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Research report

Four types of visual mental imagery processing in upright and tilted observers

Fred W. Mast*, Giorgio Ganis, Stella Christie, Stephen M. Kosslyn

Department of Psychology, Harvard University, William James Hall, 33 Kirkland Street, Cambridge, MA 02138, USA

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Abstract

We investigated the role of body position on performance in four distinct types of mental imagery processing. Previous studies used the upright body position as standard procedure and therefore do not address the issue of whether mental imagery tasks are processed in accordance with ego-centered or gravitational coordinates. In the present study, the subjects were brought into one of three different body positions: upright, horizontal, or supine. In each of these body positions, we measured performance in four imagery tasks, which assessed (1) the ability to generate vivid, high-resolution mental images; (2) the ability to compose mental images from separate parts; (3) the ability to inspect patterns in mental images; and, (4) the ability to mentally rotate patterns in images. Not all processes were affected in the same way when subjects performed them in different body positions. Performance in the image composition and detection tasks depended on body position, whereas there was no such effect for the transformation and resolution tasks.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Reference frame; Posture; Visual cognition; Mental rotation

1. Introduction

Visual mental imagery is accomplished by a host of individual subsystems, and different combinations of these processes are used to accomplish different tasks. For example, Kosslyn et al. [20,25] studied individual differences in imagery abilities, and found that such differences reflected variations in the operation of a set of individual processes; these processes are used in forming images, 'inspecting' them, reorganizing them, and transforming them. Wallace and Hofelich [40] provided evidence that at least some distinct processes are used in transforming objects in mental images and in maintaining images over time. In addition, Hegarty and Kozhevnikov [17] showed that shape imagery (i.e. constructing vivid and detailed images of objects) and spatial imagery (i.e. representing spatial relationships between objects and imaging spatial transformations) rely on at least some distinct mechanisms. Moreover, neuroimaging studies have revealed that different types of mental imagery processes do in fact engage different brain areas; for example, mental rotation relies on distinct networks from those used in generating and inspecting images [4,19,34].

In short, there is good reason to infer that imagery (even imagery in a single sensory modality, i.e. visual) relies on a set of distinct processes. However, the operation of those processes remains to be specified. To date, researchers have not even begun to address a key issue: the nature of spatial reference frames used in different imagery processes. The present study was designed to investigate the role of body position in mental imagery processes.

Mental imagery tasks require a subjective reference frame within which the task is performed. In principle, we can distinguish between two different types of coordinates that define a spatial frame of reference, egocentric and exocentric coordinates. An egocentric frame of reference is defined by an axis of the observer's body, such as the

*Corresponding author. Department of Psychology, University of Zurich, Treichlerstrasse 10, CH-8053 Zurich, Switzerland. Tel.: +41-1-634-1560; fax: +41-1-634-4342.
E-mail address: f.mast@psychologie.unizh.ch (F.W. Mast).

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longitudinal body axis, the normally vertical retinal meridian, the midline of the trunk, or the head's z-axis. In the current context, we will consider only the unitary frame of reference of the body as a whole. In contrast, an exocentric (also known as an allocentric) reference frame is defined with respect to external space. It can be anchored to the midline of the visual environment, or the midline of individual objects or perceptual units. An allocentric reference frame can also involve other environment-centered coordinates, such as the direction of gravity. In the study reported here, we will focus on the role of the gravitational frame of reference, which is crucial for perceiving orientation, guiding movements and postural control. In the present study we investigate whether specific mental imagery processes are more closely tied to egocentric or gravitational coordinates.

Most previous behavioral studies of mental imagery have been conducted with perfectly upright subjects, and thus do not yield information about the frame of reference used in a particular type of processing. In the upright body position, the egocentric body reference frame is perfectly aligned with a gravitationally based allocentric frame of reference. Tilting the body, however, enables us to decouple the egocentric from the gravitational reference frame. The egocentric reference frame is bound to the organism, whereas the gravitational reference frame is maintained with respect to the world despite head-, body- and eye-movements. Therefore, measuring performance in different body positions can lead to insight about the reference frames involved in mental imagery tasks.

