TRANSFORMATION PROCESS OF THE VISUOMOTOR MEMORY REPRESENTATION OF A TARGET IN FAR SPACE AFTER BODY ROTATION

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We examined the transformation process of visuomotor memory representation in far space. We conducted two experiments in which participants were asked to memorize target locations and, after a short delay, to point to the memorized target after body rotation to particular angles. The results were that (1) after body rotation, participants pointed to the locations displaced toward the body position before, not after, rotation, and the magnitude of the displacement increased as the rotational angle of the body increased, and (2) that participants reproduced the memorized space for pointing as shrunken after body rotation, and the ratio of reproduction decreased as the rotational angle of the body increased, to approximately 90% and 45% of the original space after 10-deg and 140-deg body rotation, respectively. We concluded that the effect of body rotation on the body-centered spatial representation and the compensative contribution of the environment-centered spatial representation in transforming the spatial memory after body rotation is considerable.

Key words: spatial memory, body-centered coordinate system, environment-centered coordinate system, pointing, body rotation

In order to produce precise movements in space using visual cues, we must be able to take into account the spatial relationships among objects in the environment and the position of our body. While visual space is recognized as a uniform entity, neuropsychological and neurophysiological studies have suggested that the external space of humans is encoded in different brain regions according to the spatial distance from the body. At least three regions of external space have been identified, including the pericutaneous space, which is the region immediately proximate to the surface of the body, the space within arm’s length, and the space beyond arm’s length (Brain, 1941; Previc, 1998).

When we attempt to operate or access a visual object, information regarding the location of the target is important. This information can be represented in different coordinate systems, including body-centered coordinate systems, in which the observer’s own body or parts of the body are referenced, and environment-centered coordinate systems, in which the localization information of the object is represented relative to other

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external objects. The location of an object can be represented in a variety of body-centered coordinate systems that depend on the type of task and the available cues. The location of an object can be represented in different body-centered coordinate systems such as eye-centered, hand-centered, and shoulder-centered systems, or a combination of eye-centered and hand-centered coordinate systems (Chieffi, Allport, & Woodin, 1999; Gentilucci, Daprati, Saetti, & Toni, 1997; Gentilucci & Negrotti, 1994, 1996; McIntyre, Stratta, Droulez, & Lacquaniti, 2000; McIntyre, Stratta, & Lacquaniti, 1997, 1998; Sochting & Flanders, 1989; Woodin & Allport, 1998). Chieffi et al. (1999) conducted a pointing task in which participants memorized the location of a target within reaching distance either under light or in the dark and were then asked to localize the target by pointing with eyes closed. The results indicated that “undershoot errors” were based on the initial location of the hands, regardless of the lighting condition. Specifically, when participants attempted to localize a target and the pointing attempt was initiated from a position near the participant’s body (between the body and the target), the final pointing position underestimated the distance to the target location, and the hand remained between the body and the target. In contrast, when the starting position was further from the body than the distance of the target from the body, the final pointing position was between the target location and the starting position. In addition, the magnitude of errors was greater when the target was observed in the dark rather than under light. It was therefore suggested that hand-centered spatial information of the target was used for pointing to memorized targets within arm’s length.

In the external space beyond arm’s length, i.e. in far space, spatial behaviors such as heading toward a destination or pointing toward a target in order to draw the joint attention with others are observed. For such behaviors, the location of the target should also be represented in a body-centered coordinate system. Yoshida and Inui (2003), for example, explored which body-centered coordinate system was utilized to perform such tasks by having participants memorize the location of a target presented 2 m ahead from them, and then asking the participants to localize the target by pointing following a three second delay. Their findings revealed that, in pointing to a memorized target in complete dark, an error occurred toward the front of the body, and the magnitude of the error could be described by a linear function of the distance between the front of the body and the target. This suggested that when a target is presented beyond arm’s length, its location is represented in the body-centered coordinate system, which is referenced to the entire body, including the head. Their results also revealed that if the frame of the target presentation area can be observed, then pointing errors decreased and relatively precise pointing could be performed. These findings demonstrated that errors directed toward the center of the body-centered coordinate system for a target in far space occurred in the same manner as when pointing to objects in near space under dark conditions. These findings also suggested that the environment-centered coordinate system, for which the reference point is based on visual objects in the environment other than the target, could be used; and on this basis, the target location is represented to enable precise pointing.

