The aim of this study was to evaluate the influence of gravity on the representation and storage of visual orientation information. On earth, measurements of response time and variability for a task of aligning remembered visual stimuli showed a distinct preference for horizontally and vertically oriented stimuli when the body and gravitational axes were aligned. This preference was markedly decreased or disappeared when the body axis was tilted with respect to gravity but was maintained for tests performed in microgravity. We conclude that subjects acquire and store visual orientation in a multi-modal reference frame that combines proprioceptive and gravitational information when both are available. NeuroReport 10:1085–1089 © 1999 Lippincott Williams & Wilkins.

**Key words:** Gravity; Human visual perception; Oblique effect; Reference frames

**Introduction**

In performing tasks requiring sensorimotor coordination the central nervous system (CNS) needs to use internal reference frames to interpret sensory information and control movement [1–3]. The CNS probably uses different systems of internal representation depending on the sensory information to be processed, the specific task for which this information is to be used and the environmental conditions. We are, however, a long way from thinking that the CNS builds internal representations from only one source of afferentation, except at the very lowest levels of processing. To the best of our understanding, the CNS combines information from any and all pertinent, perhaps redundant, sensory modalities. Experimental studies of visual mechanisms suggest that the CNS represents image information with respect to preferred horizontal and vertical axes, as shown by a phenomenon known as the oblique effect [4]. For example, subjects identify more quickly and with fewer errors axes of symmetry for objects that are aligned vertically or horizontally as opposed to obliquely oriented figures [5]. It is not clear, however, how the CNS defines the preferred vertical and horizontal orientations. There are at least three possibilities: ‘vertical’ may be defined in terms of retinal, head or body coordinates; the CNS may represent images with respect to vertical references in the visual surround; and the CNS can use the constant direction of gravity to receive a perception of the vertical. In the current study we evaluated the influence of gravity on the representation and storage of visual orientation information.

**Materials and Methods**

Eleven subjects (eight men and three women) aged 26–46 participated in this investigation. All gave informed consent prior to starting the experiment and were free to stop the procedure at any time. The subjects were seated in a special chair which could be tilted and fixed at any angular orientation in frontal plane. Subjects looked straight ahead through a form-fitting face mask, and the head was supported by a head rest such that the head remained aligned with the body axis, independent of the orientation of the chair. A video monitor was attached to the chair, centered on the line of gaze at a distance of ~60 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. Each trial started with the presentation of a 33 mm stimulus line on the video monitor that emanated from the center along one of seven different directions (−22.5°, 0°, 22.5°, 45°, 67.5°, 90° or 112.5°, where 90° is aligned with the subject’s head axis and 0° points to the right). This line was drawn inside an 18 cm diameter circle. Subjects were instructed to look at and remember the position of this reference stimulus. On 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 rotary knob, 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 after-images of either stimulus from the retina, a distracter 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 60 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.

We tested subjects in three positions of the chair: upright and tilted ±22.5° to the left and right. Each participant performed 42 trials in each chair position. The sequences of reference line orientations were quasi-random and each orientation was shown six times. To avoid influences of training effects, the order of the chair positions was different for different subjects. For each trial, we recorded the final orientation of the variable stimulus and the time required to perform the task. We computed the constant error (measured as the average mean error), the variable error (measured as the s.d. about the mean for multiple trials to the same stimulus) and average response time as a function of stimulus orientation and chair inclination for each subject. We then computed the average of these three values across all subjects and looked for effects of stimulus orientation and chair tilt.

