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Two reference frames for visual perception in two gravity conditions

Mark Lipshits¶, Ana Bengoetxea§, Guy Cheron§, Joseph McIntyre#
¶ Institute for Information Transmission Problems, Russian Academy of Sciences, Moscow, Russia;
§ Unité de Recherche de Biomécanique de Mouvement, Université Libre de Bruxelles, Brussels, Belgium; # Laboratoire de Physiologie de la Perception et de l'Action, CNRS—Collège de France, 11 place Marcelin Berthelot, 75005 Paris, France; e-mail: joe.mcintyre@college-de-france.fr
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Abstract. The processing and storage of visual information concerning the orientation of objects in space is carried out in anisotropic reference frames in which all orientations are not treated equally. The perceptual anisotropies, and the implicit reference frames that they define, are evidenced by the observation of 'oblique effects' in which performance on a given perceptual task is better for horizontally and vertically oriented stimuli. The question remains how the preferred horizontal and vertical reference frames are defined. In these experiments cosmonaut subjects reproduced the remembered orientation of a visual stimulus in 1*g* (on the ground) and in 0*g*, both attached to a chair and while free-floating within the International Space Station. Results show that while the remembered orientation of a visual stimulus may be stored in a multimodal reference frame that includes gravity, an egocentric reference is sufficient to elicit the oblique effect when all gravitational and haptic cues are absent.

1 Introduction

The question what reference frame is used to process, store, and interpret visual information remains a key topic for studies of spatial perception mechanisms (Appelle 1972; Essock 1980; Gentaz and Ballaz 2000; Luyat and Gentaz 2002). From experimental evidence showing the so-called 'oblique effect' one can conclude that human subjects manifest a clear bias toward vertically and horizontally oriented stimuli when perceiving visual information. For example, a human observer detects whether a figure is symmetric more quickly and with fewer errors when the axis of symmetry is vertical or horizontal than when it is oriented at an oblique angle (Appelle 1972). The question is: what defines the 'vertical' and 'horizontal' that are at the source of these effects?

There are at least two possible classes of reference frames that may be used to define the vertical and horizontal axes for the internal representation of visual stimuli. The orientation of the image on the retina coupled with proprioceptive and efference-copy information about eye, neck, and joint angles could be used to store the visual orientation in an egocentric reference frame linked to some axis of the body (eg head, trunk, eyes). Alternatively, the orientation of the visual stimulus may be referenced to allocentric cues, such as the horizon, vertical and horizontal walls in the visual scene, bodily contact with stable elements in the environment, or the perceived axis of gravity (Mittelstaedt 1983) or balance (Stoffregen and Riccio 1988). While it has been suggested in a number of studies that gravity can play an important role in defining the vertical for visual perception, it is also known that many visual oblique effects—including that observed for symmetry detection—can persist in the absence of gravity (Leone et al 1995). In the study reported here we continued to explore how proprioceptive and exteroreceptive cues interact to provide the canonical orientations used for visual perception.

In our previous studies (Lipshits and McIntyre 1999; McIntyre et al 2001) we used a matching task in which human subjects aligned an adjustable visible stimulus

Author to whom all correspondence should be addressed.

(a line presented on a video screen) with the remembered orientation of a similar visual stimulus presented 1 s earlier. Under normal gravity conditions we showed that subjects sitting upright produced a clear oblique effect in the performance of this task: response times were shorter and response variability lower for stimuli with horizontal and vertical orientations than for stimuli presented at other orientations. This effect was evident even in the absence of visual cues (subjects viewed stimuli through a circular tunnel). Remarkably, however, the preference for horizontal and vertical stimuli decreased or disappeared when the body axis was tilted with respect to gravity (Lipshits and McIntyre 1999). This disappearance was not connected with ocular counterrolling induced by whole-body tilt, nor could we find a preference of any other intermediate orientation between the gravity-aligned and body-aligned axes (McIntyre et al 2001). Note, however, that in similar studies an oblique effect has been found in subjects who were tilted with respect to gravity, with the preferred axis of the oblique effect aligned with the perceived vertical reported by the subject (Luyat and Gentaz 2002). Despite this discrepancy in results (see section 4), both of these observations argue for a role of allocentric graviceptor information in defining the orientation of a visual stimulus, because the perceived vertical axis is known to result from a weighted contribution of both graviceptive and proprioceptive information (Mittelstaedt 1983). On the other hand, the preference for vertical and horizontal axes persisted when tests were performed in the absence of gravity over the course of a six-month spaceflight (Lipshits and McIntyre 1999; McIntyre et al 2001). We concluded that subjects normally process visual orientation information in a multimodal reference frame that combines both proprioceptive and gravitational cues when both are available, but that an egocentric reference frame is sufficient for this task in the absence of gravity after a short period of adaptation.