In particular, in far space out of arm’s length, it is frequent in everyday life to address or access a particular visual object when transferring or moving our own body to another
place. Any form of transferring the body in far space can be described as a combination of parallel translation and rotation of the body. In order to conduct an appropriate visuomotor behavior to a particular object at different places after body transfer in space, we must update the spatial memory representation of the object in correspondence to both types of transfer. Mergner, Nasios, Maurer, and Becker (2001) examined the updating process of visual memory for localization after body rotation. After body rotation at a rather low velocity, participants showed localization errors for all targets that deviated toward the body after rotation. If the locations of targets are represented and retained in reference to the body before rotation, as was claimed, then we would expect that, especially for the targets nearer to the body after rotation, the localization errors appear against the direction actually observed, that is in the counter direction of body rotation (McIntyer et al., 1997, 1998; Yoshida & Inui, 2003). Noting that their task was a kind of visual reproduction task of the memorized target location, it is possible to consider that the memory characteristics they revealed are dissociable from the characteristics of body-centered spatial memory for the visually guided motor tasks. Therefore, in order to reveal the update process of the visuomotor representation of target locations after body rotation, it is necessary to examine the behavioral characteristics through motor tasks directing the body to the memorized visual targets.

As evidenced by navigation in everyday life, the utilization of various objects other than the goal, including landmarks, could be more effective in appropriately addressing the memorized goal. Previous studies using pointing tasks to a memorized target with the body kept static demonstrated that the observability of objects other than the target decreased pointing errors to the target at any location (Chieffi et al., 1999; Conti & Beaubaton, 1980; Yoshida & Inui, 2003). Therefore, even in pointing to the memorized target after body rotation, the environment-centered memory representation of target locations could be expected to allow appropriate pointing. What function is served by updating the visuomotor memory representation corresponding to body rotation? In order to discuss this problem, the evidence revealed by Mergner et al. (2001) is insufficient. Thus, the behavioral characteristics of pointing to memorized visual targets after body rotation in light must be examined in detail.

In pointing to the memorized location of a target in far space after body rotation, how is the spatial memory representation in a form available to visually guided motor behavior transformed/updated? At the same time, how would the environment-centered memory representation of target location function to guide an appropriate pointing behavior with less error after body rotation? In order to examine these problems, we designed two experiments. In Experiment 1, we conducted a pointing task to a memorized target after rotating the body both under normal light and in complete dark. Under the normal light condition, participants could make use of spatial information about the target location relative to various visual objects in the environment as well as to their own body, whereas in the complete dark condition, participants could observe only the target and no other objects. Therefore, the location of the target would have to be memorize and remembered solely on the basis of the participants own body. Comparison of the pointing errors between the light and dark conditions helps us to reveal the effect of the environment-
centered spatial memory representation on pointing behavior after body rotation. In Experiment 2, we asked participants to point to the memorized target after rotating the body to different angles, which was comparable to previous studies, in complete dark in order to systematically examine how the body-centered memory concerning target location is updated after body rotation.

**EXPERIMENT 1**

*Method*

**Participants**: A total of 16 healthy adults (6 men and 10 women) participated in this experiment. Participants were randomly assigned to one of two groups of eight participants. All participants were right-handed and had normal or corrected visual acuity.

**Apparatus and stimulus**: The participants sat on a swivel chair (Fig. 1). The seat height was adjustable for each participant so that her/his eye level was at 120 cm above the floor. The rotational angle of the chair was adjustable in 10-degree steps. A revolver ring having a total of 36 holes, each 10 degrees apart, was fixed to the rotational axis below the seat. The rotational angle and direction were determined by inserting two blocks into two holes on the ring. In addition, an adjustable-length metal bar was attached vertically to the bottom of the backrest. The length of the bar was adjusted to the distance between the seat and the revolver ring. Participants could rotate their own body through a given angle by swiveling the seat and moving this bar between the blocks.

