Exp Brain Res
DOI 10.1007/s00221-011-2884-8

RESEARCH ARTICLE

Spatial localization investigated by continuous pointing during visual and gravitoinertial changes

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Received: 1 June 2011 / Accepted: 17 September 2011

Abstract In order to accurately localize an object, human observers must integrate multiple sensory cues related to the environment and/or to the body. Such multisensory integration must be repeated over time, so that spatial localization is constantly updated according to environmental changes. In the present experimental study, we examined the multisensory integration processes underlying spatial updating by investigating how gradual modifications of gravitoinertial cues (i.e., somatosensory and vestibular cues) and visual cues affect target localization skills. These were assessed by using a continuous pointing task toward a body-fixed visual target. The "single" rotation of the gravitoinertial vector (produced by off-axis centrifugation) resulted in downward pointing errors, which likely were related to a combination of oculogravic and somatogravic illusions. The "single" downward pitch rotation of the visual background produced an elevation of the arm relative to the visual target, suggesting that the rotation of the visual background caused an illusory target elevation (induced-motion phenomenon). Strikingly, the errors observed during the "combined" rotation of the visual background and of the gravitoinertial vector appeared as a linear combination of the errors independently observed during "single" rotations. In other words, the centrifugation effect on target localization was reduced by the visual background rotation. The observed linear combination indicates that the weights of visual and gravitoinertial cues were similar and remained constant throughout the stimulation.

Keywords Target localization · Multisensory integration · Continuous pointing · Visual cues · Vestibular cues · Somatosensory cues

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Introduction

The spatial localization of an object relies on the integration of multiple sensory cues available to the observer. In daily life, the environment and the observer are rarely static. In this context, localizing an object requires a continuous updating of its position based on motion cues about the body and the environment. Such updating mainly relies on sensory cues such as vestibular and somatosensory cues, here referred to as gravitoinertial (**Gi**) cues, and visual cues. In the present study, we examined the multisensory integration processes underlying spatial updating by investigating how environmental changes (i.e., experimental manipulations of both visual and **Gi** cues) affect target localization, as assessed through a continuous pointing task.

In changing visual surroundings, the invariant properties of gravity constitute a relevant reference for spatial localization (Howard 1982; McIntyre et al. 1998; Mittelstaedt 1983; Pozzo et al. 1998). However, it is well known that a modification of the **Gi** environment (e.g., in weightlessness or during linear acceleration) impairs object localization (for a review, Lackner and DiZio 2004). Specifically, during a forward linear acceleration such as that produced by off-axis centrifugation, a false sensation of object elevation usually happens (i.e., the oculogravic illusion, Clark and Graybiel 1951). This perceptual illusion has been mostly explained as a consequence of the lowering of the visual horizon, considered as a main reference for the judgment of objects' height (Cohen et al. 2001; Graybiel 1952). At the same time, when the observer has to reach the perceived object during centrifugation, he/she is submitted to an illusory perception of body tilt (i.e., the somatogravic illusion, Graybiel 1952), which may lead to compensatory arm responses. In addition, a perceptual drift of the arm position relative to the body could influence pointing movements toward the perceived object during centrifugation (Bourdin et al. 2006). Hence, multiple and complex factors appear to be at work while pointing toward a visual target in a modified **Gi** environment.

Some studies investigated whether adding visual cues could attenuate the behavioral consequences of **Gi** modifications upon spatial localization. Such attenuation was found by adding visual information relative to the physical horizon or by using optic flow to induce an antero-posterior displacement (Eriksson et al. 2008; Lessard et al. 2000; Tokumaru et al. 1998). Although de Graaf et al. (1998) have already tested the effectiveness of rotating the visual scene in order to reduce the somatogravic illusion, the effect of moving visual cues on target localization during centrifugation has never been investigated, to our knowledge. This may, however, constitute a promising way of investigation since it is well established that, in a non-modified **Gi** environment, moving the visual background strongly influences target localization (i.e., induced-motion illusion, Duncker 1929; Post et al. 2008). Specifically, when a static visual target is presented, a moving visual background usually produces an illusory perception of target motion, in a direction opposite to the background motion, while the visual background is perceived static.

The purpose of the present study was to investigate how continuous and synchronized visual and **Gi** changes affect the spatial localization of a body-fixed visual target. To that aim, the visual background and/or the **Gi** vector were gradually rotated during a continuous pointing task. We assumed that a continuous pointing task, already used by Siegle et al. (2009) and Bresciani et al. (2002), allows the continuous inference of the target localization process. Besides, this task allows a better understanding of multisensory integration processes involved in spatial localization. Based on recent suggestions that sustained weights are attributed to the different sensory modalities available to the observer (Barnett-Cowan and Harris 2008; Bourrelly et al. 2010; Bringoux et al. 2008), we hypothesized that despite gradual modifications of visual and **Gi** stimuli, the weight attributed to visual and **Gi** cues would be preserved when both stimuli are simultaneously presented. With respect to how visual and **Gi** cues would be combined, several studies have shown that various sensory cues are integrated in a manner consistent with a weighted linear combination of the responses obtained with individual cues (for a review, Angelaki et al. 2009). We thus hypothesized that the pointing errors observed during the combined manipulation of visual and **Gi** cues would correspond to the linear combination of the visual influence (i.e., target elevation due to the "induced-motion" illusion) and the **Gi** influence (i.e., mainly issued from the coupled somatogravic and oculogravic illusions).