The experiments described above allow one to exclude gravity as an essential requirement for what we will call the 'visual alignment oblique effect', but several questions remain open about how proprioceptive and graviceptive cues combine to provide the reference frame used in this task. There are two main possibilities to explain why cosmonauts continued to produce an oblique effect in the absence of gravity. In the first, subjects may have used proprioceptive cues to process and store visual orientation information exclusively in egocentric terms with respect to the eye, head, or body axes. In the second, subjects may have relied on tactile receptors and the stable attachment of the body to the floor of the space station (in a seated position) to perceive their body orientation, and hence the orientation of the visual stimulus, with respect to the floor and walls. Furthermore, subjects might also have relied on visual memory even in the absence of orienting visual landmarks. When a participant gets ready to perform these experiments, he or she sees the walls and the entire surrounding visual scene. How long this scene remains in memory is unclear. If the subject is aware of the fact that body orientation will not change with respect to this initial view, the remembered visual scene can serve as a stable reference frame for orientation estimation. Thus, under the conditions studied so far in the absence of gravity, allocentric information might still have contributed to the perception of visual orientation for this task.

The study reported here was conceived to further tease out the possible contribution of egocentric and allocentric cues for visual orientation perception. Cosmonauts performed the same experiment as in our previous study, but this time they floated freely within the International Space Station (ISS). Under these conditions, subjects had no contact with the stable reference frame provided by the station nor could they be assured that the body axis would remain aligned with respect to the remembered visual field. We compared the results of these trials with those performed in an attached posture in the absence of gravity and with trials performed in a normal 1*g* environment.

2 Materials and methods

Subjects looked straight-ahead through a form-fitting face mask. A video monitor was centred on the line of gaze at a distance of ~ 30 cm from the eyes. The monitor was viewed through a cylindrical tunnel, thus removing any external visual references.

Subjects performed a matching task for visual stimuli (figure 1). Each trial started with the presentation of a 65 mm stimulus line on the video monitor that emanated from the centre along one of seven different directions ($-22.5°$, $0°$, $22.5°$, $45°$, $67.5°$, $90°$, or $112.5°$, where $90°$ was aligned with the subject's head axis, and $0°$ pointed to the right). This line was drawn inside a 165-mm diameter circle. Subjects were instructed to look at and remember the position of this 'reference' stimulus. At the push of a button by the subject, the original stimulus disappeared, and a second line of the same length but in a different orientation appeared. Using a trackball, the subject rotated this 'variable' stimulus to the same orientation as the first. By repeated pushes of this button, the subject had the option of switching back and forth between the reference and the variable stimuli. To erase afterimages of either stimulus from the retina, a distractor screen comprised of many crossing lines at different orientations was presented for 1 s during the transition from one stimulus to the other. The number of transitions was left up to the subject, but the duration of each trial was limited to 45 s. When the subjects were satisfied that the two stimuli were identical, they pressed a second button to indicate the end of one trial and to initiate the next. Each series of experiments lasted not longer than 20 min and included 42 trials, divided into 3 blocks of 14 each, with a short rest interval between them.