The possibly selective effects of this manipulation are especially intriguing; not all processes need be affected in the same way by differences in body orientation. In fact, several previous studies have varied the orientation of the subjects while requiring them to perform imagery tasks. However, all of these studies have focused exclusively on mental rotation. For example, Corballis et al. [7,8] tested subjects either while seated upright or with the head and/or the body tilted sideways while they mentally rotated alphanumeric characters. These researchers found that the subjective reference frame was more closely tied to gravitational than to retinal coordinates. Friedman and Hall [14] confirmed this finding, but also found strong effects of retinal stimulus misorientation. More recently, Gaunet and Berthoz [15] studied how well people recognize familiar environments when their bodies are tilted versus upright. The results support the claim that viewpoint-dependent information about spatial layout is stored in memory; subjects required more time with larger angles of orientation. However, Gaunet and Berthoz [15] found only slight effects of the gravitational frame of reference for the moderate roll tilt angle of 33° used in their study. Furthermore, studies of mental rotation with astronauts in microgravity (which eliminates gravity-receptive sensory information) initially suggested an increase in the intercept of the function relating reaction time and angular discrepancy [31]. However, a subsequent study by Leone et al. [26] showed no effect of microgravity on mental rotation. Moreover, Friederici and Levelt [13] demonstrated that people in microgravity can quickly reassign spatial coordinates from a gravitational to a retinal frame of reference. Taken together, the results from microgravity and ground-based experiments are ambiguous; no clear conclusion emerges on whether mental rotation is affected by changes in body position.

In contrast to the dearth of evidence about mental imagery, numerous researchers have studied the role of reference frames in visual perception and oculomotor control. These studies consistently demonstrate effects of the observer's position relative to gravity. For example, Buchanan-Smith and Heeley [1] have shown that discrimination thresholds for orientation are mapped onto gravitational and not retinal coordinates. Furthermore, Marendaz et al. [28] found that visual search asymmetries between a tilted line (target) among numerous vertical lines (distractors) and a vertical line (target) among numerous tilted lines (distractors) depends on gravitational coordinates. Specifically, the subjects performed best when the tilted target line was among vertical lines that were aligned with what the subjects perceived as upright. An earlier study by Corballis et al. [5] tested performance of upright and tilted subjects in a letter identification task using tachistoscopic stimulus presentation. Again, the gravitational frame of reference was key for producing effects of orientation on performance.

Several studies have also shown that the effects of visual context depend on a gravitational frame of reference; for instance, Dichgans et al. [10] demonstrated such effects with roll vection stimulation, and Zoccolotti et al. [42] demonstrated them with a rod and frame paradigm. More recently, Prinzmetal and Blake [35] have shown that the magnitude of visual illusions such as the Poggendorff- and Zöllner-illusion are increased when subjects are tilted sideways. The findings from numerous studies suggest that early visual processing is not entirely fixed to a retinal frame of reference but rather includes extra-retinal information about the head's orientation relative to gravity. The role of a gravitational frame of reference in early visual processing has also been documented in studies of reflexive eye movements, such as the vestibulo-ocular reflex [32] and the optokinetic afternystagmus [9]. Moreover, studies using single cell recordings in awake monkeys have provided striking evidence that head position relative to gravity is registered by neurons in low-level visual cortices [37] (see also [18,39], for comparable results in cats).

How might these findings be relevant to visual mental imagery? Research on mental imagery has shown that it can engage early visual processing mechanisms [8,27]. Indeed, neuroimaging studies have found that even the first cortical area to receive visual input from the eyes, Area 17, can be activated during visual mental imagery—even when the eyes are closed [23]. Additional support that early visual areas are in fact functionally involved in some forms of mental imagery comes from neuropsychology [12], and from the combined use of neuroimaging and repetitive transcranial magnetic stimulation [21]. The fact that imagery can affect early visual areas is intriguing if only because these structures contain neurons that are modulated by the gravitational frame of reference [37].

In the present study, we wanted to investigate whether there is a functional overlap between two — prima facie — distinct mechanisms: those that establish a gravitational frame of reference and those that underlie visual mental imagery. To our knowledge, only the rotation task has been previously examined when subjects are in tilted positions. We chose to administer a battery of four different imagery tasks for two reasons: (1) the different tasks tap the major types of imagery processing, and we wanted to ensure that any effects of rotation were in fact distinct from other sorts of processing. (2) The four imagery tasks were designed to draw on distinct mental imagery processes. Therefore, the reference frame manipulation induced by tilting the body offers a way to investigate further the mechanisms that underlie the different imagery processes. It is possible that not all processes are affected in the same way in different body positions. More specifically, the following expectations led us to investigate the influence of body position on performance in these four imagery tasks:

First, the combination of two completely different findings motivated our investigating the effect of body position on the resolution task of visual images: (1) Neuroimaging studies have shown that early visual areas are activated when people generate high-resolution mental images [38]. (2) A separate line of research in neurophysiology has provided evidence that orientation selectivity in early visual cortex is affected when the body is tilted sideways. These two findings together led us to study whether the ability to form high-resolution mental images is influenced by tilting the body. We expected impairment in the resolution task for the lateral body position but no specific effect for the supine position, in which the gravity-based and visual reference frames are not in conflict.