At a point 2 m ahead of the seated position of the participant, the tablet of a wireless graphic digitizer (height: 95 cm, width: 125 cm) was set up fronto-parallel to the participant, with the mid-point of the digitizer positioned 120 cm above the floor. This digitizer was used to present the target and record the pointing location of the participant. Using a PC and an LCD projector, a red light of 0.72 deg in diameter was projected onto the digitizer as a target. A total of five target projection locations were aligned at a level equivalent to the mid-length of the digitizer: the center of the digitizer (hereinafter referred to as 0 deg), and

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**Fig. 1.** Swiveling chair used for the experiments. **A.** Overview of the chair. Participants rotated their entire body until braking while remaining seated. **B.** Close-up view of the parts used for adjustment of the rotation angle. 36 holes were drilled in the revolver ring every 10 degrees. The experimenter could adjust the angle of rotation by inserting two block-shaped stoppers at the desired locations. Participants rotated their entire body until the bar, placed vertically below the seat, was braked by the stopper.
10 degrees and 5 degrees to the left of center of the digitizer (−10 deg and −5 deg), and 5 degrees and 10 degrees to the right of center (5 deg and 10 deg). The 0-deg target was just in front of the participant. The target was presented in one of five locations per trial.

During the experiment, participants wore LCD shutter goggles and a laser pointer on the index finger of their right hand in order to allow the experimenter to identify the pointing location of the participant. When a participant finished pointing, the laser pointer was turned on, and then the pointing location was projected onto the digitizer. Onset and offset of the laser pointer was controlled by the experimenter using a switch. The LCD shutter goggles were used to prevent the participants from using visual cues in learning of the target location before trial onset and during retention time. In this experiment, the participant’s pointing locations were indicated by the light of the laser pointer. The shutters were therefore closed after pointing, in order to prevent the participants from receiving visual feedback on their actual pointing performance. The experimenter controlled the onset and offset of the LCD shutter goggles using a switch. The locations of the light spots were recorded using a PC as (X, Y) coordinates (X: horizontal location, Y: vertical location) by having the experimenter touch the light of the laser pointer projected onto the digitizer with a stylus.

Procedure: The task was to memorize the location of a target presented out of the participant’s reach and, after a 3 second delay, to recall and point toward the memorized target location with the index finger of the dominant hand, either under light or in complete darkness.

Participants wore LCD shutter goggles and a laser pointer positioned on the forefinger of the dominant hand, and sat on a swiveling chair maintaining the height of their eyes at 120 cm above the floor. The shutters of the goggles were closed prior to trial onset. At the beginning of the trial, the shutters were opened, and the participants observed the target for 2 seconds. The participants could adjust only their head position so that they were fixating directly at the target when it was presented. After 2 seconds, the shutter goggles were closed, and the target was simultaneously removed. The shutters remained closed for 3 seconds. During this delay period, the participants swiveled the chair seat to rotate their entire body, including their head, 70 degrees to either the right or the left. After the delay, the shutters were reopened and participants were instructed to point to the location of the memorized target. The participants were asked to recall and point toward the target location previously presented with the index finger of their dominant hand while their bodies remained rotated. When the participants finished pointing, the shutter glasses were closed again so as not to provide visual feedback on their actual pointing locations. After the shutters had been closed, the experimenter turned on the participants’ fingertip laser pointer so as to project the participants’ pointing location onto the digitizer. The experimenter touched the projected light from the laser pointer with a stylus and then recorded the pointing locations to complete the trial.

Each of ten experimental conditions, that is for five target locations in two rotational directions, were conducted for 8 trials in pseudo-random order, which was designed so that each half of the trials included each parameter of both target locations and rotational directions in the same frequency.

Calibration of pointing locations: The participants performed pointing while wearing a fingertip laser pointer. The position of the laser pointer is slightly different from that indicated by the fingertip of the participant. Thus the projected position of the laser beam was slightly displaced from the exact position indicated by the participants’ bare fingertip. Therefore we devised a correction to account for the difference in the pointing created by wearing the laser pointer. After all experimental trials had been completed, we measured the difference between the pointing location intended by the participant and that indicated by the laser beam projection. The participant asked to sit 75 cm from the tablet of the digitizer. From this location, the participant observed the 0-deg target without body rotation (i.e. facing forwards). While watching the target at 0 deg, the participant pointed towards the target, stretching out their arm so that their fingertip pointed exactly at the target. After the participant finished pointing, we closed the shutter glasses and recorded the pointing location. We repeated this measurement eight times. After taking eight measurements, we found the direction and average angular displacement between the pointing locations and the 0-deg target for each participant. We considered these values as the corrected differences between the intended pointing location and the projected location of the laser beam, and then adjusted the pointing locations for all trials performed by a given participant.

Pointing errors: We computed pointing errors on the basis of the corrected pointing locations. For all pointing results, we identified the direction and magnitude of the horizontal displacement between the target location and the pointing location as a visual angle. For the direction of the errors, we used the sign “−” to indicate pointing deviation to the left of the target and “+” to indicate pointing deviation to the right. We
computed the average and standard error of the pointing errors after eight trials for each participant.