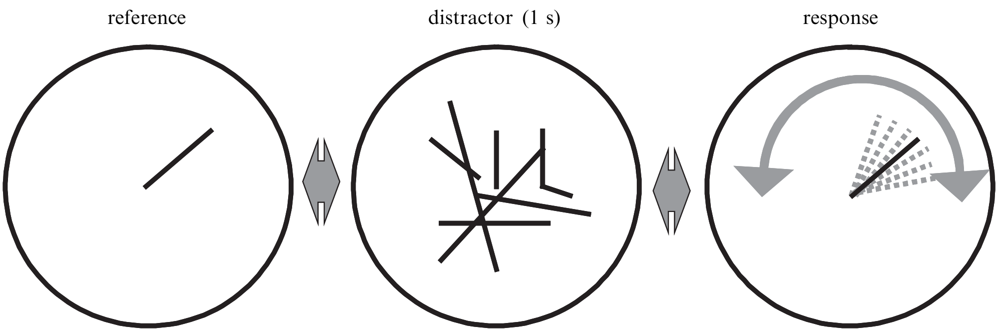

Figure 1. Three visual stimuli (black lines) viewed sequentially by subject through a cylindrical tunnel. Subjects could move back and forth between the reference and response screens, via the distractor screen, by pressing a button. Response stimulus was adjusted by the participant by turning a potentiometer to match the orientation of the reference stimulus.

On the Earth, subjects performed the experiment while seated upright in front of the computer. During spaceflight they performed the experiment in two conditions. In the attached position the cosmonauts used belts, foot straps, and a tabletop to reproduce essentially the same seated posture as that used on the Earth. In the free-floating condition subjects held the experimental apparatus (laptop computer and tunnel) in their hands, with an elastic band used to hold the face against the mask. An assisting cosmonaut then positioned the subject in the centre of the free working volume within one of the spacestation modules. The subject was then released and both subject and apparatus floated free from any contact with the station. The assisting cosmonaut remained in place to assure that no contact with the walls of the station occurred. To accomplish this, the assistant applied short tugs on the clothing of the subject to adjust the position without giving strong directional cues. Very few such corrections (one to two per session per subject) were required.

Six cosmonauts (five men and one woman) participated in this investigation during the joint Russian – French 'Andromeda' mission (subjects S1 – S3) and the Russian – Belgian 'Odissea' mission (subjects S4 – S6) to the ISS in 2001 and 2002. All gave informed consent prior to starting the experiment and were free to stop the procedure at any time. Each cosmonaut was tested on the ground before flight, during space flight aboard the ISS, and on the ground soon after her/his return to the Earth. Details of the testing schedules for each subject are shown in figure 2. In flight, subjects were tested on two days over the course of their ten-day space flights, with at least one day between sessions. Prior to flight, subjects were tested in two pairs of sessions over the two months prior to the lift-off. Sessions within each pair were separated by at least one day, corresponding to the testing schedule to be used in flight. Subjects were tested on three days during the week immediately following the landing, starting on the day of landing. Three of the subjects were tested two more times two weeks after returning to the Earth.

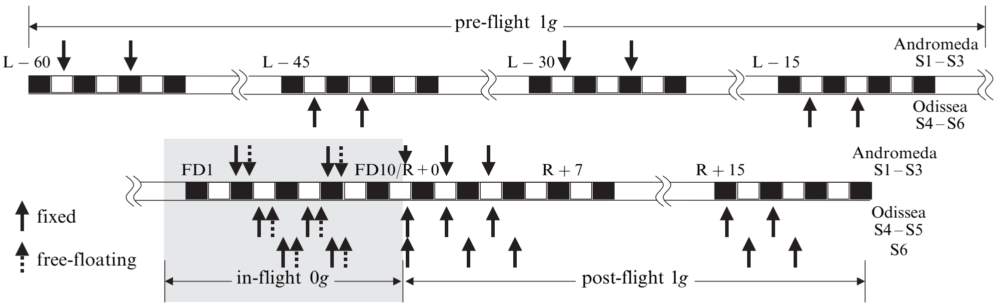

Figure 2. Testing schedule for cosmonauts who performed the experiment during the Andromeda and Odissea space flights to the International Space Station. Testing on the Earth before the flight started as early as sixty days prior to launch (L – 60) and continued up to twenty days after return to the Earth (R + 20). Subjects performed the experiment at 0*g* on two different days during a ten-day mission (FD1 – FD10), in both attached and free-floating conditions (except S1, who worked only in free-floating in-flight).