Even when objects are partially hidden, most people can figure out what the object is. The composition task draws on this ability. Only in this task are the subjects exposed to visual characters. The characters are gravitationally and retinally upright as long as the subject is in the upright body position. Tilting the body, however, leads to a misalignment of retinal and gravitational coordinate systems. Because of this misalignment, we expected the subjects to be impaired in the composition task while they were in the lateral body position, when the retinal and gravitational frame act in the same plane and are therefore competing. Because the reference frames are not in conflict in the supine position, we expected comparable performance in the supine and upright body positions.

In the inspection task the subjects have to parse and 'to look for' individual segments within the image. To our knowledge, there is no previous research on the potential effect of body position on this ability, with the exception of one study by Marendaz et al. [28]. In this study, the subjects performed a visual search task faster when they were supine compared to when they were upright. This result showed that the ability to find a target in a visual display can be influenced by extra-retinal information. We had no specific expectations for this task, but the rather surprising finding by Marendaz et al. [28] would seem to imply that we should find improved performance when the body is supine.

Finally, the transformation task requires the subjects to mentally rotate a previously memorized character. The question of whether the subjects mentally rotate to the gravitational vertical or to the retinal vertical (defined by the normally vertical retinal meridian) has been addressed in the previous studies mentioned above. In all of these studies, however, upright and tilted subjects were actually exposed to misoriented visual stimuli. Therefore, it remains unclear whether body tilt influences the perceptual encoding of misoriented stimuli and/or whether body tilts selectively affect the mental transformation process operating on an internal representation. In our task, we were able to isolate the mental transformation from processes involved in perceptual encoding. We did not expect an effect of body tilt in the supine position, and previous studies produced ambiguous results for lateral body positions.

We tested performance in not simply two body positions, as used in previous studies, but three: upright, 90° roll body tilt (i.e. lying horizontally on the side), and a 90° pitch body tilt (i.e. lying supine on the back). It is important to note that the two non-upright positions differ substantially; the supine position does not produce a spatial reference frame conflict whereas the lateral body position does.

2. Materials and methods

2.1. Subjects

Thirty-five people (17 female, 18 male, mean age 19 years, range: 18–25 years) volunteered to take part in this study, which was conducted in William James Hall, on the Harvard University campus. The subjects gave their informed consent and completed a health history questionnaire prior to participating. None of them reported any health problems and all subjects had normal or corrected-to-normal vision. The subjects were Harvard students or professionals from the Boston area. All subjects were naïve regarding the purpose of this study and they were paid for their participation. The study was approved by the Harvard University Institutional Review Board.

2.2. Visual cognition test battery

We assessed specific visual cognition processes with a novel set of four computerized tasks, which were programmed in Psyscope [3]. The visual cognition test battery was extensively pre-tested prior to this experiment. We attempted to equate task difficulty as closely as possible by pursuing an iterative test procedure, in which about 100 different subjects were tested in total. In particular, using an item-based analysis, we were able to eliminate those items that were either too difficult to be solved reliably (more than 25% of the subjects got it wrong) or generally too easy (no errors). The final set of items used for this study could be solved correctly by at least 80% of the subjects in the pilot study.

In all of the tasks, subjects see a circle with three radii that divide it into three equal-sized wedges. The wedges could be oriented in any way. A third of the circle that defines the boundary of one wedge is drawn in heavy black; a third of the circle that defines another wedge is drawn with a dashed line; and the remaining third of the circle is drawn with a fine line. The specific tasks are as follows.

2.2.1. Resolution task

The resolution task was designed to assess a person's ability to form high-resolution images. Subjects first memorize the appearance of 16 simple block letters and four numbers. Following this, they see a circle stimulus (divided into three equal segments, as described earlier) with a lowercase script character beneath. They are to visualize the corresponding block character in the circle, upright, and decide whether more of it would have been in the wedge defined by the heavy black border or the wedge defined by the dashed line. The wedge lines are positioned so that the discrimination is difficult, requiring high-resolution imagery of the characters. In this and all other tasks: (1) We administered 24 trials, with each response occurring an equal number of times and no more than three of the same response occurring in succession. (2) We recorded both response times and error rates. (3) The subjects were asked to respond as quickly as possible while remaining as accurate as possible. (4) The subjects performed four practice trials prior to the test trials. During the practice trials, they received auditory feedback and repeated the practice stimuli when their response was incorrect. The characters from the practice trials were not included in the actual test trials. The tasks are illustrated in Fig. 1.

