RESEARCH ARTICLE

Ease of hand rotation during active exploration of views of a 3-D object modulates view generalization

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Abstract
Active exploration of views of 3-D objects by manually controlling a device, such as a trackball, facilitates subsequent object recognition, suggesting that motor simulation contributes to object recognition. Further, biomechanical constraints, such as range of hand rotation, can affect mental rotation. Thus, the ease with which an object can be rotated by hand may modulate the facilitative effect active exploration through manual control has on object recognition. In our experiment, participants performed two sessions of a view-matching task, with a learning task administered between the two. In the learning task, one group of participants (active group) viewed and explored a novel 3-D object using their hand to rotate a handle attached to a cathode-ray tube monitor. The other group (passive group) observed on the monitor a replay of the movements of the 3-D object as manipulated by an active-group participant. Active-group participants were interviewed to determine the direction they found easiest to rotate their hand. The view-generalization performances were compared between the pre and post sessions. Although we observed a facilitative effect on the view-matching process in both groups, the active group exhibited view-dependent facilitation. The view-generalization range of the active group in the post-session was asymmetric in terms of the rotation direction. Most intriguingly, for most participants, this asymmetric change corresponded to the direction that afforded the easiest hand rotation (ulnar deviation). These findings suggest that the object-recognition process can be affected by ease of hand rotation, which is based on the biomechanical constraints of the wrist joint.

Keywords Active exploration · Embodied recognition · Mental rotation · Object recognition

Introduction

In our daily lives, we interact with the environment through our bodies. This interaction influences and imposes constraints upon our understanding of the outer world and, consequently, the role of our body and body schema in regard to recognition of outside stimuli has been emphasized in several embodiment theories (e.g., the motor theory of speech perception (Liberman et al. 1967)). In recent studies, visual mental imagery has also been explained in terms of embodiment: mental imagery is a consequence of predicted sensory feedback generated by a forward model based on motor commands, which are in turn based on the body schema (Grush 2004; Schubotz 2007). Underpinning this view, interaction between the visual and motor systems during mental rotation tasks has been reported in previous research. For instance, in one study, when participants rotated a joystick by hand in the same direction as their mental rotation, their mental-rotation performance was found to improve (Wexler et al. 1998; Wohlschläger and Wohlschläger 1998). Furthermore, it has been reported that the biomechanical constraints of the body can affect the performance of mental rotation and mental imagery of body parts; studies have shown that laterality judgments of line drawings of hands in physically awkward postures, such as a palm in a large rotation away from the midsagittal plane of the body, take longer (Sekiyama 1982; Parsons 1987, 1994). Further, Parsons (1994) conducted an experiment in which participants made various

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hand postures or performed mental imagery of making hand postures, reporting that time required to assume the hand postures or perform the imagery depended on the awkwardness of the target hand posture, a finding consistent with the performances in the abovementioned laterality judgment task. These observed effects of biomechanical constraints on mental rotation performance strongly support the theory that motor simulation affects mental imagery transformation.

Several brain-imaging studies have further shown that, during mental-rotation tasks, both motor-related areas, such as premotor and supplementary motor areas, and posterior parietal areas, which are involved in spatial processing, are activated (Cohen et al. 1996; Richter et al. 1997, 2000; Wraga et al. 2003; Lamm et al. 2007; Zacks 2008; Sasaoka et al. 2014). Considering this finding, it could be tentatively suggested that motor-related areas play a functional role in motor simulation, updating the mental imagery represented in the posterior parietal areas.