**Results**

Figure 1A presents the average constant error for all 11 subjects in each of the three chair positions, and for each of the seven possible stimulus orientations. The reference line orientation is reported with respect to the head/body axis of the subject. In all conditions subjects were highly accurate, generating constant errors most often in the range ±1°. A qualitative inspection suggests that a cyclic pattern of constant error might exist for reference line orientations, and that the phase of this cyclic pattern appears to shift for different orientations of the chair. We tested this observation with a two-factor (stimulus line × chair orientations) ANOVA analysis. For stimulus line orientations with respect to the head in the range 0–90°, the main effect for stimulus orientation did not reach statistical significance ($p < 0.0698$) at the 0.05 level of confidence, but there was a significant interaction ($p < 0.0103$) between the chair and the stimulus orientation factors. Similarly, if the stimulus line orientation with respect to gravity is considered, the main effect of this factor was not quite significant ($p < 0.0721$) and the interaction effect persisted ($p < 0.0187$). We cannot conclude that there is a definite dependence of constant error on the orientation of the reference stimulus. However, if such a pattern does exist, we can say that constant errors depend on the reference line orientation with respect to both the head/body and the gravitational axes.

Measurements of response variability (variable error) show a clearer dependence on the stimulus orientation (Fig. 1B). An ANOVA analysis revealed a significant effect of both the reference line orientation with respect to the head ($p < 0.0032$) and the chair orientation with respect to gravity ($p < 0.0265$) on the variability of repeated measures to the same reference. For the upright chair position, variable error for vertically and horizontally oriented reference lines was remarkably lower than for any oblique orientation ($p < 0.05$, Newman-Keuls post hoc test), indicating a clear preference for these two canonical directions. Note that in the upright chair position, the body axis and the axis of gravity are aligned. Chair tilt induced changes in the pattern of response variability, as indicated by a significant

![FIG. 1. Errors produced during the matching of visual orientations by subjects tested on the ground as a function of stimulus line orientation on the screen and chair orientation with respect to gravity. (A) Constant bias in repeated responses for seven stimulus orientations and three chair tilts. (B) Variable error (s.d. around the mean response) for the upright chair position. (C) Variable errors for right and left inclination of chair (±22.5°).](image-url)
cross effect between the chair and the reference line orientations \((p < 0.0027)\). When the subject was tilted to the right or left (Fig. 1C) there was no longer a clear preference for horizontal or vertical stimuli, measured in either reference frame, as indicated by the lack of a significant effect of stimulus line orientation on the variable error \((p = 0.2170\) and \(p = 0.3716\) for right and left chair tilt, respectively). Variable errors for vertical and horizontal stimuli (with respect to the head) increased significantly when the body was tilted to the right or left, compared with the upright position \((p < 0.0066)\). For oblique reference lines, chair tilt had no significant effect on response variability \((p < 0.8988)\).

We found further confirmation of the saliency of vertical and horizontal stimuli in an analysis of the response time as a function of stimulus and chair orientation. Note that the subjects were not asked to work quickly. On the contrary, they were advised not to hurry so as to maximize the accuracy of their responses. Subjects were instructed to switch a minimum of two times between the reference and variable stimulus presentations and to terminate the trial only when they were sure that the orientations of both lines were the same. The response time data presented in Table 1 (ground group) indicate that subjects in the upright position took less time, on average, to judge that the variable stimulus was aligned with a vertical or horizontal reference line than when the task was performed for oblique reference lines. In the upright position, the effect of reference line orientation on response time was highly significant \((p < 0.0001)\). The lack of a significant main effect for the reference line orientation when the chair was tilted to the left or right \((p = 0.7249\) and \(p = 0.0581\), respectively) and a significant interaction effect between the reference line and chair orientations in a two-factor ANOVA analysis \((p < 0.002)\) indicate that chair orientation also influenced the time required to accurately judge the stimulus alignment. More specifically, the preference for vertically and horizontally oriented stimuli is reduced or disappears when the body is tilted with respect to gravity.

These 1 \(g\) results lead us to conclude that the CNS represents visual orientations in a reference frame having clearly defined vertical and horizontal axes. Furthermore, the CNS uses both body-fixed (head, retinal or trunk axis) and gravity-fixed information to define the horizontal and vertical directions. The data do not suggest that either source of information dominates in the perceptual processes. If visual information was predominant, one should continue to see minimal variable error and response time for stimulus lines aligned with 0° and 90° in the head/body reference frame for all chair inclinations.