Experimental conditions: We manipulated the extent of the indoor illumination to set up two experimental conditions.

(A) Dark condition. One group of the participants performed all test trials in complete darkness. As such, the participants could observe only the light spot at the target location, but no other visual stimuli were apparent. Thus, they were able to encode and memorize the target location solely on the basis of the body-centered coordinate system. In order to perform pointing after body rotation, the body-centered memory representation of the target location should be transformed into the appropriate location solely on the basis of somatosensory information about the rotational direction and angle. Thus, the results of this condition should allow an exploration of how body-centered memory representation of target location is transformed to accommodate body rotation.

(B) Light condition. The other group of the participants performed all test trials with normal indoor illumination, which allowed participants to observe a variety of visual objects other than the target to be memorized. Therefore, participants were able to encode and memorize the target location in both the body-centered and environment-centered coordinate systems. In order to recall and point to the appropriate target location, the participants should transform each of the body-centered and environment-centered memory representations of target location into the appropriate position in proportion to the direction and angle of body rotation. This condition therefore would allow an examination of the basic characteristics of the pointing behavior on the basis of the transformed visuospatial memory representation of target location following body rotation.

If participants point to a target location while keeping their body stable, the magnitude of the pointing errors to the memorized target under light is much smaller than those in complete darkness, both within near space (Chieffi et al., 1999) and in far space (Yoshida & Inui, 2003). In our experiment, similar to these previous studies, the magnitude of pointing errors under light might be predicted to be smaller than that in the dark. In the dark condition, in order to transform the body-centered memory representation of target location, participants should utilize only the somatosensory information of the body rotation to perceive the direction and the amount of visuospatial memory transformation to be needed. On the other hand, under light, participants could observe a variety of visual objects other than the target. If a given participant rotates her/his body in space, the visual field may look different depending on the direction and amount of the rotation. Thus, the change in the visual field configuration could affect the perceivability of the direction and amount of the rotation of the participant’s body. If this is true, then how would be the environment-centered memory representation of target location involved in the transformation process following body rotation? A comparison of the results of the experiments under these two conditions should allow us to realize this process.

Results

Fig. 2 shows the averages and the standard errors of pointing errors for each target location under each illumination condition.

We conducted three-way ANOVA (illumination condition × rotation direction × target location). The main effects of both rotation direction and target location were significant ($F(1, 28)=16.74, p<.001$; $F(4, 112)=24.90, p<.001$). The interactions between illumination and rotation direction and between illumination and target location were also significant ($F(1, 28)=6.34, p<.001$; $F(4, 112)=11.60, p<.001$).

The pointing errors shown in Fig. 2 and the significant main effect of rotation direction revealed that when participants recalled and pointed to a memorized target location out of the participants’ reach after body rotation, the participants indicated pointing errors displacing along the counter direction to the body rotation. In addition, the significant main effect of target location revealed that for the targets nearer to the body position after rotation, the greater magnitudes of pointing errors were after body rotation. These two effects of body rotation on the direction and magnitude of pointing errors were
stronger in the dark than under light, as indicated by the significant interactions between the illumination conditions and rotation direction and/or target location.

Discussion

Three main results were obtained in this experiment.

First, when participants memorized a target location, rotated their body by 70 deg, and then pointed to the memorized target, they pointed to the deviated location along the counter direction of body rotation: if the body was rotated to the left, pointing positions were indicated to the right of the target, whereas if the body was rotated to the right, pointing positions were to the left of the target.

Second, participants showed the larger pointing errors for targets relatively nearer to the body position after rotation. As mentioned previously, Mergner et al. (2001) investigated the transformation of visual memory reproduction of targets by body rotation. They revealed that the farther targets relative to the body position after rotation were recalled in locations displaced along the direction of body rotation. In our experiment using a pointing task to the memorized targets after body rotation, we found the opposite effects on both the direction and the magnitude of the error. These results suggested that visuospatial memory representation of target locations for motor tasks such as pointing might have different behavioral characteristics from the visual memory of target location.