In previous studies regarding visual object recognition, the role of motor processing has been somewhat underestimated. Nevertheless, recent studies in this field have shown that visual recognition of scenes (Christou and Bülthoff 1999), novel 3-D objects (Harman et al. 1999; James et al. 2001; Sasaoka et al. 2010; Meijer and Van der Lubbe 2011), and faces (Liu et al. 2007) can be facilitated by allowing the perceiver to actively view various perspectives of the scene/object/face (e.g., through manipulating a control device such as a computer mouse or a track ball); these findings are based on comparisons with perceivers who passively observed a sequence of perspectives of objects being actively explored by other participants. This suggests that motor-system-sourced information is used for visual object recognition. However, as most previous studies adopted an explicit old/new task to test the facilitative effect of active exploration, in which the same stimulus set was used both in the recognition and learning (exploration) phases, it is not clear whether the active exploration of views facilitates the encoding of object representations or matching between learned and test stimuli. To address this issue, Sasaoka et al. (2010) investigated the effect active exploration and passive observation of a variation of views of a novel 3-D object have on view generalization performance. In this study, participants in one group (the active group) actively observed variations of novel paper-clip objects (Bülthoff and Edelman 1992) that they could rotate around the *x*-axis (horizontal axis) by manipulating a trackball with their right hand. Meanwhile, participants in the other group (passive group) passively observed, through a replay, the movements of the objects as they were actively explored by a participant in the active group. Before and after the learning task, both groups of participants performed a matching task featuring two sequentially presented views of a paper-clip object (view-matching task). The effect of active exploration/

passive observation was then assessed by comparing view-generalization performances before and after the learning task. Consequently, after the learning task, only the active group showed a significantly expanded view-generalization range for *x*-axis-rotated views. None of the objects used in the active exploration or passive observation were used in the view-matching task. These results suggested that active exploration facilitates the view-matching process, but not the encoding process. This finding again implies the involvement of the motor system in visual-object recognition; however, it remains unclear whether active hand movements (i.e., information from the motor system) are required to elicit the facilitative effect of active exploration on object recognition. If object recognition does indeed involve motor simulation based on the body schema, this suggests that the body's biomechanical constraints, such as ease of hand rotation, could affect object recognition. However, previous object-recognition studies have not addressed this issue.

Taken together, these findings lead us to the hypothesis that the biomechanical constraints of hand rotation affect the view-matching process when object recognition is being performed. To verify this hypothesis, in the present study we examined whether ease of hand rotation modulates active exploration's facilitative effect on view generalization of 3-D objects. In the present study, one group of participants observed virtual 3-D objects that they could rotate around the horizontal axis (*x*-axis) by rotating a "handle" attached to the side of a cathode-ray tube (CRT) monitor. In an attempt to give the participants a realistic sensation of physically rotating the object with their hand, we aligned the rotational axis of the handle with the horizontal axis of the object. We expected that this setting would reveal a clear effect of ease of hand rotation on view-matching performance (i.e., facilitation of view generalization for views rotated in the direction to which it was easiest to rotate the hand). We further noted that in the study by Sasaoka et al. (2010), the views that the participants could explore were limited to rotations on a single axis (*x*- or *y*-axis); here, the facilitative effect of active exploration was evident through the participants' improved ability to match views rotated around the same axis as they had used to actively explore the objects, which suggests that performing hand rotation around a certain axis affects view-matching performance for views of objects that are rotated in a corresponding fashion. Therefore, in the present study, we predicted that (1) we would observe a difference between the active and passive groups regarding the matching performances and the view-generalization range, depending on the rotation axis and views applied, and (2) we would observe asymmetric facilitation of the view-generalization range for the direction to which it was easiest to rotate the hand, particularly in the active group. Consequently, we tested for the presence of the facilitative effect regarding *x*-axis-rotated views, which corresponded to the

rotation used in the active exploration, and *y*-axis-rotation views separately.

Methods

Participants

Forty-two adults (26 males and 16 females, aged 20–33 years) participated in the experiment. All were right-handed and reported normal or corrected-to-normal vision. The Edinburgh Handedness Inventory was used to confirm their reported handedness (mean laterality coefficient 0.94, SD 0.13). Before the experiment, participants were asked to view through liquid crystal shutter glasses a stereoscopically presented stimulus (described later), and self-reported that they had normal stereo vision. The study was approved by the Unit for the Integrated Studies of the Human Mind, Kyoto University, and all participants gave written, informed consent prior to the study.

Apparatus

A personal computer (Dell Precision T7400, Dell Computers, TX, USA) was used to present stimuli and to collect participants' responses. Stimuli were displayed on a 21-inch CRT monitor (SONY GDM-F520), with a stereoscopic presentation conducted using liquid crystal shutter glasses (StereoGraphics, CrystalEyes). A custom-made handle, 10-cm long with a metal disk on the end that was 1-cm thick and 5 cm in diameter (Takei Kiki Kogyo, Japan), was attached to the right side of the CRT monitor (Fig. 1). During the learning task (described later), participants could rotate virtual stimuli displayed on the monitor around the horizontal axis by rotating the handle using their right hand. The stimuli subtended a maximum visual angle of 8° at a viewing distance of 40 cm. A chin rest was used to maintain the viewing distance. The experiment was conducted in a dark room, with one participant entering at a time.