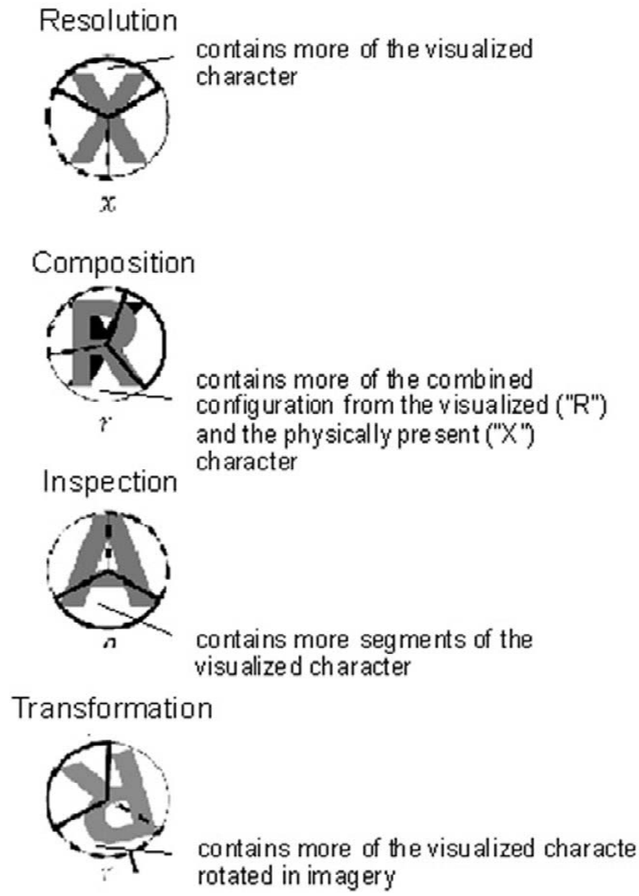

Fig. 1. The four tasks of the visual cognition test battery. The grey characters represent the imagined information the subjects were instructed to form according to the lowercase cues indicated beneath the circle. The judgments were based on comparing the wedge defined by the solid black line with the wedge defined by dashed black line. The position of the wedges was varied between trials.

2.2.2. Composition task

The composition task was designed to assess a person's ability to compose images from separate parts. The task is the same as the resolution task, with two changes: First, the discrimination is not very difficult, and thus high-resolution images are not crucial. Second, a block character now is physically presented in the circle and the subjects must meld the visualized character (cued by a lowercase script letter beneath the stimulus) with the character that is present. The subjects made their judgment on the combination of the two stimuli, the one physically present added to the visualized one. Thus, the critical aspect of this task is the ability to compose shapes to form a new whole.

2.2.3. Inspection task

This task was designed to assess a person's ability to inspect the individual parts of images. The task is the same as the resolution task, with two changes: First, the discrimination is not very difficult, and thus high-resolution images are not crucial. Second, the subjects now must decide which wedge has more segments of the visualized character. Each segment of a letter corresponds to a stroke typically made when drawing the block character.

2.2.4. Transformation task

The transformation task was designed to assess a person's ability to rotate mental images. This task is the same as the resolution task, but again with two changes: First, the discrimination is not very difficult, and thus high-resolution images are not crucial. Second, there is a 'tick mark' on the border of the circle, and the subjects were to mentally rotate the visualized character until its top was directly under the tick mark. Once the subjects mentally rotated the visualized character until its top was directly under the tick mark, they made the same judgment as in the resolution task—with the only difference being that the discrimination was easier and thus not the rate-limiting factor.

2.3. Apparatus and design

All 35 subjects were tested on all four visual cognition tasks, but body orientation was a between-subjects variable. The subjects were assigned to one of three body tilt conditions: upright, horizontal (lying horizontally on the side, right ear down), or supine (lying supine on the back). We chose these three body positions because they create the desired reference frame manipulations, as noted in Table 1.