Methods

Participants

Seventeen right-handed subjects (9 men and 8 women; mean age ± SD: 25.2 ± 4.0 years) participated in this experiment. They reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. All gave informed consent prior to the study, in accordance with the local ethics committee and the 1964 Declaration of Helsinki.

Apparatus

As illustrated in Fig. 1, subjects sat on a bucket seat fixed to a rotating platform. They were positioned off-axis, facing the platform center, with their inner ear radially positioned 1.90 m away from the rotation axis. A four-point safety belt was used to prevent subjects' trunk displacement. Clockwise centrifugation was servo-controlled to fit a pattern of angular velocity increasing linearly from 0° to 120° s^{-1} in 30 s (Fig. 2). During the platform rotation, centrifugal force ($\vec{c}$) was added to gravitational force ($\vec{g}$), producing a non-linear rotation of the **Gi** vector.[1]

A 3D head-mounted display (HMD, 3D Cybermind hi-Res900®, Cybermind Interactive Nederland, The Netherlands; resolution: 800 × 600 pixels; field of view: 31.2° diagonal for each eye) was used to display a stereoscopic visual background. The HMD was fixed to the adjustable headrest used to prevent head motion. Customized software was used to create a visual background composed of an octagonal 3D prismatic structure that reinforced horizontal and vertical reference lines (Fig. 1). A pink virtual target of 1 cm in diameter was projected at the center of the visual background and was always static relative to the observer. Nevertheless, subjects were not informed that the target was static and positioned at the center of the visual screen. The visual background and target appeared at 1.5 and .8 m from eye position, respectively. It should be noted that the HMD device prevented subjects from having visual

[1] $\text{Gi\_angle} = a\tan\left(\frac{\vec{c}}{\vec{g}}\right)$

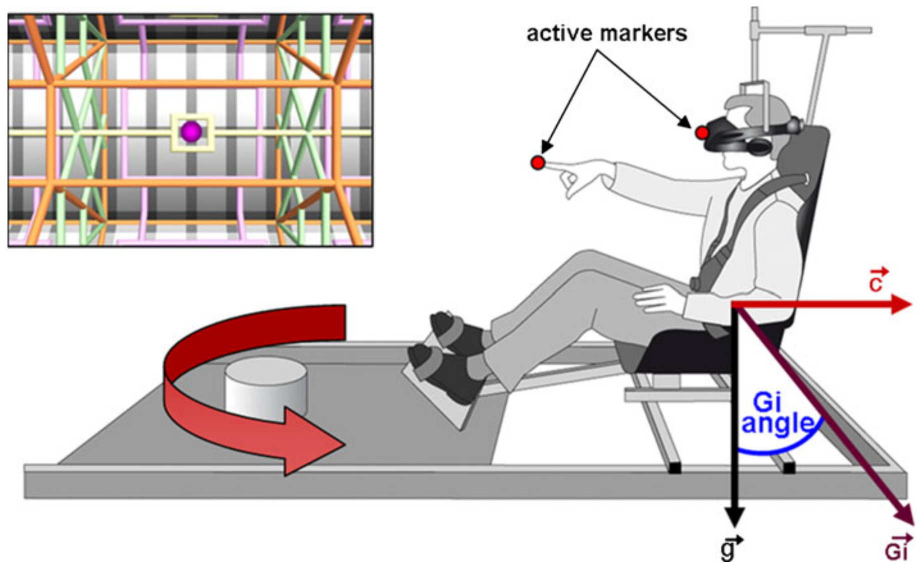

Fig. 1 Experimental setup. Subjects wore a head-mounted display showing a central body-fixed target and, for most conditions, a structured background as illustrated in the *upper-left panel*. The platform could rotate and thus modify the **Gi** angle relative to the vertical. *Dots* on the hand and head represent active markers for data acquisition. **c** Centrifugal force, **G** gravitational force, **Gi** gravitoinertial force

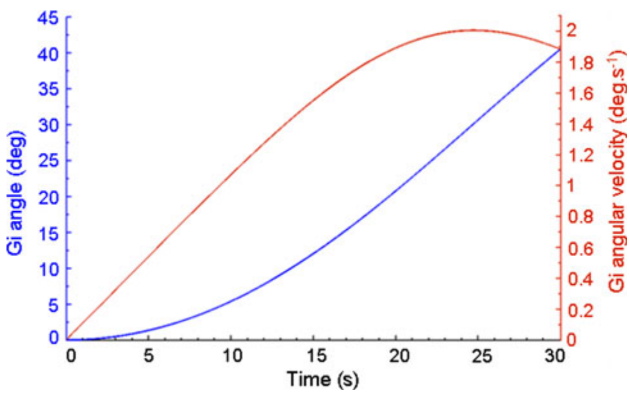

Fig. 2 **Gi** angle (*higher curve*) and angular velocity (*lower curve*) modifications during the centrifugal platform rotation from 0 to 120° s^{-1} in 30 s

feedback about the experimental setup and about their current arm location.