Stimuli

To exclude the factor of previous experience of specific objects, novel 3-D objects (paper-clip objects; Bülthoff and Edelman 1992; Fig. 2) were used as stimuli. Each stimulus was created by randomly generating eight equally distant points within a unitary cube. Dodecagonal prisms centered on the line connecting two points were rendered using the Lambertian surface reflectance model. Objects for which any two lines overlapped were discarded. The stimuli were presented in the center of the monitor, on a grey background.

Fig. 1 The handle device used for active exploration, allowing participants to rotate the objects presented on the display. **a** Photograph taken from the participant side. **b** An example of extreme radial and ulnar deviations of the hand when rotating the handle device. During the learning task, participants in the active group rotated the handle, which was attached to the right side of the CRT display. See "Methods" for details

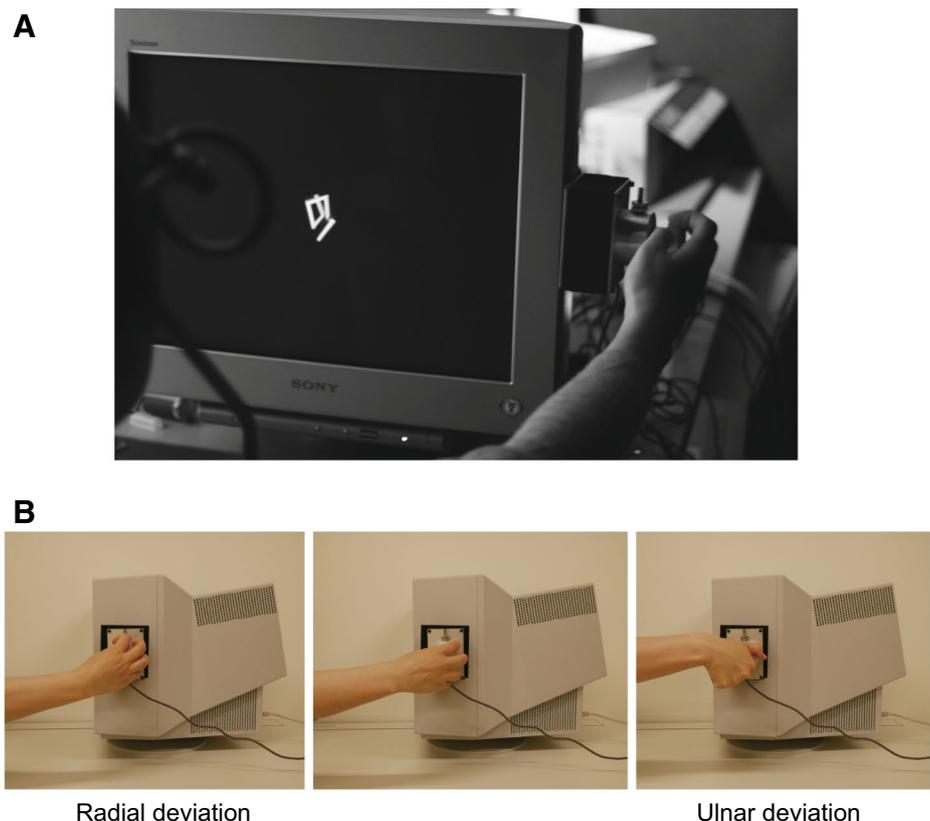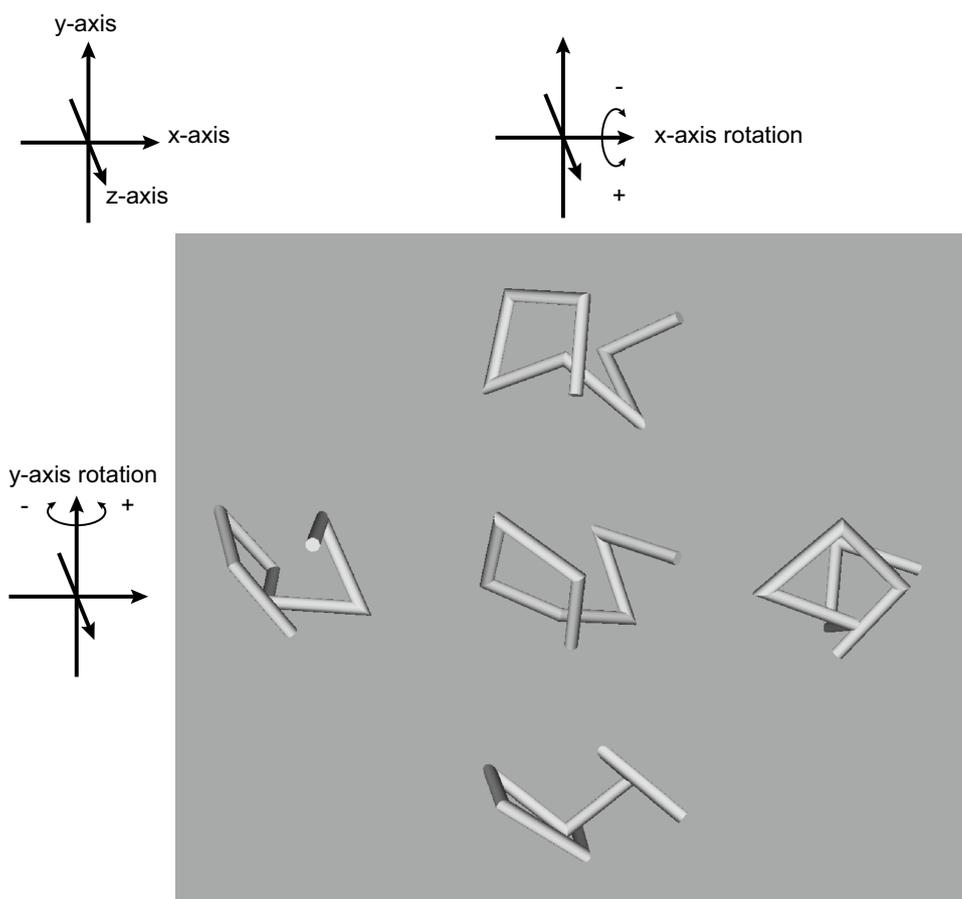Radial deviation   Ulnar deviation

