation condition: 0.41°).

Localization errors versus head rotation

Figure 5 the observed localization errors are plotted against the head yaw (5a) and roll (5b) rotation in the Head-free session. The data were fitted well by a linear regression for head yaw rotation (R^2=0.78) but not for head roll rotation (R^2=0.14). This suggests that localization responses were at least partly inversely proportional to head yaw rotation but not significantly correlated to head roll rotation.

Because target mislocalization during modified gravitoinertial force background was also observed in the head-fixed condition, the change in targets position perception could not be only due to head movements in the head-free session. Therefore, mislocalization might also result from a possible shift of the egocentric reference frame. As a consequence, we were particularly interested to see whether VSA changed with the experimental conditions.

Evaluation of the visual straight-ahead (VSA)

As presented above (Eq. 1), we computed the VSA during both experimental sessions. Statistical analyses were performed to test whether the different experimental conditions had an effect on the C_0 factor representing the subjective VSA direction. The ANOVA revealed a significant interaction (rotation×session) on the subjective VSA direction ($F(2,18)=14.90$, $P<0.001$) (Fig. 6). The post-hoc test revealed a significant shift of VSA to the left (that is in the direction of the head rotation) during the rotation of the platform for both head-free and head-fixed sessions with a greater shift when the head was not restrained than during head-fixed session (on average −8.81° and −3.41°, respectively). However, VSA direction was almost aligned with the actual straight ahead direction in PRE and POST-rotation conditions, irrespective of whether or not the head was fixed or free to move (on average −0.74° and 0.63°, respectively). It seems that rotation of the platform induced a shift in the perception of

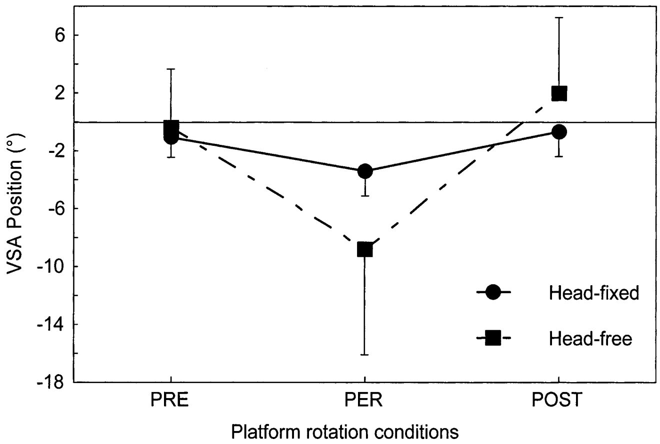

Fig. 6 Mean position and *SD* of the visual straight ahead (*VSA*) with respect to the rotation conditions (PRE-, PER-, and POST-rotation) for both sessions (head-fixed and head-free)

the VSA, which was opposite to the direction of the centrifugal force and to the direction of the errors in localizing the visual memorized targets.

Discussion

The goal of this study was to investigate the accuracy with which subjects perceived target position in a perturbed gravitoinertial force field. Furthermore, as head position was submitted to the mechanical influence of the centrifugal force, we also investigated the effect of head position on the accuracy of the localization task.

During platform rotation (PER-rotation), subjects exhibited a significant shift of target localization towards the direction of the inertial force whatever the head session (head-fixed or head-free). This deviation might result from variations in the perceived distance between the body and the flashed targets along the experiment. However, the lack of statistical difference of localization performance between PRE and POST-rotation indicates that a potential drift of the perceived target location over the time course of the whole experiment is not present. Consequently, we need to consider other sources of error. One possibility could be the interaction between the otolith signal (informing subjects about orientation and amplitude of the gravitoinertial force vector) with neck and tactile afferents. Actually, even though their body was firmly fixed on the chair, all subjects reported a strong sensation of body tilt in the direction of the inertial force during rotation of the platform. This sensation is known as the somatogravic illusion (Clement et al. 2001; Cohen 1977) and was experienced during both head sessions. The CNS cannot distinguish between the sensory activation which arises from centrifugal forces from that arising from gravitational forces. This leads to the perception of the gravitoinertial force vector as the earth vertical axis. This perception is coherent with both the pressure information provided by the body support and the neck proprioceptive information resulting in a body orientation being perceived as tilted to the right. Considering that the subject's body and head were firmly attached to the chair holding the targets presentation board, from a purely egocentric point of view, there is no reason for the subjects to mislocalize the targets, relative to their body. Thus such perceived body orientation, in the rotating frame of reference, which is different from the actual position of the body in space in the Earth-fixed, Galilean referential, could not alone be the origin of the perceptual errors observed.

To better explain the shift of target localization to the direction opposite to the gravitoinertial force vector we rather propose the following interpretation. According to the sensation of a body tilt in the direction of the inertial force, the subject might code target location in a reference frame aligned with the perceived gravitoinertial vector (interpreted as the earth vertical axis) leading to a shift of the subjective straight ahead in the opposite direction to the inertial force. Such an interpretation implies that the orientation of the "egocentric" reference frame (as assessed by the VSA measurement) is influenced by the gravitational vector and by the idiotropic vector, and thus cannot be defined as purely egocentric.