Infrared active markers were placed on the right index fingertip and at the cyclopean eye location on the HMD. These locations were sampled at 200 Hz using an optical motion tracking system (Codamotion Cx1®, Charnwood Dynamics Ltd, Leicestershire, UK; accuracy: .05 mm). A real-time acquisition system (ADwin-Pro®, Jäger, Lorsch, Germany) driven by customized software was used to control visual background and **Gi** vector rotations and to collect data.

Procedure

Throughout the experimental trials, subjects were required to maintain their gaze on the virtual target and to point as accurately as possible toward the virtual target with their right index finger, arm outstretched. All participants were rotated once before the beginning of the experiment, in order to familiarize them with centrifugation effects.

During the experiment, we manipulated the **Gi** and/or the visual background pitch rotation in 5 experimental conditions (Fig. 3). The **GI** condition involved a centrifugation (causing **Gi** vector rotation) without visual background. The **GI–Vis^{F}** condition replicated the **GI** condition with an additional structured **Vis**ual background, which was **F**ixed relative to the observer and presented throughout the centrifugation. The **Vis^{R}** condition involved a **R**otation of the **Vis**ual background without centrifugation. **GI**, **GI–Vis^{F}** and **Vis^{R}** conditions were the so-called single conditions. Kinematics of the visual background rotation was the same as those of the **Gi** vector rotation (Fig. 2), and the rotation was performed in the same pitch downward direction. The **GI–Vis^{R}** condition involved both **Gi** vector and **Vis**ual background **R**otations. In this so-called combined condition, the rotations of the visual background and **Gi** vector were synchronized.

Before each trial, subjects had to place their right index finger at the starting position, indicated with a standardized tactile mark on the right leg. A trial began with the appearance of the visual target accompanied by the static visual background, except in the **GI** condition. A concomitant auditory signal prompted the participant to point toward the target and to keep the index finger on its perceived location until the end of the trial. Seven seconds after the auditory signal, the visual background and/or the **Gi** vector could be rotated with an increasing velocity during 30 s (Fig. 2). A second auditory signal and the suppression of visual cues (i.e., the HMD screen became black) indicated the end of the trial, prompting subjects to bring their arm back on the tactile mark. In the conditions including centrifugation, a deceleration phase began,