Aside from the differences in test schedules shown in figure 2, performance of the experiment by the two different crews (Andromeda and Odissea) differed in two other respects. First, the response mode differed slightly in the software used for each mission. For the Andromeda flight, subjects could rotate the response line 360° or more in either direction to arrive at the final response position. For example, if the reference stimulus was presented at 45° and the initial position of the response stimulus was at 130°, subjects could rotate the response either 85° clockwise or 275° counterclockwise to reach the reference orientation. This was in contrast to the response conditions allowed by the Odissea software, and by software used in previously cited studies, in which movements of the variable response line were limited to a range of −30° to +120°. In the latter case, subjects could only take the 'short route' from the initial response line orientation to the desired response condition. This difference could have had an influence on the time it took to perform each trial (it takes longer to turn the stimulus 275° than 85°). A second difference was the location in the ISS in which the experiments were performed. The free-floating trials were performed in the node module of the ISS during the Andromeda mission—a large, symmetric volume with few visual cues about a locally defined 'up' and 'down'. During the Odissea mission, free-floating was performed in the ESO module—a narrower workspace that affords a more oriented visual environment. These differences could have played a role in the visual memory available to subjects during the trials. Owing to these variations in conditions, we looked for potential differences between the two missions in the results.

2.1 *Analysis*

The sequences of reference-line orientations were quasi-random and each orientation was shown 6 times. For each trial, we recorded the final orientation of the variable stimulus when the subject pressed the button to validate her/his response and the time required to perform the trial from the moment when the reference stimulus first appeared to the moment when the final response position was recorded by pressing on the button. We computed the constant error (measured as the average mean error), the variable error (measured as the standard deviation about the mean for multiple trials to the same stimulus) and average response time as a function of stimulus orientation for each subject. To look for effects of stimulus orientation and gravitational conditions on the responses, we used multifactor ANOVA analysis followed by Sheffé tests for a posteriori analyses. We used primarily a $2 \times 4 \times 7$ factor design with mission (Andromeda or Odissea) as a between-subjects factor and gravity conditions (1*g* pre-flight, 0*g* free-floating, 0*g* attached, or 1*g* post-flight), and reference-stimulus orientation ($-22.5°$, $0°$, $22.5°$, $45°$, $67.5°$, $90°$, and $112.5°$) as within-subjects factors. Owing to operational constraints, subject S1 performed the experiment in only the free-floating condition in 0*g*. The $2 \times 4 \times 7$ ANOVA design was therefore applied to the results of only five subjects (S2 – S6). ANOVA tests were repeated on data from all six subjects by removing the 0*g*-attached level from the gravity conditions factor, yielding similar results (not reported here) in terms of the comparison between 0*g* free-floating and 1*g* performance of the experiment.

3 Results

Figure 3 presents the average constant error for subjects S2 – S6 in each experimental condition, and for each of the seven possible reference-stimulus orientations. A negative error means that the response line was oriented erroneously in the clockwise direction with respect to the reference stimulus. In all conditions and for all reference angles subjects worked carefully and demonstrated a high level of attention—average constant error was less than 1.5° in all cases. As we already saw in our previous investigation, constant error showed a consistent cyclic pattern across reference-stimulus orientations, independent of the condition of gravitational and fixation conditions. The pattern was similar between pre-flight, in-flight (attached and free-floating), and post-flight tests. These observations were confirmed statistically—the ANOVA analysis revealed a significant

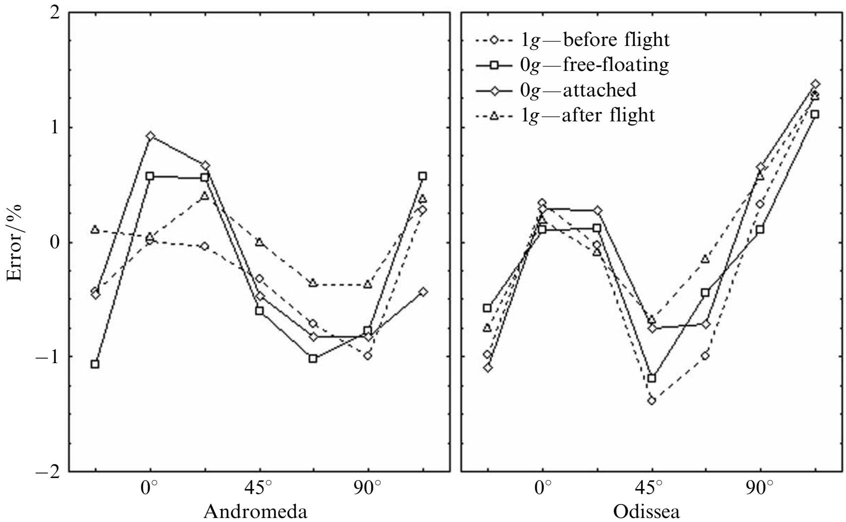

Figure 3. Constant error as a function of gravity conditions and reference-stimulus angle.