To test this hypothesis, the direction of the VSA in each rotation condition was deduced from the localization data. The direction of the subjective VSA was almost aligned with the actual VSA in PRE- and POST-condition of rotation whatever the head position. Thus, there was no drift of the VSA direction over the time course of the experiment. During the PER-condition of rotation, the significant shift of the VSA in the direction opposite to the inertial forces clearly shows that the "egocentric" frame of reference is unexpectedly affected by gravitoinertial forces and thus is in some way linked to geocentric cues. We propose that the subjects localized the targets in a mixed reference frame (Bringoux et al. 2003), not really egocentric nor geocentric, the origin being attached to the body while the axes are influenced by both corporal and inertial cues.

Moreover, subjects exhibited greater errors (PER-rotation) with greater variability (PRE-, PER-, and POST-rotation) in their responses when their head was free to move than when it was fixed. One explanation could be a decrease in the accuracy of the perceived head position. The increase of head-position variability observed during platform rotation, approximately matched the increase in variability in the verbal estimates of target position when the head was free to move (Figs. 3a and 3b). Thus, the lower reliability of the localization responses could be due to less accurate head coding. Moreover, inaccuracy of head coding might be amplified in a perturbed gravitoinertial force field because of the modification of the proprioceptive signals (Sarès et al. 2004). Hence, the shift in the perceived target location could therefore partly result from misperception of body in space position and also from misperception of head position.

Such deviation was concomitant with a larger shift of the VSA in the direction opposite to the inertial force. A possible shift of the egocentric frame of reference so as to be aligned with the gravitoinertial vector could have modified the orientation of the two other reference axes of the egocentric frame of reference. This would consequently lead to a shift of the straight ahead reference in the direction opposite to the inertial forces (as we have observed) responsible for a shifted perception of the visual targets in the direction of the inertial force (as we have observed).

If one considers that subjects coded target location in a head-centered reference frame, one could argue that the shift of target localization, when the head was turned, should be at least proportional to the amplitude of the head rotation (R^2=0.78, Fig. 5a). However, it has to be noted that the extra shift of the perceived target localization (difference between the errors in the head-fixed and head-free sessions is 2.99°) was smaller than the head rotation itself (7.2° of head yaw rotation). This means that a non-negligible part of head rotation is compensated for, or more probably that the straight-ahead direction depends not only on head orientation but also on body orientation (Soechting et al. 1990). Nevertheless, the contribution of head rotation to the localization errors might follow from reduced accuracy in the perception of head position. Indeed, increased activity in muscle spindle afferents during exposure to a modified gravitoinertial force level (Fisk et al. 1993) would have led to misperception of head position (under-estimation of head rotation) inducing an erroneous perception of target position as we observed in our study. This is supported by the increase in the variability of the responses when the head was free to move than when it was fixed (Fig. 3b). Object localization with respect to the head was found to be affected by an erroneous perception of the head rotation (Maurer et al. 1997). This point of view is in accordance with that of Fookson et al. (1994) who analyzed azimuth errors in pointing to remembered targets under extreme head rotation. They showed that the space representation shifted in the opposite direction to head rotation in yaw, as observed in our study. This shift was attributed to influences from the neck muscle proprioceptors, which indicate changes in the head position on the trunk, rather than to vestibular reaction indicating movements of the head in space. The influence of neck proprioception on the straight ahead direction has been confirmed in studies using vibration of the neck muscles (Karnath et al. 1994). The effects on the VSA seem to be similar to those elicited by an actual rotation of the head (Biguer et al. 1984). Such interpretation seems to correspond to our observations, because the head was not only tilted in roll but also turned in yaw toward the center of rotation (to the left). This rotation in yaw might have partly induced the observed mislocalization of the memorized visual target, due to a shift of the VSA direction.

In conclusion, varying the orientation of the gravitoinertial force background led to a shift in localizing memorized visual targets. Moreover, this study argued in favor of target mislocalization as one origin of pointing errors observed in modified gravitoinertial force fields. Indeed, previous results (Bourdin et al. 2002) have shown that the magnitude of the shift of localization accurately matched the magnitude of pointing errors we observed in a correlated experiment under similar conditions. Furthermore, the shift of perceived target location increased when the head was free to move, giving some evidence of misperception of head position from neck proprioceptive afferent during gravitoinertial changes. On the other hand, the observed straight ahead deviation, even if the head was firmly restrained, leads us to consider that the orientation of the egocentric reference frame was influenced by geocentric cues (i.e. the gravitoinertial vector). This leads us to hypothesize that egocentric localization in poor visual environment is based on an internal representation of the world elaborated on the perceived orientation of the gravitational force, that is a mixed egocentric and geocentric frame of reference. More specifically, a mixed egocentric and geocentric frame of reference would be a frame of reference centered on the body (on the head in this particular task), with one axis depending on gravity and on the body's longitudinal *Z*-axis (Bringoux et al. 2003). One other hypothesis highlights the occurrence of ocular torsion in order to align the eye meridian axis with the gravitoinertial vector (McDougall et al. 1999; Moore et al. 2001). A shift in the perception of the target location might occur if the CNS did not take into account the whole torsion (through efference copy or extra-ocular proprioception), leading to a discrepancy between the perceived and the actual position of the eyes. However, we did not analyze the ocular movements. Further experiments have to be done to test this hypothesis.

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