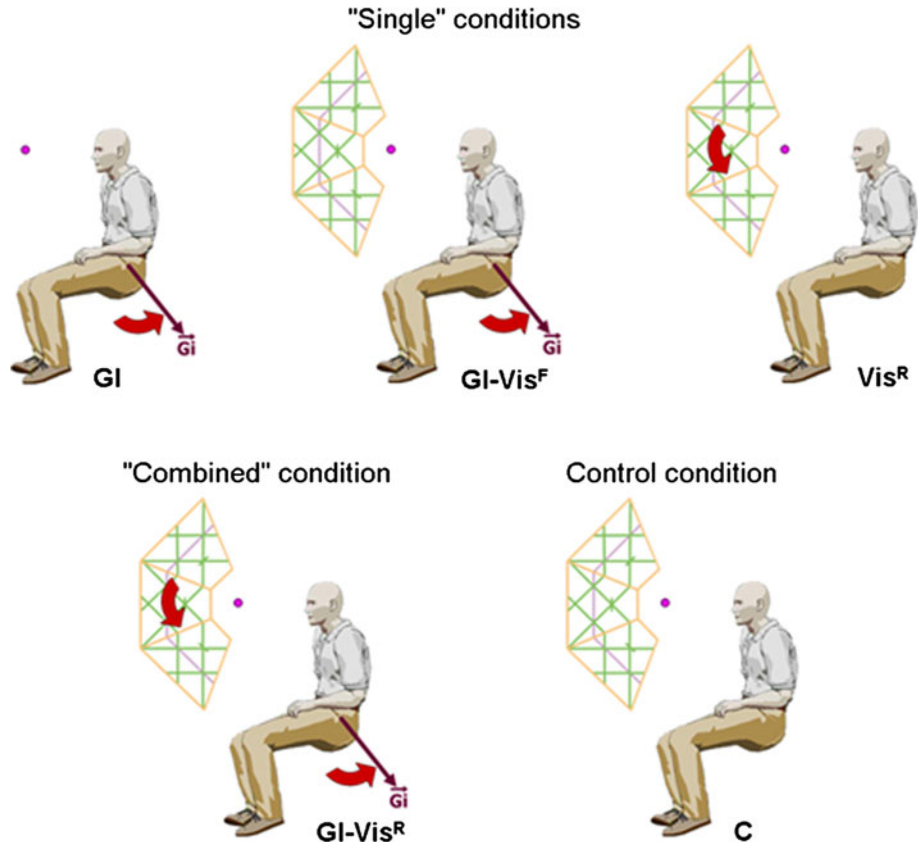

Fig. 3 Experimental conditions. **GI** **Gi** vector rotation without visual background. **GI–Vis^F** **Gi** vector rotation with fixed visual background. **Vis^R** visual background rotation without **Gi** vector rotation. **GI–Vis^R** **Gi** vector and visual background rotation. **C** fixed visual background without **Gi** vector rotation. *Arrows* represent the rotation of the visual background and the **Gi** vector. The target, presented at eye level, always remained fixed relative to the observer

following a profile inverse to the acceleration phase. A 30-s period of rest was finally allowed before the next trial started. This resting period allowed for the suppression of post-rotational effects due to semi-circular canal stimulation (Benson 1990), and limited possible fatigue or motion sickness.

All 17 subjects performed 4 trials in each of the 4 aforementioned conditions. The experimental session thus consisted of 16 trials presented in a pseudo-random, counterbalanced order. Following these 16 trials, a control trial of an equivalent duration was presented and involved a fixed visual background without centrifugation (Fig. 3). This **C** control condition was used as a baseline for comparison analyses. The complete experimental session lasted approximately 1 h.

Data processing

Data were first low pass, Butterworth-filtered (cut-off frequency: 10 Hz; order: 2). Angular errors of continuous pointing in the sagittal plane were analyzed from the beginning of the trial to the end of the visual background and/or **Gi** vector rotation (i.e., $t = 30$ s; see Fig. 2). For each trial, the markers on the cyclopean eye and the right index indicated the angle between the pointing finger and eye level. Pointing errors were determined by referring the current pointing angle to the initial angle reached prior to any rotation (i.e., $t = 0$ s).

Statistical comparisons were made on the means and standard deviations of pointing errors for all experimental conditions. To that aim, we used analyses of variance (ANOVAs) with repeated measures and post hoc tests (Newman–Keuls) or t tests for dependant samples. The effect size ($\eta^2 p$) and the power ($1 - \beta$) of each test were provided.

Multiple linear regression analyses were performed on the mean pointing errors (i.e., the between-subjects mean) and individual pointing errors (i.e., the within-subject mean of the 4 trials per condition) observed in the **GI–Vis^R** condition. Based on the least squares method, these analyses were achieved to find a model that could better predict the data obtained in the "combined" condition with the "single" conditions as predictors. The coefficient of determination (R^2) was used to determine the quality of fit of the multiple linear regressions on the mean pointing errors in the **GI–Vis^R** condition. The predictive power of the models was estimated by the calculation of the root mean square error (RMSE) on individual pointing errors. RMSE evaluates the differences between predicted and observed pointing errors, lower values of RMSE indicating a better fit. The level of significance was .05 for all analyses.

Results

Final pointing errors

For each participant, the rotation of the **Gi** vector or of the visual background affected final pointing accuracy (assessed at $t = 30$ s). Figures 4 and 5 show that even though the target always remained stationary, the rotation of the visual background (**Vis^R** condition) yielded an upward shift of the pointing response (**Vis^R** mean = +1.9°), whereas the rotation of **Gi** vector (**GI** and **GI–Vis^F** conditions) yielded errors in the opposite, downward direction (**GI** mean = −2.4°; **GI–Vis^F** mean = −2.0°). Strikingly, when the **Gi** vector and the visual background were synchronously rotated, pointing accuracy was not substantially affected (**GI–Vis^R** mean = +.1°) compared with the control condition (**C** mean = −.4°).

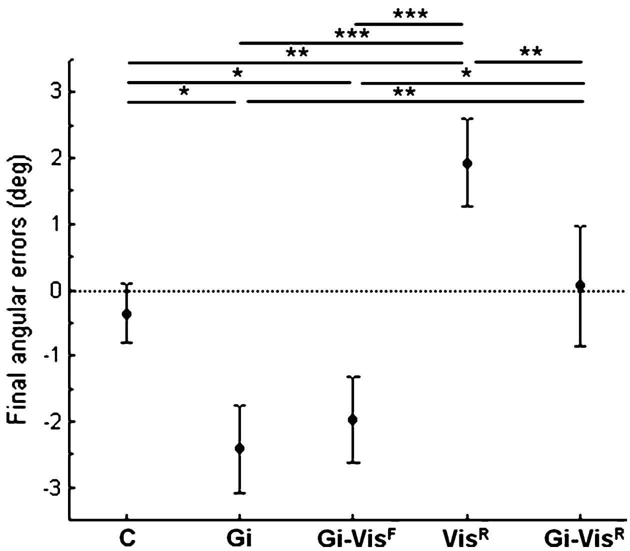

Fig. 4 Mean final pointing *errors* as a function of experimental conditions. Negative pointing *errors* correspond to downward pointing. *Error bars* represent standard errors. *$P < .05$; **$P < .01$; ***$P < .001$