main effect of the stimulus orientation factor ($F_{3,6} = 2.77$, $p < 0.05$), but there were no other significant main effects or cross interactions ($p > 0.25$). Note, however, that this pattern of constant error does not constitute the oblique effect observed for this reproduction task. In terms of the absolute value of the error, subjects in fact performed worse for vertical and horizontal reference stimuli. The oblique effect instead manifested itself in measurements of response time and response variability, as described below.

The response-time data presented in figure 4 indicate that subjects took less time, on average, to judge that the variable stimulus was aligned with a vertical or horizontal reference line compared with the time to perform the task for oblique reference lines. Note that the subjects were not asked to work quickly. On the contrary, they were advised not to hurry so as to maximise the accuracy of their responses. Subjects were instructed to switch a minimum of two times between the reference-stimulus and variable-stimulus presentations and to terminate the trial only when they were sure that the orientations of both lines were the same. The effect of reference-line orientation on response time was highly significant ($F_{6,18} = 4.72$, $p < 0.01$). Conversely, there were no differences between different gravitational conditions (neither a significant main effect of the gravitational conditions factor, nor an interaction effect between stimulus orientation and gravitational conditions). In a planned comparison to test for the persistence of the oblique effect in the free-floating condition, response times for horizontal stimuli differed from those for oblique angles for the critical case of free-floating in 0g tested separately ($p < 0.05$ in all cases). Average response time also appears to have been less for vertical stimuli than for oblique angles; however, planned comparisons between these references did not reach significance at the 0.05 level ($p = 0.07$). Visual inspection suggests that there was a greater range of response times for the Andromeda crew than for the Odissea crew, with a trend toward lower durations as time went on, but there was no significant main effect or interaction effect involving the mission factor. It is unlikely that lower response times observed in-flight for the Andromeda crew can be specifically attributed to the microgravity conditions of space flight, even if the effect were statistically significant, because the response times were even lower after return to the Earth. The difference is more likely due to a learning effect linked to the choice that subjects could make about whether to turn the response knob clockwise or counterclockwise for any given stimulus. When this choice was not available (for the Odissea crew and in our previous experiments) no such overall

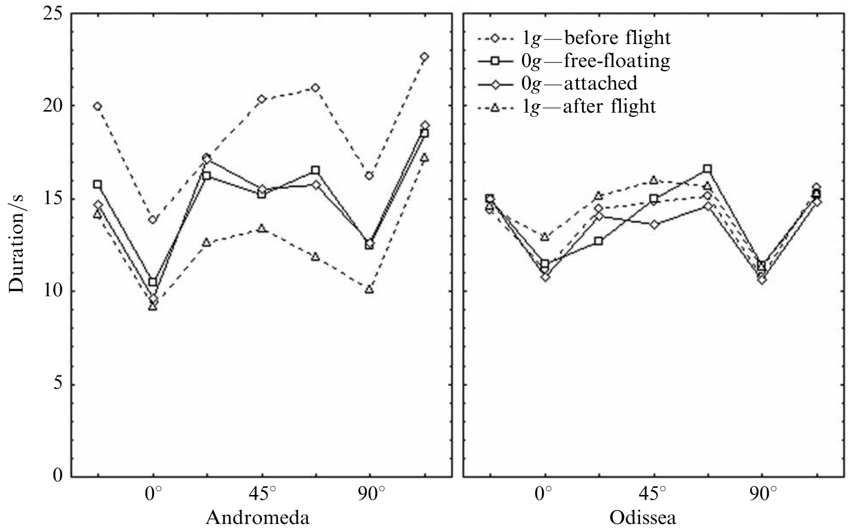

Figure 4. Response time as a function of gravity conditions and reference stimulus angle.

effect appeared. More importantly, planned comparisons showed that there were no statistical differences between the free-floating and attached conditions of the experiment for either crew.