We did not distinguish between the retinal and head/body-centered frame of reference. The gain of ocular counterrolling, which is an otolith driven reflex, is limited to about 9° when subjects are lying horizontally on the side, and is negligible when they are supine [2]. Ocular counterrolling only marginally influences the perception of visual orientation [16], and therefore can be disregarded in the current context of mental imagery.

In the upright position, the subjects sat on a chair and faced the screen of a Macintosh Powerbook G3, which was placed on a desk directly in front of them. The center of the screen was raised to eye level, 30 cm from the eyes. This distance was maintained in the supine and horizontal body orientations and thus kept the visual angle of the stimuli constant at 8°. To prevent the subjects from tilting or moving their heads, we placed a headband around each subject's forehead, which was attached to the headrest of the chair. In pilot studies, we observed that some subjects did in fact move their heads during the transformation task. When asked about their strategy, they indicated that they tended to align their head with the orientation of the tick mark, which indicates the degree of rotation—as if they were trying to replace the mental rotation by a physical rotation of the head.

Table 1
Relation of body tilt and reference frames

Body tilt condition	Reference frame alignment	Reference frame conflict
Upright	Aligned	No
Horizontal	Misaligned	Yes
Supine	Misaligned	No

The subjects responded on each trial by pushing the response keys on an external button box used in conjunction with the Psyscope software package. There were three buttons on the button box, one for the dotted section (if the subject believed that more of the character would have been in the wedge defined by the dotted line), one for the bold section (if the subject believed that more of the character would have been in the wedge defined by the heavy black border), and one to indicate that they were ready for the trials to start. Each subject kept the index and middle finger of the dominant hand on the two response keys. The keys were marked distinctly with velcro, which ensured that subjects could correctly identify the keys throughout the task. The entire lab room was darkened and a circular mask (8 cm in diameter) placed directly in front of the screen. Thus, only the part of the screen that contained the stimuli (the circle and the character underneath) was visible. We used a circular mask because Corballis et al. [5] demonstrated that a rectangular surround biases subjects to use a gravitational frame of reference.

In the horizontal position, the subject was horizontal on the right side of the body, supported by a smoothly padded foam mattress. A chunk of square foam was placed between the lower legs and the thigh, forming a 90° angle between the legs and the thighs. This ensured that the angle between the legs and the trunk remained as similar as possible in the different body tilt conditions. A pillow was used to support the subject's head, so that the position of the subject's head was in line with the trunk. The laptop computer was oriented sideways and mounted onto a standing frame in front of the subject. The screen was opened 180° relative to the keyboard. In the horizontal position, the visual stimuli and cues were kept in the same orientation with respect to the subject's head as in the upright condition, but now they were misaligned with the direction of gravity.

In the supine position, the subject was now horizontal on his or her back, on the same foam mattress. A chunk of square foam was placed under the subject's leg so that the angle of the legs with respect to the body resembled the sitting position. The laptop was mounted vertically on a standing frame, and the screen was opened 90° relative to the keyboard. The screen was parallel to the ground and the subjects were lying directly beneath the screen. Again, we used a headband to keep the subject's head in place. As in the supine and upright conditions, this arrangement ensured that the stimuli were presented parallel to the retinal vertical, but now there was no conflict between retinal and gravitational reference frames because the orientation of gravity ran exactly orthogonal to subjects' frontal plane. The gravitational cues were not relevant to the task in the supine position. This is one of the reasons why ground-based studies often use the supine position in order to explore potential effects of microgravity [13].

2.4. Questionnaires

Two questionnaires were administered after the subjects completed the computerized visual cognition test battery. These data were collected as an independent assessment of individual mental imagery ability. The VVIQ (vividness of visual mental imagery questionnaire) consists of four familiar scenes, for each of which four specific aspects have to be visualized (e.g., a rising sun: the sky clears and surrounds the sun with blueness). The items are rated on a five-point scale. The VVIQ has a high reliability [29] and is relatively unaffected by social desirability biases [36]. The SUIS (spontaneous use of imagery scale) consists of 12 separate statements, which subjects rate on a five-point scale to indicate the degree to which each statement applies to the test-taker (e.g., 'When I think of visiting a relative, I almost always have a clear mental picture of him or her'; [22]).

3. Results

We analyzed the data from the four computerized imagery tasks, examining both response time (RT) and error rates (ERs). All subjects were included for the analysis of ER. They were all correct on at least 66% of the trials in at least two tasks. Specifically, two subjects had ERs ≤ 0.33 in two tasks, nine subjects had an ERs ≤ 0.33 in three tasks, and 24 subjects had ERs ≤ 0.33 in all four tasks.