A 5-condition repeated-measures ANOVA on final pointing errors revealed a significant effect of the main factor [$F_{(4,64)} = 11.98$, $P < .001$, $\eta^2 p = .43$, $(1 - \beta) = 1.00$]. As illustrated in Fig. 4, post hoc analyses showed that final pointing errors observed when a "single" stimulus was manipulated (either visual or **Gi** cues) significantly differed from the final pointing errors in the **C** control condition. On the other hand, final pointing errors in the "combined" condition did not statistically differ from those in the **C** condition (**C** vs. **GI–Vis^R**, $P = .55$). The ANOVA performed on the within-subject standard deviation of the final pointing errors in **GI**, **GI–Vis^F**, **Vis^R** and **GI–Vis^R** conditions did not reveal any significant difference [$F_{(3,48)} = 1.82$, $P = .16$, $\eta^2 p = .10$, $(1 - \beta) = .44$].

Further analysis indicated that our data were not substantially affected by fatigue or learning effects. Indeed, final pointing errors were negligible in the last, control condition trial (mean = −.4°). Moreover, a 4-condition × 4-trial position ANOVA confirmed that there was no significant trial position effect on final pointing errors [$F_{(3,30)} = .25$, $P = .86$, $\eta^2 p = .03$, $(1 - \beta) = .09$] and no significant interaction [$F_{(9,90)} = 1.01$, $P = .44$, $\eta^2 p = .09$, $(1 - \beta) = .47$].

Time course of pointing errors

Figure 5 shows that in **GI**, **GI–Vis^F** and **Vis^R** conditions, pointing errors gradually increased after stimulation onset (i.e., $t = 0$ s). Relative to the **C** condition, pointing errors

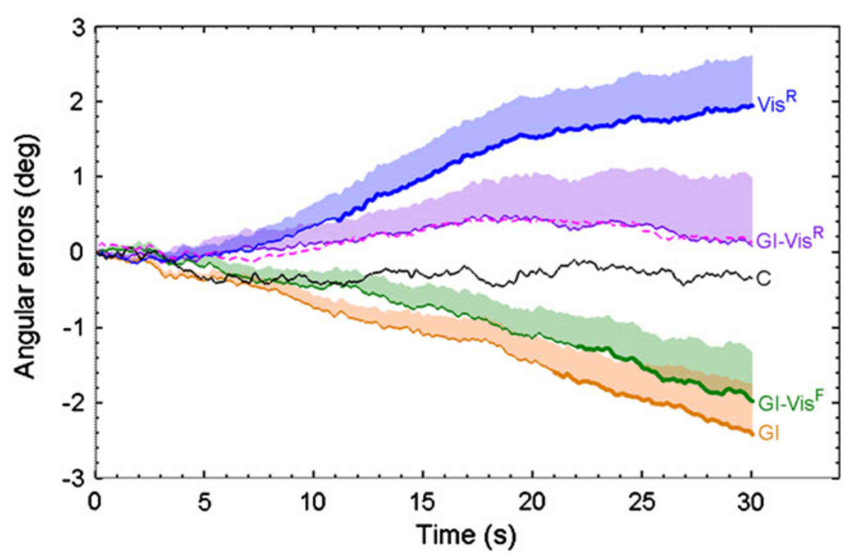

Fig. 5 Mean pointing *errors* as a function of time. Negative pointing *errors* correspond to downward pointing. *Thick lines* illustrate significant differences between a given condition and the **C** control condition ($P < .05$). *Areas* represent positive standard errors (note that the standard error for the **C** condition is not represented because trial number differed from the other experimental conditions). The *dotted line* corresponds to the data predicted by the multiple linear regression on the mean pointing errors (see "Time course of pointing errors")

Table 1 Latency (in s) of the first significance in mean pointing errors between conditions

	C	GI	GI–Vis^F	Vis^R	GI–Vis^R
C	–	21.0	22.0	11.1	ns
GI		–	ns	9.0	10.1
GI–Vis^F			–	11.1	13.7
Vis^R				–	20.0
GI–Vis^R					–