If gravity was the dominant factor, the minima should appear for stimulus lines at 0° and 90° with respect to gravity (i.e. at orientations of \(-22.5°\) and \(67.5°\) for leftward chair tilt, and \(22.5°\) and \(112.5°\) for rightward chair tilt, with respect to the head). Instead, both types of data combine to form a coherent representation of the visually acquired line orientation. When the body and gravity axes are co-aligned, the preference for stimuli aligned with these axes is striking. When the two reference frames diverge, sharply defined reference orientations no longer emerge.

If indeed the CNS represents line orientations with respect to both a body axis and the gravitationally defined vertical, what will happen if one of these two reference frames is removed? Three cosmonauts performed the same task both on the ground (three times before and 2–3 times after flight) and aboard the space station Mir (1-2 times) after spending at least 3 weeks in the microgravity environment. The cosmonauts performed the experiment for the upright position only. Inflight, the subject was secured by belts to a chair that was in turn fixed to the space station. Thus, in-flight subjects maintained the same posture as on the ground and were held upright with respect to the stable reference provided by the station floor.

Figure 2 presents the effect of reference line orientation on response constant and variable error for cosmonauts tested on the ground and in-flight. This group of subjects does not show the cyclic pattern of mean response errors (Fig. 2A) that was
suggested by Fig. 1A, either inflight or on the ground. Nevertheless, both variable error (Fig. 2B) and response time (Table 1, flight group) show a distinct preference for vertically and horizontally oriented stimuli in both gravitational environments. 

An ANOVA analysis of variable error confirms this preference for vertically and horizontally aligned reference stimuli (stimulus orientation main effect, \( p < 0.0053 \)). This is further supported by a similar analysis for the average response times (\( p < 0.0001 \)). There was no interaction effect between the gravitational factor (0 \( g \) or 1 \( g \)) and the stimulus line orientation for constant error (\( p = 0.2107 \)), variable error (\( p = 0.6323 \)) or response time (\( p = 0.7900 \)), indicating that the preference for vertical and horizontal stimuli is equally strong in the presence or absence of gravity. We measured no significant main effect of gravity on either the constant error or the response time, indicating that subjects were able to carryout the task equally well in 0 \( g \) and 1 \( g \).

**Discussion**

The data from our ground experiments indicate a multi-sensory reference frame for the internal representation of visual orientations. This interpretation is consistent with data on the perception of the subjective vertical. When asked to indicate which way is up, subjects consistently indicate an intermediate direction between the body axis, the gravitational axis and the visual surround [6,7]. The data from the current study take this analysis a step further. Not only does the CNS use multiple sensory cues to define the subjective vertical direction, it also acquires and stores stimuli with respect to this multi-modal reference frame. It might seem that the comparison of two images should most easily be carried out in a head/retinal reference frame in the absence of head movements. However, the memory requirements of the task invoked by the sequential presentation of stimuli may be the reason that the CNS transforms visual orientations into a more general reference frame that includes gravity.

Whereas tilting the subject with respect to gravity on Earth reduced or eliminated the oblique effect for this visual task, removing gravity had no significant effect. This need not have been the case. The observed oblique effect in 1 \( g \) might conceivably depend on the presence of gravity and on the coherence between these two primary sources of orientation information (proprioceptive and gravitational). The lack of an effect of microgravity on task performance indicates that subjects can, in fact, replace the gravity-dependent reference frame identified on Earth with a body-aligned reference used on orbit. These results are also consistent with 0 \( g \) tests of subjective vertical [8] and relative object positions [9]. Note that in our experiment, subjects were not explicitly asked to identify a vertical axis, or to use terms such as above or below when generating responses. These cognitive terms are somewhat ambiguous in the absence of gravity. Instead, subjects were required to match objectively the orientation of two visual stimuli. Nevertheless, subjects performed this task more consistently and more quickly when stimuli were aligned with perceived vertical and horizontal orientations.