Fig. 2 An example of a paper-clip object used as a stimulus. The center view is a 0° view of this object, arbitrarily decided. The left and right views are rotated from the center view around the *y*-axis, − 60° and 60°, respectively. The top and bottom views are rotated from the center view around the *x*-axis, − 60° and 60°, respectively

Procedure

The experiment consisted of two sessions of view-matching tasks (pre- and post-sessions; Fig. 3a), with a learning task performed between.

View-matching task

Figure 3b shows the procedure for a trial of the view-matching task. Each trial began with a presentation of a fixation cross in the center of the monitor, which remained in place for 500 ms. Then, a blank screen was shown for 500 ms, before a single view of one paper-clip object (first stimulus) was presented for 1500 ms. Participants were required to memorize the shape of this stimulus. This was followed by another blank screen, this time 1000-ms in duration, a fixation cross for 500 ms, a blank screen for 500 ms, and then a single view of another paper-clip object (second stimulus). At this point, participants were asked to indicate whether the second stimulus was identical to the first stimulus (was an "old" object) or was a new object by pressing a corresponding key on a numeric keypad ("4" for "old," "6" for "new"). They then rated their confidence in their response using a two-point scale ("confident" or "not very confident"), reporting their answer by pressing a corresponding key ("1" for "confident," "2" for "not very confident"). In cases when the second stimulus was an old object, it was presented with a rotation difference of 0°, ± 15°, ± 30°, ± 45°, ± 60°, or ± 90° around the x (horizontal) or y (vertical) axis in comparison to the first stimulus. Immediately after the participant self-reported his/her confidence in his/her response, the second stimulus disappeared, and the next trial began after a 1000-ms inter-trial interval. One session of the view-matching task consisted of 252 trials, and in half of these the 2nd stimulus was an old object. The object used as the first stimulus differed in every trial.