Latencies are given relative to the stimulus onset, i.e., rotation of **Gi** vector and/or visual background ($t = 0$ s). ns indicates that no statistical difference was found. Similar latencies were obtained when data were normalized with respect to the control condition (i.e., by subtracting, for each subject, the pointing errors in the control condition from the mean pointing errors in a given condition)

first appeared in the **Vis^R** condition and then in **GI** and **GI–Vis^F** conditions (Table 1). Pointing errors remained negligible throughout the trial in both **C** and **GI–Vis^R** conditions. To investigate more precisely how the experimental manipulations dynamically affected pointing accuracy over time, a 5-condition ANOVA was carried out on pointing errors every 5 ms throughout the trial. When the ANOVA revealed a significant main effect (starting 8.6 s after trial onset [$F_{(4,64)} = 2.53$, $P = .049$, $\eta^2 p = .14$, $(1 - \beta) = .68$] to the end of the trial), post hoc analyses were performed. This method (e.g., Sarlegna et al. 2003) was used to obtain the latency of the first significant difference between two given conditions, even though sensory integration likely started before the statistical analysis reached significance. This analysis confirmed that, relative to the **C** condition, pointing errors first differed in the **Vis^R** condition (Table 1). Errors then differed between **C** and **GI** or **GI–Vis^F** conditions. Across the trials, no significant difference was found between the pointing errors in the two "single" conditions including **Gi** vector rotation (**GI** vs. **GI–Vis^F**, $P > .05$) or between that in **GI–Vis^R** and **C** conditions. Comparisons were then made between the pointing errors in the trial achieved in the **C** condition and that in the different trials of each other condition to verify the consistency of response latencies. These were similar across trials for the **GI** condition (mean = 21.9 ± 1.8 s), **GI–Vis^F** condition (mean = 19.3 ± .5 s) and **GI–Vis^R** condition (no trial latency could be extracted since no significant differences were found). However, latencies in the **Vis^R** condition appeared more variable (mean = 12.8 ± 7.3 s), even though it had no effect upon the final pointing errors, as attested by the non-significant trial position and trial position × condition effects (see "Final pointing errors").

To further investigate the pointing errors observed in the **GI–Vis^R** condition relative to those observed in the "single" conditions (constituting the "combined" condition), we first tested the hypothesis of a simple additive effect (i.e., **GI–Vis^R** = **Vis^R** + **GI–Vis^F**). A paired t test was conducted every 5 ms between the pointing errors observed in the **GI–Vis^R** condition and the sum of the pointing errors observed in the "single" **Vis^R** and **GI–Vis^F** conditions. No

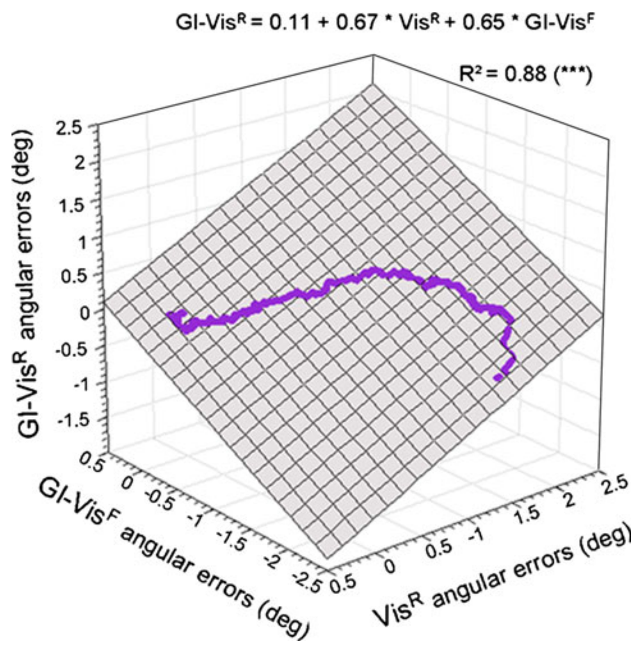

Fig. 6 Multiple linear regression on between-subject mean fitted to the **GI–Vis^R** mean pointing errors (*line*) as a function of the mean pointing *errors* observed in the single conditions **Vis^R**. The multiple regression *plane* is represented by the *hatched area* following the equation given above the *graph*. ***$P < .001$

statistical difference was observed throughout the trial ($P > .05$, as illustrated in Fig. 5). In addition, no significant difference was found between the pointing errors in the **GI–Vis^R** condition and the sum of the pointing errors in **Vis^R** and **GI** conditions. The R^2, used to evaluate the quality of the model **GI–Vis^R** = **Vis^R** + **GI–Vis^F**, was .36 ($P < .001$).

We tested how better a multiple linear regression would explain pointing errors in the **GI–Vis^R** condition. First, we investigated the origin of the pointing errors obtained in the "combined" condition by performing multiple linear regressions on individual pointing errors (mean of the 4 trials for each subject) and averaging each equation parameter (ordinates to the origin and **Vis^R** and **GI–Vis^F** weights). The average equation (**GI–Vis^R** = −.22 + .05 × **Vis^R** + .72 × **GI–Vis^F**) did not explain a large part of variance when applied on the mean pointing errors ($R^2 = .39$, $P < .001$). Second, we assessed the quality of fit of a multiple linear regression on the mean pointing errors in the **GI–Vis^R^** condition based on the mean pointing errors observed in the "single" conditions. Figure 6 presents the multiple regression plane that best explained **GI–Vis^R^** mean pointing errors (plane equation: $\mathbf{GI\text{–}Vis^R} = .11 + .67 \times \mathbf{Vis^R} + .65 \times \mathbf{GI\text{–}Vis^F}, R^2 = .88$, $P < .001$). The similar equation parameters .67 and .65 suggest that the weights of visual cues and **Gi** cues were similar in the "combined" condition.[2] In addition, these weights seemed to be constant across the trial as attested by the close planar relationship between the predictors and the data observed in the $\mathbf{GI\text{–}Vis^R}$ condition ($R^2 = .88$). Figure 5 also illustrates the quality of the fit by plotting the observed data in the $\mathbf{GI\text{–}Vis^R}$ condition and the data predicted by the multiple linear regression. In order to estimate the predictive power of these models, the RMSE was calculated for each subject. We found that the predictive power of the model of multiple linear regression on the mean pointing errors was significantly higher than the model of averaged parameters based on multiple linear regressions on individual pointing errors (mean RMSE = $1.19 \pm .90$ and 1.74 ± 1.62, respectively; $t_{(16)} = 2.70$; $P < .05$).