Third, as the significant interactions between illumination and rotation direction of
body and/or target location, these two behavioral characteristics were revealed to be much more noticeable in complete darkness than under normal light. This suggested a contribution of the environment-centered memory representation of target locations to the transformation of the target location following body rotation, and the transformation process of the body-centered memory representation of target locations following body rotation. Concerning the first finding, even in our experiments involving the pointing task after body rotation, pointing behavior characteristics were similar to those reported in previous studies (Chieffi et al., 1999; Yoshida & Inui, 2003): The pointing errors under light were much smaller than those in the dark. This result suggests that the environment-centered memory representation of target locations contributes to the errorless transformation of target location after body rotation. Yoshida and Inui (2003) argued that the average pointing errors indicated by the stable body could be well explained quantitatively as the weighted sum of two types of pointing errors. One type of pointing error was the egocentric function $D_{ego}$, which is occurred in pointing executed only based on the body-centered memory representation of target location. This type of error was observed in the complete darkness condition, and showed the displacement toward the reference point of the body-centered coordinate system which was estimated upon the entire body facing forward (see Fig. 3A). The other type of pointing error was the allocentric function $D_{allo}$, which can be estimated by assuming to be occurred in pointing executed only based on the environment-centered memory representation of target location (see Fig. 3B). Through a well-controlled experimental visual configuration, Yoshida and Inui (2003) estimated that this type of error might be indicated toward the reference point of the environment-centered coordinate system, the frame of the digitizer tablet for target presentation, similar to pointing errors that are based only on the body-centered target representation. These errors were summed with particular weights to explain the actual observed pointing errors. The weight of each of these pointing errors was considered to illustrate a contribution ratio of each memory representation for executing the actual pointing. In our experiment, the frame of the tablet as described by Yoshida and Inui (2003) was observed in the light condition. Thus the following two points can be assumed: (1) both the pointing errors in the dark conditions $D_{Dark-Left}$ and $D_{Dark-Right}$ are based solely on the body-centered memory representation of memorized target location transformed after body rotation (Fig. 3A), and (2) for the light condition, participants could utilize the environment-centered, at least the frame-centered, memory representation of target location for pointing after body rotation, and their pointing errors would include the estimated allocentric function $D_{allo}$ (Fig. 3B). Based on these assumptions, pointing errors under light were well approximated with the weighted sum model proposed by Yoshida and Inui (2003) (Fig. 3C):

$$D_{Light-Left} \approx 0.15D_{Dark-Left} + 0.85_{allo}$$
$$D_{Light-Right} \approx 0.32D_{Dark-Right} + 0.68_{allo}$$

These approximations accounted for the data in two light conditions very well ($R^2=0.986$ and 0.996, respectively). It should be noted that under the light conditions of the present
Fig. 3. Weighted sum model and its approximations to pointing errors after body rotation. A., B.: The lines in the upper row illustrate average pointing errors for every target location. Formats of abscissas and ordinates are as described in Fig. 2. Figures in the lower row demonstrate schematic illustrations of the deviation of pointing positions in reference to the body and the frame of the digitizer, respectively. The black line in Fig. A for the pointing errors only in reference to the static body, are quoted from Yoshida & Inui (2003). The light- and dark-gray lines are for the errors in pointing after rotating the body, without any cues in the environment-centered spatial memory. The line in Fig. B illustrate the estimated errors on the assumption as derived from pointing solely based on the environment-centered spatial memory in reference to the frame of the digitizer. C. Filled/unfilled circles and triangles illustrate average angular displacements in our rotation conditions of left in the dark, left in the light, right in the dark, and right in the light, respectively. Solid lines were for approximations by the weighted sum model consisting of the egocentric functions $D_{ego}$ as seen in Fig. A (same values as errors after rotation to left/right in the dark condition, $D_{Dark-Left}$ and $D_{Dark-Right}$) and the allocentric function $D_{allo}$ as seen in Fig. B. The values on abscissa and ordinate were obtained as described in Fig. 2. The equations to the right of the graphs are the approximation models; Pointing errors after rotation under two light conditions were well explained by the weighted sums of the errors under the two dark conditions, $D_{Dark-Left}$ and $D_{Dark-Right}$ and $D_{allo}$. Pointing errors $D_{Dark-Left}$ and $D_{Dark-Right}$ were described as linear functions of target location relative to body position before rotation $x$. 