Measurements of variable error (response variability for repeated trials to the same reference orientation) showed a remarkable dependence on the reference-stimulus orientation for all experimental conditions, as seen in figure 5. On average, variable error was slightly greater than 1° and showed clear minima for reference stimuli at 0° (horizontal) and 90° (vertical): ie there is a very strong oblique effect in terms of response variability. This observation was supported by a significant main effect for the reference-stimulus orientation factor ($F_{6,18} = 5.49$, $p < 0.01$). There was an unexpected significant main effect for the gravitational condition factor ($F_{3,9} = 14.69$, $p < 0.01$), but also a significant interaction between this factor and the mission ($F_{3,9} = 10.18$, $p < 0.01$). The manifestation of this cross effect is evident in figure 5. Crew members from the Andromeda mission showed increased variability for the 0*g* in-flight measures compared to pre-flight and post-flight measures, while results from the Odissea mission were unaffected by gravitational conditions. A posteriori analysis showed a significant difference between ground and flight conditions for the Andromeda mission ($p < 0.05$), but no difference between the attached and free-floating conditions in flight. Note, however, that there was no interaction between the gravitational factor and the stimulus-orientation factor ($p > 0.25$), ie the overall increased variability shown for the Andromeda crew at 0*g* did not change the oblique effect for stimulus orientation. This is illustrated in figure 6, in which variable errors for each stimulus orientation were normalised as a function of the average variability across all stimulus orientations within each session. It appears that the relative preference for vertical and horizontal stimuli was maintained when free-floating in 0*g* whatever the overall level of variability.

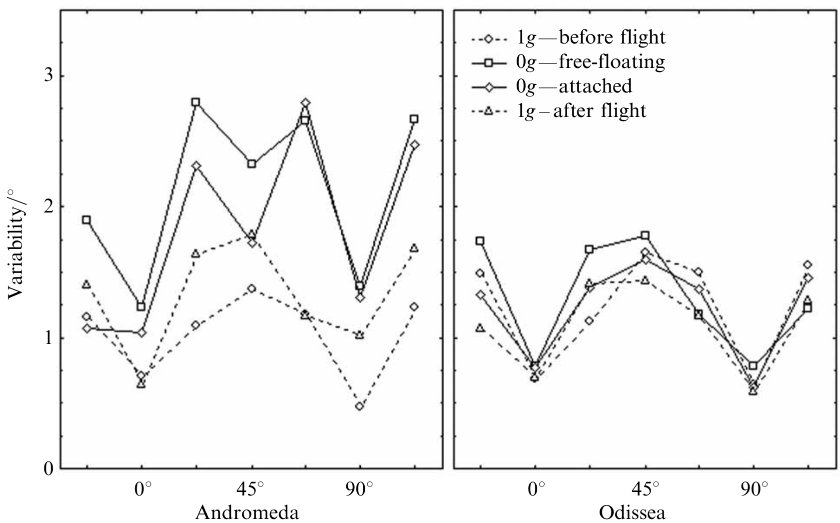

Figure 5. Variable error as a function of gravity conditions and reference-stimulus angle.

To test the specific hypotheses that the oblique effects were maintained in the free-floating condition, we conducted an ANOVA analysis on the variable error for the free-floating condition alone, with mission as a between-subjects factor and reference-stimulus orientation as a within-subjects factor. We found a significant main effect of the reference-stimulus orientation on variable error ($F_{6,24} = 3.49$, $p < 0.05$). Planned comparisons of the vertical and horizontal (computed separately) versus oblique angles were both significant ($p < 0.05$).