In our ANOVA on ER, we treated body position as a between-subjects independent variable (with three levels: upright, horizontal, and supine) and task type as a within-subjects variable (with four levels: resolution, inspection, composition, and transformation). This analysis revealed a main effect of task type, $F_{3,32}=15.45$, $P<0.0001$. Post-hoc analyses with Bonferroni adjustment revealed that the resolution task was more difficult than the inspection and composition tasks ($P<0.0001$), whereas there was no significant difference between the resolution and transformation tasks. There was no main effect of body position, $F_{2,32}=1.38$, $P=0.27$. However, and most important, the effects of the two variables (task type and body position) interacted, $F_{6,32}=3.33$, $P=0.005$. Separate ANOVAs on each of the four tasks revealed that performance depended on body posture in the inspection task, $F_{2,32}=3.68$, $P=0.04$, and in the composition task, $F_{2,32}=3.75$, $P=0.03$. Post-hoc analyses with Bonferroni adjustment revealed higher error rates for the inspection task in the upright orientation compared to the horizontal orientation ($P<0.02$). The opposite pattern was present for the composition task: the subjects in the upright condition made fewer errors than those in the horizontal body tilt condition ($P<0.02$). Contrary to some previous reports, the results from the transformation task did not show any effect of body posture, $F_{2,32}=0.89$, $P=0.42$. Performance in the resolution task also did not depend on body position, $F_{2,32}=1.14$, $P=0.33$. The mean ERs are shown separately for each imagery task in Fig. 2.

For the analyses of RT, we did not consider RTs from trials on which there was an error, and we excluded outliers prior to analysis; an outlier was defined as an RT greater than 2.5 times the mean of the remaining RTs in that condition for that subject.

Our ANOVA of the RTs included the same variables as the one on the ERs, but we considered only RTs from those subjects who had ERs ≤ 0.25 in each of the four tasks. This analysis revealed no main effects of body position, $F_{2,13}=0.82$, $P=0.46$, or task type, $F_{3,13}=2.60$, $P=0.07$. Moreover, the two variables did not interact, $F_{6,13}=0.29$, $P=0.94$. These data are important, however, because they demonstrate that the ER results were not a result of a speed-accuracy tradeoff. Fig. 3 shows the mean RTs for each imagery task separately.

The effect of body position on ER did not arise because of differences among subjects in the different conditions. There were no differences in VVIQ scores and SUIS scores between the subjects who were tested upright, supine, or horizontal, as revealed by separate ANOVAs with body position as between-subjects independent variable, $F_{2,32}=0.06$, $P=0.94$ for the VVIQ, and $F_{2,32}=1.08$, $P=0.35$ for the SUIS. The mean score for the VVIQ was 61.05 (range 45 to 73; maximum score: 80) and the mean score for the SUIS was 39.86 (range 27 to 50; maximum score: 60).

4. Discussion

The present study explored the role of body position on four types of mental imagery processes. Performance in the composition and inspection tasks interacted with body position, whereas there was no such effect for resolution and transformation. The fact that there was no effect of body position in the transformation task is in contrast to findings from some previous studies [6,7]. However, in the earlier studies on mental rotation, the subjects actually viewed visual stimuli of rotated alphanumeric characters while they were in a tilted body position. Unfortunately, the non-alignment of gravitational and retinal coordinates could have affected the perceptual encoding of rotated stimuli, and not simply mental rotation. We rarely see letters or numbers in any orientation other than retinally upright, and when the retinal and gravitational frames are not aligned, the apparent orientation of rotated stimuli may seem ambiguous. With the transformation task used in this study, we were able to exclude any such effect on the encoding processes; the subjects did not see the characters they had to rotate mentally. Therefore, it was possible to isolate the process of mental rotation from any processes