A. Egocentric function $D_{ego}$

B. Estimated allocentric function $D_{allo}$

C. Approximations by the weighted sum model
study, participants could observe a variety of visual stimuli other than the target. Therefore, many environment-centered coordinate systems were available for the memorization of target locations and the execution of pointing. However, the actual observed pointing errors can be well explained by assuming only the frame-centered memory representation, which is the same estimated function \( D_{\text{allo}} \). In addition, we can deduce from equations (1) and (2) that the environment-centered memory representation of the target location has a greater contribution to the transformation of the target location after body rotation. These findings suggest that in order to point toward a memorized target location after rotating the body, among a variety of visual objects configuring the visual field, the frame of the tablet must be selected as an important visual object to serve as the environment-centered coordinate system for memorizing and recalling target locations.

We should next consider the reason why only the frame of the digitizer tablet was selected as especially important environmental information. After rotating the body in the light condition, participants could not observe the edge of the frame on the side farther from the body after rotation; however, the side nearer to the body after rotation was observable in the peripheral visual field. Thus the frame of the digitizer was one of the objects observable both before and after body rotation among the objects making up the environment. Observing these kinds of objects after body rotation would help participants to make use of the spatial information on target locations in an environment-centered coordinate system and to reduce the errors derived from pointing solely based on the body-centered target location (Yoshida & Inui, 2003). In addition, the different appearance of the frame between the before and after body rotation condition could have allowed participants to apply the frame as an effective visual cue in order to evaluate the current position of their own body relative to the environment. This would allow appropriate estimation of the direction and angle of body rotation and could be accompanied by somatosensory information of body rotation in order to guide appropriate updating of the body-centered memory representation of target locations. Therefore, participants consider the frame of the digitizer tablet as an informative object with respect to the environment for pointing after body rotation.

We will now discuss the transformation of the body-centered memory representation of target locations following body rotation. Pointing errors observed in the dark condition deviated in the counter direction to the rotation direction. Pointing behavior based only on the body-centered memory representation of the target location revealed two important characteristics: the direction toward the reference point of the body-centered coordinate system and the magnitudes of the errors increased as a linear function of the distance between the body and the target (Yoshida & Inui, 2003; Fig. 3A). This means that an error is produced in the direction of the front of the body before rotation, if pointing is performed after body rotation in the dark condition. In the results of the present experiment, pointing errors were directed toward the body position before rotation, rather than toward the current body position after rotation, suggesting that for pointing the memorized target after body rotation, participants encoded target locations in the body-centered coordinate system, for which the point of reference was set on the entire body.
before rotation and then transformed by a particular rotational angle into the appropriate location. Therefore, in the dark, pointing errors for a target nearest to the body (i.e., 0 degrees) should be at a minimum for either rotation direction. However, when participants pointed toward a target at 0 degrees, they performed pointing errors with a displacement to the right by approximately 5.7 degrees after body rotation to the left, and a displacement to the left by approximately 5.6 degrees after body rotation to the right (see the data for the target at 0 deg in Fig. 2). These results suggest that participants overestimated the angles of body rotation. Under complete darkness, it should be harder to perceive the exact angle of body rotation based only on the somatosensory information of body rotation.

In addition, the greater magnitude of the errors for the targets nearer the body after rotation illustrates that the memorized visual space shrinks after body rotation. This is considered to be one of the effects of body rotation upon the transformation of visuospatial memory representation. However, the body was rotated through 70 degrees in this experiment, which is a relatively large degree of rotation. In contrast, for instance, Mergner et al. (2001) used very small rotational angles, such as 10 degrees and 18 degrees. It is possible that, especially in complete darkness, larger rotational angles induced misperception of body rotation, resulting in 5- to 6-degree pointing errors for a target at the body center. Thus, the objective of Experiment 2 was to examine in detail the effect of the different angles of body rotation on the transformation of the body-centered memory representation of target location.

**EXPERIMENT 2**

**Method**

*Participants:* A total of 9 healthy adult (3 men and 6 women) participated in this study. All of which were right-handed and have normal or corrected visual acuity.

*Apparatus and stimulus:* The apparatuses and stimuli used for this experiment were almost identical to those used in Experiment 1. However, for this experiment, all trials and tests were performed in complete darkness.

*Procedure:* Similar to the methodology of Experiment 1, the task was to memorize a target location out of arm’s reach and, following body rotation, to point to the location of the memorized target. In Experiment 2, participants rotated their entire body, including the head, to the left or right by either 10 or 140 degrees during the 3-second delay period. Following the delay, participants attempted to recall the original target location by pointing toward the target location with the index finger of their dominant hand.

Each of twenty conditions, that is for five target locations by two rotational angles in two rotational directions, were conducted for 8 trials in pseudo-random order, which was designed in the same manner as Experiment 1.