If cosmonauts perform this task equally well in 0 \( g \) and in 1 \( g \), why then does chair tilt modify performance on Earth? It is likely that the CNS uses a weighted combination of visual, vestibular, tactile and other cues to define the internal reference frame on Earth. When the chair is tilted, these different sources of information conflict. This might increase the uncertainty in the internal representation of the vertical and horizontal axes, or it may be that these conflicting signals combine to form an intermediate reference frame in which the canonical vertical and horizontal directions fall between the stimulus and chair orientations tested in this study. Both of these hypotheses are consistent with the tilt-induced reduction of the oblique effect for visual stimuli on the ground. In 0 \( g \), the gravitational contribution to the multi-modal reference frame is simply removed. In this case, there is no conflict between competing sensory signals, and thus the body-fixed reference frame is entirely adequate. We cannot exclude, however, an adaptation period in which the absence of gravity might perturb the internal representation of visual orientations. For verbal reports of relative

| Table 1. Mean response time ± s.d. for different stimulus line and chair orientations |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                | -22.5°          | 0.0°            | 22.5°           | 45.0°           | 67.5°           | 90.0°           | 112.5°          |
| Ground group   |                 |                 |                 |                 |                 |                 |                 |
| Upright        | 21.7 ± 8.6      | 18.1 ± 5.3*     | 20.7 ± 6.6      | 20.3 ± 6.1      | 21.7 ± 7.7      | 16.7 ± 3.5*     | 21.1 ± 6.6      |
| Right          | 21.0 ± 6.3      | 22.6 ± 8.3      | 18.1 ± 4.8      | 20.9 ± 5.7      | 19.9 ± 5.7      | 19.3 ± 6.0      | 19.9 ± 6.1      |
| Left           | 20.0 ± 6.2      | 18.5 ± 5.6      | 18.4 ± 4.7      | 19.6 ± 5.1      | 19.4 ± 4.7      | 18.5 ± 4.4      | 18.9 ± 3.9      |
| Flight group   |                 |                 |                 |                 |                 |                 |                 |
| Ground         | 16.7 ± 3.6      | 10.8 ± 2.9*     | 16.5 ± 4.5      | 16.5 ± 5.1      | 16.7 ± 5.2      | 11.2 ± 3.3*     | 14.2 ± 3.3      |
| Flight         | 14.5 ± 5.9      | 9.9 ± 4.3*      | 13.1 ± 3.7      | 14.2 ± 5.4      | 15.2 ± 4.3      | 10.1 ± 4.1*     | 12.2 ± 3.7      |
object locations, subjects shifted from a gravitational to a head-fixed reference frame after only several hours on orbit [9], but this task is not directly comparable to the matching of visual orientations. Subjects may have been forced to change their definition of ‘above’ in the absence of gravity. Indeed, for tasks more directly related to the orientation matching task described here, cosmonauts showed a slow modification of the ‘upright’ posture over the first several days of space flight [10], indicating a gradual shift to a proprioceptive reference frame. Furthermore, returning cosmonauts show an increased dependence on visual cues both in estimating the direction of the perceived vertical [11] and in the maintenance of posture [12]. We intend to test these different hypotheses during an upcoming mission aboard Mir, by testing cosmonauts during the first few days of flight and shortly after their return to Earth.

Conclusions

Measurements of response time and variability for a task of aligning visual stimuli showed a distinct preference for horizontally and vertically oriented stimuli when the body and gravitational axes are aligned. This preference was markedly decreased or disappeared when the body axis was tilted with respect to gravity but was maintained in microgravity. We conclude that subjects normally process visual orientation information in a multi-modal reference frame that combines both proprioceptive and gravitational cues, but that a proprioceptive reference frame is sufficient for this task in the absence of gravity.

References


Acknowledgements: The authors thank Professor A. Berthoz for comments on the manuscript, and the participating cosmonauts: N. Boudarin, M. Foale, A. Latzukin, J. Linenger, T. Musabaev, V. Tisbiiev and J. Voss. This work was supported by the French space agency (CNES), the Russian Fund for Fundamental Research and the program AFIRST.

Received 22 December 1998; accepted 9 February 1999