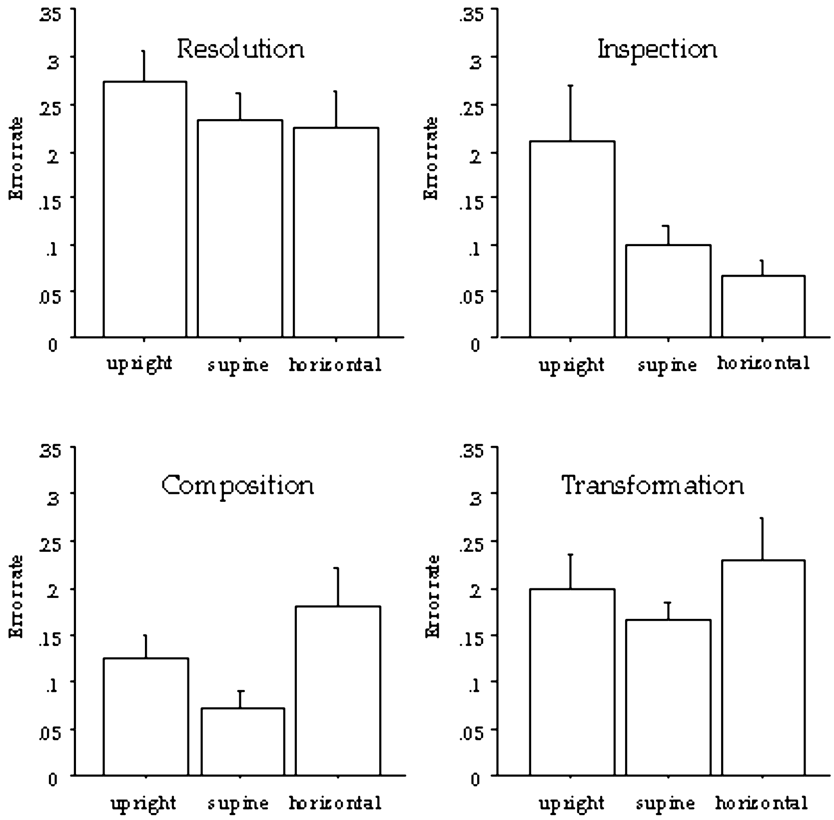

Fig. 2. The mean error rates (ER) shown separately for each visual mental imagery task in the upright, supine, and horizontal body position. Error bars indicate standard deviations.

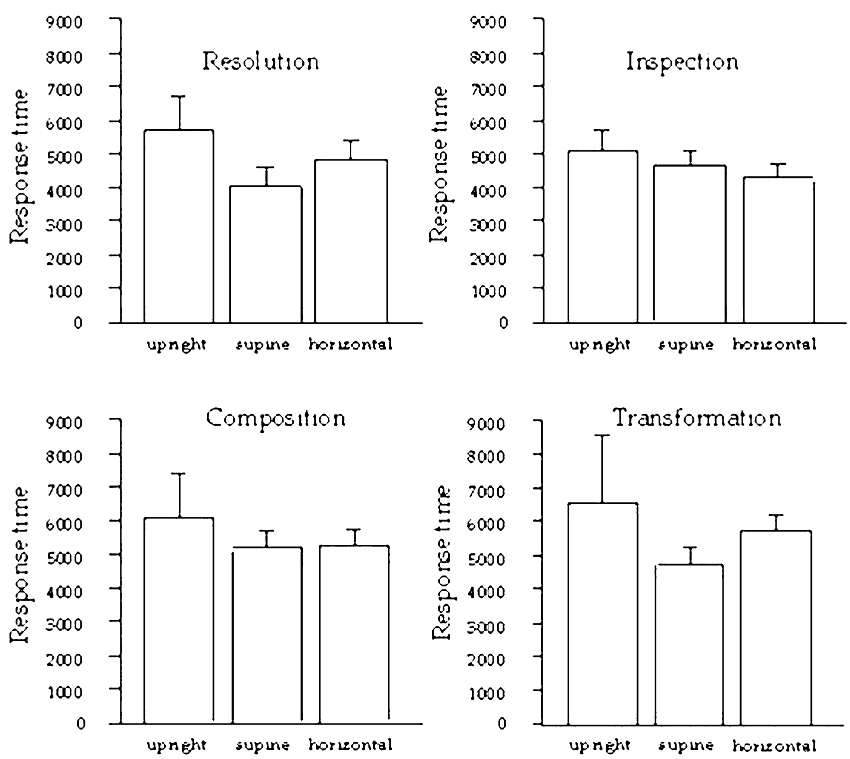

Fig. 3. The mean response times (RT) shown separately for each visual mental imagery task in the upright, supine, and horizontal body position. Error bars indicate standard errors of the mean.

involved in the perceptual encoding of rotated stimuli. Our results show that the mental transformation process itself was not influenced by body tilt (at least in the three body tilt conditions used in this study).