Discussion

The aim of the present study was to determine the multisensory integration processes underlying spatial localization during "combined" changes of visual and **Gi** cues. To do so, we investigated how, during **Gi** vector rotation, a visual background rotation influenced the localization of a body-fixed target, as inferred from a continuous pointing task. Our results showed that the "single" rotation of the **Gi** vector or the visual background specifically affects the pointing accuracy, since downward and upward errors were observed, respectively. More interestingly, the synchronous rotation of the visual background and the **Gi** vector yielded a cancelation of the pointing errors, which were similar to that of the control condition. In terms of multisensory integration processing, our data suggest a linear combination of **Gi** and visual cues whose weights remained constant across the range of the tested stimulation.

Before dealing with the combined influences of **Gi** and visual cues, we will first discuss the specific effect of the modified **Gi** environment upon target localization, assessed by continuous pointing. Target localization impairments during centrifugation have been largely explained by the oculogravic illusion (Carriot et al. 2005; Graybiel 1952), which leads, for instance, to a false sensation of target elevation during a forward linear acceleration. In parallel during the same stimulation, the observer is submitted to an illusory sensation of backward body tilt (i.e., the somatogravic illusion; Benson 1990; Graybiel 1952). Since it is widely assumed that both illusions are intimately linked, one could expect that in our task, the illusory target elevation (i.e., oculogravic illusion) concomitantly occurred with an illusory elevation of the arm in space as a consequence of the illusory backward body tilt (somatogravic illusion). If both illusions simultaneously appeared with the same magnitude, the observer would not have to modify his/her arm position relative to the target, as both would be sensed elevated to the same extent. However, our data do not support this hypothesis since the arm moved downward in the **Gi** condition. One possibility is that, in the present study, the somatogravic illusion was stronger than the oculogravic illusion and that compensatory arm responses resulted in downward pointing errors. Dissociation between oculogravic and somatogravic illusions would be consistent with recent findings of Carriot et al. (2006). Indeed, these authors investigated the effect of centrifugation upon the subjective visual horizon (considered as a reference for target localization and reflecting the magnitude of the oculogravic illusion) and the subjective proprioceptive horizon (reflecting the magnitude of the somatogravic illusion). Carriot et al. (2006) observed that the subjective proprioceptive horizon and the subjective visual horizon were differently affected when facing the rotation axis. This is in line with our aforementioned interpretation as it suggests that the somatogravic illusion and the oculogravic illusion differed in magnitude.

The centrifugation resulted in pointing errors that arose at a similar latency in **GI** and $\mathbf{GI\text{–}Vis^F}$ conditions (~21 s relative to the control condition). Incidentally, this latency is close to the time constant of the semi-circular canals (i.e., 20 s; Howard 1982). The latency that we found may reflect the slow build-up of the oculogravic and somatogravic illusions (Curthoys 1996). This latency may also reflect the time at which the somatogravic condition differed from the oculogravic condition.

Adding a fixed visual background ($\mathbf{GI\text{–}Vis^F}$ vs. **GI**) did not significantly reduce the effect of centrifugation upon continuous pointing toward a body-fixed target. This might appear surprising because in a non-modified **Gi** environment, adding a static visual landmark or a structured visual background to a dark environment improves the localization of targets in space (Lemay et al. 2004; Magne and Coello 2002). However, Eriksson et al. (2008) pointed out that spatial localization should not be improved during centrifugation if the visual background is not related to the

[2] These values should not be viewed as relative weights of **Gi** and visual cues whose sum would necessarily correspond to 100% in the multisensory integration process.

external Earth-fixed reference frame but instead is related to the body. Based on this idea and given that we used a head-mounted display (the visual background was thus anchored to the head), the somatogravic and oculogravic illusions may not have been affected in our study. Indeed, in our study, adding a visual background during centrifugation does not appear to help the observer to have a more precise idea of his body configuration and target location in space and thus to improve continuous pointing accuracy.