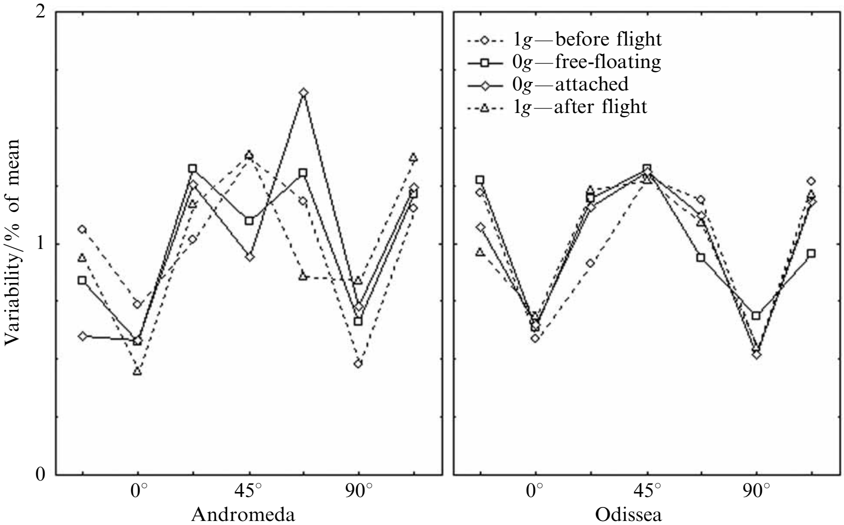

Figure 6. Normalised variable error (relative to average variability for a given session) as a function of gravity conditions and reference-stimulus angle.

4 Discussion

In these experiments, we found further evidence for the salience of vertical and horizontal stimuli in the visual perception of orientation, both in terms of response time and response variability in a visual matching task. Subjects responded more quickly and more accurately to vertical and horizontal stimuli than to any other oblique orientation. As in previous studies (Lipshits and McIntyre 1999; McIntyre et al 2001), we found that gravity is not an essential requirement for the emergence of the oblique effect. Experiments performed by cosmonaut subjects showed the same patterns of response time and variability as a function of stimulus orientation both on the ground and during orbital flight. This is in contrast to ground results in which tilting subjects with respect to gravity eliminated the oblique effect, indicating that, when present, gravity sensation is nevertheless involved in the perceptual processing.

The current study went a step further by comparing performance of subjects in free-floating versus attached conditions at 0*g*. It is possible to see from video recordings obtained during the execution of these trials that the position of the subject with respect to the walls changed from trial to trial in the free-floating state. Subjects had no tactile information about their body orientation with respect to the local environment and they could not rely on visual memory to relate the visual stimuli to their surroundings. Indeed, subjects reported that in free floating they very quickly lost their sense of orientation. Nevertheless, the oblique effect for the visual matching of orientations was maintained in both the attached and free-floating conditions. The lack of difference between these conditions shows not only that direct perception of the direction of gravity is unnecessary to produce the oblique effect but also that a stable haptic reference frame is not essential. The observed oblique effect is clearly egocentric at 0*g*.

In the current study, a specific group of subjects showed an overall increase in response variability for trials performed at 0*g*. In contrast to the lower reaction times observed progressively over the entire mission, measurements of variable error returned to pre-flight levels during post-flight tests. Thus, the differences in variability cannot be explained by habituation or loss of attention over the course of the study, nor by a speed – accuracy trade-off in which lower reaction times cause higher response variability.

The increased variability at 0*g* could instead be taken as evidence for a diminished ability for some subjects to remember the orientation of visual stimuli in the absence of gravity. However, the fact that different crews produced different results in this respect and the fact that such an overall increase in variability was not observed in our previous space-flight experiments, suggest that the increased variability for one crew was probably due to some other uncontrolled factor.

One confounding factor was introduced by the slight difference in the test methods for the two different missions. Crew members in the Andromeda mission could turn the knob clockwise or counterclockwise to reach the desired response condition, while Odissea crew members could only take the shortest route. This may have increased the task complexity for the Andromeda subjects. Note, however, that this difference in response method did not significantly affect the response variability on the ground. If this indeed is the pertinent difference between the two missions, it implies a cross effect between the gravitational conditions and the task complexity, rather than a specific effect of task complexity alone. In any case, the more important point is that, whatever the overall level of variability, the relative advantage of vertical and horizontal stimuli over oblique orientations was maintained, both in free-floating and when attached to a stable platform.