Learning task

After the pre-session of the view-matching task, participants performed a learning task. The procedure of the learning task was the same as that used in Sasaoka et al. (2010). Participants were divided into two groups (active and passive groups); each group consisted of 13 males and eight females. Participants were then presented with five different paper-clip objects, one at a time, for 20 s each; these five objects
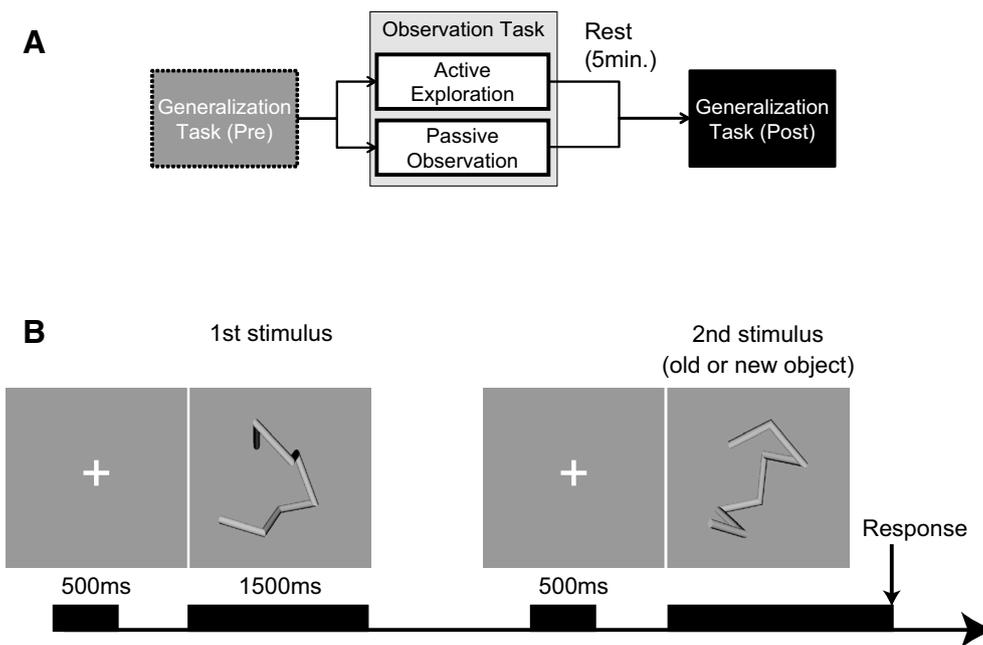
Fig. 3 Experimental design. **a** Experimental protocol. **b** Procedure for a trial in the view-matching task. See "Methods" for details

were not used in the view-matching tasks. Participants in the active group could vary their view of each paper-clip object within a range of $\pm 45°$ around the x-axis by rotating the handle on the right side of the CRT monitor using their right hand. The handle was attached to the middle of the right side of the monitor to align the rotational axis of the handle with the horizontal axis of the stimuli. Meanwhile, the i-th participant in the passive group observed, through a replay, the movements of the object in response to the active exploration of the i-th participant in the active group. Participants in both groups were instructed to pay attention to how such an object changed its appearance depending on its rotation within a $\pm 45°$ range around the x-axis, but they were informed that they did not need to memorize the shapes. After a 5-min rest, participants performed the post-session of the view-matching task. After the experiment, each participant in the active group was interviewed regarding the direction, away (ulnar deviation) or toward (radial deviation), they found easiest to rotate the handle. Before the pre-session, participants in both groups performed 20 practice trials, in which a different set of stimuli from that of the main experiment was used. Here, when the participants made an error response a beep sound was presented as feedback for 150 ms. This sound was not present during the actual experiment.

Data analysis

To assess participants' performance regarding discriminating between old and new objects, we used the area under the curve (AUC); this corresponds to the area under the receiver operating characteristic (ROC) curve, which is computed using signal-detection theory. The ROC curve is defined as the trajectory of the hit and false alarm rates in a unit square when a receiver's criterion varies continuously (e.g., when a ROC curve corresponds to a diagonal line in the square from (hit rate, false alarm rate, respectively) 0, 0–1.0, 1.0, the AUC equals 0.5, which corresponds to $d' = 0$; when a ROC curve passes through the upper left corner of the square (hit rate, false alarm rate = 1.0, 0.0, respectively), the AUC approaches 1.0, which corresponds to $d' = \infty$). The AUC is an index of accuracy that is independent of the participants' decision criteria. RScore Plus software (Harvey 2007) was used to estimate AUCs, inputting confidence rating data. We chose to use AUC as an index of accuracy to compare our results with those of Logothetis et al. (1994) and Sasaoka et al. (2010).