When the visual background was rotated without any **Gi** modifications (**Vis^R** condition), we found a progressive elevation of continuous pointing which could be interpreted as a consequence of an illusory target elevation. This induced-motion phenomenon has already been described at length in the literature for localization judgments and discrete pointing movements (Bridgeman et al. 1981; Post et al. 2008). Post and Lott (1990) also suggested that the strength of induced motion is mostly related to the visual background velocity. Our results seem consistent with this idea since pointing errors gradually increased with the visual background velocity.

Strikingly, when the visual background was rotated while the **Gi** vector was simultaneously rotated (**GI–Vis^R** condition), the effects of the centrifugation were cancelled since pointing errors did not significantly differ, across the trial, from that observed in the control condition. In order to improve spatial localization skills during a linear acceleration, researchers have tried to define how the different sensory modalities participate in these illusions. In this vein, studies have demonstrated that the absence of vestibular cues does not suppress the somatogravic illusion (Clément et al. 2001), thus highlighting the importance of somatosensory cues. Studies have already tried to minimize such illusion in modified **Gi** environments by manipulating somatosensory cues (with pressure and vibration cues reinforcing the gravity direction; Rupert 2000; van Erp and van Veen 2006). However, given the importance of visual cues for spatial orientation and localization (Howard 1982), studies mostly aimed at minimizing these illusions by adding visual cues. Adding a congruent optic flow (i.e., visual cues that are coherent with the produced acceleration) has been shown to improve spatial localization skills (Eriksson et al. 2008; see also Lessard et al. 2000). Here, we found a salient way to cancel centrifugation effects on spatial localization by adding non-congruent visual cues (i.e., visual background rotation), which basically biased target localization in the opposite direction of the effects produced by a modified **Gi** environment. Conversely, one could view our findings as reflecting the cancelation of the illusory consequences of the visual background rotation (induced motion) by centrifugation.

The present study suggests that the "combined" rotation of the visual background and the **Gi** vector corresponds to the linear combination of the "single" rotations. Indeed, the multiple linear regression on the mean pointing errors shows that the proportion of explained variance by a linear equation was $R^2 = .88$. This indicates that the weights of **Gi** and visual cues remained constant across the stimulation. The present study may thus bring further insight into the way sensory inputs are integrated for spatial localization during concomitant changes in visual background and **Gi** cues. According to Howard (1997), sensory weighting processes are based on cue dominance, dissociation or cue reweighting. Here, the possibility of sensory dominance, even visual dominance, might be dismissed because the weights of **Gi** and visual cues were found to be similar. In fact, there is no consensus in the literature with respect to the dominant sensory modality since visual dominance (Gibson 1950), vestibular dominance (Mittelstaedt 1999) or somatosensory dominance (Mergner and Rosemeier 1998) has been proposed. In addition, it is commonly observed that spatial localization skills are influenced by several sensory modalities (Barnett-Cowan and Harris 2008; Bringoux et al. 2004; Cohen et al. 2001; Rossetti et al. 1995). In this vein, recent data evoked a reweighting process that characterized the relative influence of each cues, depending on the time period (Bringoux et al. 2009), the stimulus intensity (Oie et al. 2002) or the cue reliability (Angelaki et al. 2009; Ernst and Banks 2002). For instance, Angelaki et al. (2011) reported that the integration of visual and vestibular cues relied on sensory weighting processes where each weight is inversely proportional to the cue variability. It thus would have been reasonable to expect a modulation of the weight attributed to the different sensory cues over time, when both stimuli were provided. This is not what we observed since our findings support the idea of a constant weighting of both visual and **Gi** cues, despite the progressive change in stimulation intensities. Several studies have already suggested that constant weights are attributed to the sensory modalities available to the observer (Barnett-Cowan and Harris 2008; Bourrelly et al. 2010; Bringoux et al. 2008). Our study not only suggests that a constant weighting of visual and **Gi** cues takes place when both stimuli are combined but also suggests that these weights remain constant across the range of stimulation manipulated. Further experiments need to be carried out to examine whether these weights remain constant during more complex or desynchronized stimulations.

Conclusion

Our study showed that continuous pointing toward a body-fixed target is modified by a gradual change in visual or **Gi** cues. The more visual background or the **Gi** vector was rotated, the larger the pointing errors were. During the "combined" changes of **Gi** and visual cues, the centrifugation effects on continuous pointing were cancelled by the visual background rotation. The "combined" rotation of visual background and **Gi** vector thus appeared to affect target localization as predicted by a linear combination of both "single" stimulations over time. The evolution of continuous pointing errors across the different conditions suggests that the respective weights attributed to the visual and **Gi** cues were kept constant across the range of the tested stimulations. Here, we suggest that visual cues can be used to reduce illusions caused by **Gi** changes and which cause most cases of spatial disorientation (Benson 1990). Hence, these data may be of value for the ergonomic design of assistive devices in aeronautics.

Acknowledgments The authors are grateful to F. Buloup, A. Donneaud, C. Goulon and J.-M. Pergandi for their technical expertise. They also thank M. Woodman for English assistance.

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