In our previous reports (Lipshits and McIntyre 1999; McIntyre et al 2001) we proposed that under normal ground conditions subjects use a multisensory reference frame for the internal representation and storage of visual information. This reference frame could combine both egocentric and gravitational components. We argued for this conclusion on the basis of the fact that the oblique effect disappeared for this task when the subject was tilted with respect to gravity. These results would appear to be in conflict with a more recent study of a similar memorisation and reproduction task for which the oblique effect was observed with respect to the subjective vertical axis reported by the subject (Luyat and Gentaz 2002). While the discrepancy between these studies remains to be resolved, both argue for an influence of gravity on the perception and storage of visual orientation information. In fact, the subjective vertical axis, which arises from visual, vestibular, and proprioceptive cues, can be seen as another manifestation of the multimodal reference frame used to define orientation in space. What is clear from the results reported here, however, is that an egocentric reference frame alone is sufficient when visual, gravitational, and haptic information about the external world is unavailable.

The oblique effect has been observed for many different visual tasks while the reference frame that defines the horizontal and vertical varies from task to task. Essock (1980) proposed that oblique effects in visual perception can be divided into two classes, according to the task: Class-I effects concern basic discrimination functions; these tasks are usually related to the physiological properties of the low-level visual system and are thus expressed with respect to a retinotopically defined horizontal and vertical. Class-II effects involve higher levels of cognitive processing which may be carried out in a gravitational reference frame, as evidenced by experiments carried out by tilting the observer with respect to gravity (Attneave and Olson 1967; Buchanan-Smith and Heeley 1993; Ferrante et al 1995). These two classes may be considered as specific cases of the more general dichotomy of egocentric versus allocentric reference frames. Representing a visual stimulus in an entirely egocentric reference frame would facilitate the manipulation of a visually perceived physical object. One need only follow the kinematic chain from retina to hand in order to, for instance, reach out and grasp the object. Knowledge of the orientation of the object or of any body segment with respect to the external environment would be unnecessary. Alternatively, when the orientation of an external object must be remembered prior to the interaction, one might suppose that the observed entity, which is independent from the observer's body, would maintain a stable orientation with respect to the external world. In this case, an allocentric reference frame would prove beneficial. Interactions between the object and the observer's body would therefore depend on the observer's 'body scheme' within the environment, in terms of perceiving the orientation of the body segments with respect to an externally defined vertical (Pagano and Turvey 1995), perceiving the orientation of the vertical itself (Mittelstaedt 1983), or in terms of the observer's own perceived stable orientation with respect to the world (Stoffregen and Riccio 1988). The pull of gravity acting on the limbs, on the body, and on the otoliths of the inner ear most certainly contributes to the observers' perception of their orientation within the stable external environment.

Depending on the constraints of the task, it is a reasonable conjecture that the human perceptual system might use egocentric or allocentric reference frames, or both, to perceive and store the orientation of visual stimuli. The coexistence of these two potential reference frames could, in fact, reconcile the apparently paradoxical observations found on the Earth and in orbit. When tilted on the Earth, a visual stimulus can be aligned with the vertical or horizontal in only one of the two potential reference frames. Conflicting information about the verticality of the stimulus would prevent the oblique effect from emerging in either reference frame. Conversely, there would be no conflict in the $0g$ conditions of orbit as great pains were taken to remove all cues relating to the orientation of the body within the environment. As the allocentric reference frame was removed, manifestation of the egocentric reference frame would show through.

One can find other examples in the literature in which human subjects use different internal reference frames depending on the physical context and the so-called body scheme. For example, subjects standing on a slowly rotating platform (angular velocity and acceleration below the vestibular threshold), but with head attached with respect to the environment, will perceive that the head is turning and the body is fixed (Gurfinkel and Levik 1993). In these conditions, subjects will generate reflexive eye movements consistent with the perceived turning of the head in the Earth-fixed reference frame. When the subject simultaneously touches or grasps a rigid object that is also Earth-fixed, the cognitive and reflex responses are modified dramatically. On touching the Earth-fixed object with the hand, the subject immediately perceives that the body is turning while the head is fixed and reflexive eye movements diminish accordingly. Thus, subjects can use haptic cues to establish the physical context of proprioceptive information coming from the neck and reinterpret this information accordingly. The interpretation of one set of sensory information depends on the availability of other sensory cues about the context in which the sensations are to be interpreted.

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