**Results**

Fig. 4 shows the averages and standard errors of the pointing errors for each degree of rotation. Experiment 2 differs from the dark condition of Experiment 1 only in body rotational angle. We attempted to confirm the consistent effects of different rotational angles on the pointing task and, therefore, the pointing errors of Experiment 2 were analyzed in conjunction with those indicated under the dark condition of Experiment 1.
We conducted a mixed three-way ANOVA (rotational angle × rotation direction × target location). The three rotational angles were 10 degrees, 70 degrees, and 140 degrees, because the rotational angle of the body was 70 degrees in Experiment 1. In addition, the participants for this experiment were different from those for Experiment 1. Therefore, the factor of the rotational angle was assumed to be a between-subjects factor.

The main effect of the rotation direction was significant \( (F(1, 17) = 38.01, p < .001) \). No other main effects or interactions were significant.

Although the effect of target location was significant in Experiment 1, it was not significant in Experiment 2. This may be because pointing errors for a given target for both the left and right rotation directions were pooled for analysis. Therefore, we conducted a two-way ANOVA, namely, “rotational angle × target location” separately for each left and right rotational direction. For the errors after rotation to the left, we found significant the main effect of the target location \( (F(4, 92) = 14.87, p < .001) \) as well as the interaction of rotational angle and target location \( (F(8, 92) = 3.61, p = .001) \). For the errors after rotation to the right, we found the main effect of the target location \( (F(4, 92) = 16.62, p < .001) \) as well as a significant interaction of rotational angle and target location \( (F(8, 92) = 2.01, p = .05) \).

Fig. 4 and the significant main effect of rotation direction in 3-way ANOVA revealed that in pointing to the memorized target after body rotation in complete darkness, participants indicated pointing errors displaced along the counter direction to the body rotation, and the magnitude of the errors increased as the body rotational angle increased. In addition, significant main effects of rotational angle and target location as well as the significant interaction thereof revealed that participants produced larger pointing errors for targets nearer to the body after rotation and that the magnitude of the errors also increased.
Discussion

Our results illustrated that in memorizing the target location out of arm’s reach and pointing to the memorized target location after body rotation by a particular angle in complete darkness, participants indicated pointing errors along the counter direction to the rotation of the body. This finding was consistent regardless of angle of body rotation. Even in the case of much smaller body rotational angles, such as 10 degrees, pointing to the target on the reference point of the body-centered coordinate system produced errors of displacement in the counter direction of body rotation. Our results are quite different from those reported in Mergner et al. (2001), and appear to reflect one of the behavioral characteristics of pointing based solely on the body-centered memory representation of target locations. The pointing errors for the 0-deg target in all conditions, $D_0$, were also
found to be explained as a nonlinear function of body rotation angle $\theta$ (Fig. 5A).

$$D_0 \approx \begin{cases} 1.4\ln(1.1|\theta| + 1) & (\theta < 0) \\ -1.4\ln(1.1|\theta| + 1) & (\theta \geq 0) \end{cases}$$

This approximation accounted very well for the pointing errors to the 0-deg target ($R^2=0.984$), and revealed that the magnitude of pointing errors along the counter direction of body rotation increased nonlinearly as the rotational angle of the body increased.

Our results also revealed that in pointing to the memorized target after body rotation in complete darkness, participants indicated targets as being nearer to the current body position at larger displaced locations, and the magnitude of the displacement also increased as the rotational angle of the body increased. This indicates that the entire visual space, including the all target locations, is reproduced as shrunken, and that greater body rotational angles induce a greater degree of shrinkage. Thus, less visuomotor memory space than the original space is reproduced. This indicates another behavioral characteristic of the transformation of the body-centered memory representation of target locations. Here, we calculated the reproduction ratio $R$ of the size of the area including pointing positions for all targets relative to the size of the area, including all original target locations. The ratio $R$ can be described as a nonlinear function of the angle of body rotation, $\theta$, and can be approximated as

$$R \approx \exp(-0.006\theta)$$

This approximation accounts for the calculated ratio very well ($R^2=0.996$). This approximation and the graph in Fig. 5B reveal that the space reproduced by pointing after body rotation did shrink and that the ratio of reproduction decreased nonlinearly as the rotational angle of the body increased.