This finding from the transformation task fits with the results from experiments in microgravity aboard the MIR station [26]. In these experiments, mental rotation was not affected when compared to performance in the upright position on the ground. In the absence of the gravito-inertial force, there was no misalignment between reference frames and thus no problem with encoding rotated visual stimuli; the retinal coordinates provided the only spatial reference in microgravity. On the ground, however, the retinal and gravitational reference frames conflict when the subjects are tilted away from upright. Thus, these results further support the inference that the misalignment between the retinal and gravitational reference frame is responsible for the effects of body position on mental rotation reported in earlier studies.

The misalignment of reference frames might also account for the impaired performance in the composition task when the subjects were in the horizontal body position. In this task, the subjects were in fact exposed to perceptual stimuli. The subjects made more errors in the horizontal position, where the characters on the screen were still upright with respect to the subject's head reference frame but tilted with respect to gravity. Again, this finding demonstrates the consequence of an orientation ambiguity, which inevitably makes the perceptual processing involved in the composition task more difficult than in the supine body tilt condition where the reference frames are not in conflict. Presumably, the misalignment of egocentric and gravitational reference frames affects the perceptual components in the composition task rather than the internal processes used to compose mental images. It is important to note that this specific effect of body position cannot be explained by a more general effect of not being upright.

Our inference about the role of misaligned reference frames during perceptual encoding is further supported by the fact that there was no effect of body tilt in the resolution task. Although this task was more difficult than two other tasks (inspection and composition), the subjects were still able to solve it with sufficient accuracy (ER= 0.25). The resolution task shares many processes with the composition task but does not require the subjects to combine imagined information with perceptually present stimuli (or it does so to a much lesser extent). The absence of any effect of body position in the resolution task does not confirm our initial expectation, which was based on neurophysiological findings by Sauvan and Peterhans [37]. In this context, it is noteworthy that Sauvan and Peterhans [37] reported that—unlike in areas V2 and V3A—most of the neurons (83%) they investigated in area V1 preserved their retinally defined orientation selectivity when the body was tilted. It is possible that the resolution task used in this study draws more on area V1 than other early visual areas. Several neuroimaging studies have shown that high-resolution mental images of previously memorized shapes can engage Area 17 in human visual cortex [21,23,24]. The resolution task must also involve higher visual areas—if only because the mental images are generated from memory. Thus, any observed effects cannot with confidence be localized to one particular brain region. In addition, and consistent with the absence of any effect of body position in the resolution task, Fahle and Harris [11] demonstrated that subjects had comparable vernier acuity in different body positions.

Why did we find an effect of body tilt in the inspection task? Even though this finding was surprising, reports of better performance in a visual cognition task for tilted subjects are not new. Marendaz et al. [28] found that supine subjects were faster at performing a visual search task when they were tilted. It took the subjects longer to detect a straight target among tilted distractors when they were upright compared to when they were exposed to the identical stimulus but lying in the supine position. Marendaz et al.'s finding suggests that the way the subjects inspect a visual pattern depends on their own body position with respect to gravity. However, unlike in the composition task, there was no perceptual stimulus in the inspection task. One possible (entirely speculative) interpretation for this result is that it was easier to process the individual parts when the character was imagined in an apparently tilted orientation compared to when it was imagined in the upright orientation. The global level features of the upright character could have interfered stronger with the local inspection of the character's constituents.

Finally, we note that the present research not only addresses properties of basic mechanisms, but also has an applied aspect. Humans do not always maintain an upright body position when they are engaged in visual cognitive tasks. For example, a mechanic sometimes needs to put himself under the car in order to inspect different automotive parts. Pilots are often exposed to rather complex acceleration profiles, but they still need to be able to accurately operate their instruments. Moreover, microgravity is a gravitationally altered work environment, which can produce enormous perceptual consequences (known as inversion and visual reorientation illusions), which in turn can lead to severe forms of disorientation as described by Oman et al. [33]. Unlike the processing of perceptual information, we know remarkably little about how changes of the gravitational reference frame can influence performance in cognitive tasks. A better understanding of how gravity can affect cognitive functions will also help to develop potential countermeasures used for the training of astronauts to overcome the adverse effects of long-term spaceflights.

In summary, our results reveal that specific mental imagery processes can be affected by changes of body position. Sensorimotor and cognitive mechanisms are intertwined, and can mutually inhibit or facilitate each other [30,41]. Future research with combined behavioral and neuroimaging methods will help further reveal the mechanisms underlying mental imagery and whether and how these mechanisms are shared by other functions.

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