**General Discussion**

The experiments of the present study examined through the use of pointing tasks to memorized target locations after a delay how the visuospatial memory representation of target location for pointing is transformed after body rotation. The following are the findings of these experiments:

1. In pointing to memorized targets after body rotation, participants pointed at the locations displaced along the counter direction of body rotation, and the magnitude of displacement increased as the rotational angle of the body increased. This demonstrates that the spatial information of the target location is represented in the body-centered coordinate system, for which the point of reference is set in the body positioned before body rotation.

2. For targets nearer to the current body position, participants pointed at more displaced
locations, and the magnitude of displacement increased as the rotational angle of the body increased, demonstrating that the memorized space for pointing was recalled as shrunken through the transformation of the visuomotor memory representation of target locations after body rotation.

(3) Pointing errors under normal lighting decreased considerably in magnitude, relative to those in complete darkness. As has been reported in previous research, pointing errors in light can be described quantitatively as the weighted sum of two pointing errors that rely upon different types of spatial coordinate systems (Fig. 2C): one pointing error appeared in pointing based solely on the body-centered spatial representation, which was referenced to the body position prior to rotation (light- and dark-gray lines in Fig. 2A), and the other pointing error could be estimated as appearing in pointing based solely on the environment-centered spatial representation, specifically referenced to the frame of the target presenting area among a variety of visual objects (Fig. 2B).

In considering the above findings, the following processes may be required for the transformation of the spatial memory representation of location for target localization pointing after body rotation:

*Memory of the Target Location*

The body-centered coordinate system allows the locations of objects to be represented or memorized for executing visuomotor tasks. If pointing is performed only on the basis of this representation, pointing errors will direct toward the center of the coordinate system, and the magnitude of the error increases linearly as the distance between the target and the body increases.

*Transformation of Body-Centered Memory Representation Based on the Somatosensory Information of Rotation*

On the basis of somatosensory information on direction and angle of body rotation, the body-centered memory representation of object location is transformed/update to a particular location. Two attributes of the memorized space including the target object are thus affected by the rotation of the body.

*Effect of the perceived amount of body rotation on the location of memorized space:* It is necessary to reinforce the memorized location of the object after rotating the body, when the location was memorized with reference to the body before rotation. Thus, the participants imagine their body to rotate from the post-rotation back to the pre-rotation position. It is noted that, as mentioned in participants’ interviews, it is very hard to perceive the rotational angles of body accurately under complete darkness. Specifically, in our experiments, the angles of body rotation were perceived as being much greater than they actually were. If the participant imagines the body to rotate back by a larger angle than the actual angle, then the participant recalls the spatial memory represented in reference to the body as displaced with respect to the actual rotation direction from the original position. Therefore, the pointing positions to the objects in the memorized space, as well as just in front of the body, should be deviated in the counter direction of the body rotation.
The effect of body rotation on the size of memorized space: Our previous study suggested that the memorized space for pointing based on the body-centered coordinate system might slightly shrink (Yoshida & Inui, 2003). The results of the present study revealed that body rotation before pointing reproduced the memorized space as more shrunken than pointing without body rotation, and that the reproduction ratio decreased nonlinearly as the rotational angle of the body increased. Therefore, for pointing after body rotation, pointing positions to memorized objects at locations other than to that to the front of the body should have greater deviation than for pointing with the body maintained static.

When the body-centered spatial memory representation in reference to the body before rotation are to be updated based only on the somatosensory information of body rotation, the updated spatial memory are affected by both of these effects. Therefore, the objects including the memorized space are remembered at inaccurate locations deviated in the counter direction of body rotation by magnitudes that are dependent on the distance between the body and the objects.

Compensation by the Environment-Centered Memory Representation of Target Locations

The environment-centered memory representation, as well as the body-centered representation, of target locations is required in order to provide more precise information of target location. In this type of representation, a more effective object is referenced for the transformation of the target location after body rotation, such as an object that can be observed both before and after body rotation. It is possible that such an object will function as an environment-centered coordinate system to provide additional spatial information of the target location, as well as the additional information about the observer’s current body position relative to the observed space.

Therefore, this should allow the observers to perform appropriate movements by modifying the spatial memory representation appropriately. It is possible that an object that may function as a kind of “landmark” may be selected for the environment-centered coordinate system and then used for pointing following body rotation. We intend to explore this hypothesis in greater detail by controlling operational aspects of the visual target’s location and presentation (for example, as seen with and without the frame conditions in Yoshida & Inui (2003)), or by conducting a well-configured visual field, which is changeable regardless of the body rotation.

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