To evaluate the effects of active exploration and passive observation on the view-generalization range, a modified Gaussian function, which has two different values of standard deviation (σ_{minus}, σ_{plus}) (Sasaoka et al. 2010), was fitted to the AUCs for each participant. This asymmetric Gaussian function ($G_{asymmetric}$) is described by

$$G_{\text{asymmetric}}(\theta; \sigma_{\text{minus}}, \sigma_{\text{plus}}, b, c)$$
$$= \begin{cases} 1 - c & \theta = 0 \\ b + (1-b-c)\exp\left(\frac{-\theta^2}{2\sigma_{\text{minus}}^2}\right) & \theta < 0 \\ b + (1-b-c)\exp\left(\frac{-\theta^2}{2\sigma_{\text{plus}}^2}\right) & \theta > 0 \end{cases},$$

where θ is the angle of rotation from the 1st stimulus, σ_{minus} is the width of the Gaussian for $\theta < 0$, σ_{plus} is the width of the Gaussian for $\theta > 0$, b is the lower boundary, and $1 - c$ is the upper boundary. This function was originally introduced in Sasaoka et al. (2010), and is suitable for the present study for the following two reasons. First, Logothetis et al. (1994) demonstrated that a Gaussian function successfully described the profile of view-generalization performance when AUCs were plotted as a function of the rotation difference between the old and new views of objects. Second, Sasaoka et al. (2010) further found that the range of said view generalization can differ between the plus and minus directions of rotation, leading to an asymmetric view-generalization profile, which is consistent with the modified Gaussian function defined above. We thus fitted the asymmetric Gaussian function to the data of the AUCs for each participant by least squares, under the constraint that the upper bound $1 - c$ is common between the axes of rotation (x and y). This nonlinear least squares problem was solved using the quasi-Newton method.

Based on our hypothesis, it could be predicted that there would be a significant interaction between the factors of group and session, a three-way interaction among the factors of group, session, and view or axis, or even a four-way interaction (group, session, view, and axis). Meanwhile, for sigma values, there would be a significant interaction between the factors of group and session, a three-way interaction among the factors of group, session, and axis or direction, or a four-way interaction among group, session, view, and direction.

Results

Figures 4 and 5 show the AUC, averaged using the scores of 21 participants from each group, as a function of the angular difference between the first and second stimuli. Figure 4 shows the AUCs for *x*-axis-rotated views, while Fig. 5 shows the AUCs for *y*-axis-rotated views. In these figures, the results for the active group and for the passive group are shown on the left and right sides of each figure, respectively. The curves in each figure were produced by fitting an asymmetric Gaussian function (described above) to the AUCs representing the averages of the participants.

To examine the effects of active exploration and passive observation in a view-wise manner, we conducted a four-way repeated-measures analysis of variance (ANOVA) on the AUCs, using the factors of group (active, passive), session (pre, post), axis (*x*-axis, *y*-axis), and view ($0°$, $\pm 15°$, $\pm 30°$, $\pm 45°$, $\pm 60°$, and $\pm 90°$) (Table 1). In this study, our hypothesis was that there is a significant interaction between the factors of group and session, a three-way interaction among the factors of group, session, and view or axis, or a four-way interaction among group, session, view, and axis. As we predicted, we found a significant four-way interaction ($F (10, 400) = 1.886$, $p = 0.046$). Then, for every pair between the factors of group (active, passive) and axis (vertical, horizontal), we conducted a test for simple main effects and interactions. Consequently, for the *x*-axis views of the active group and the *y*-axis views of the passive group, we observed a significant interaction between session and view (*x*-axis, active: $F (10, 800) = 3.440$, $p = 0.0002$; *y*-axis, passive: $F (10, 800) = 3.201$, $p = 0.0005$). Further, to examine the effect of session for each view, we conducted analyses of simple
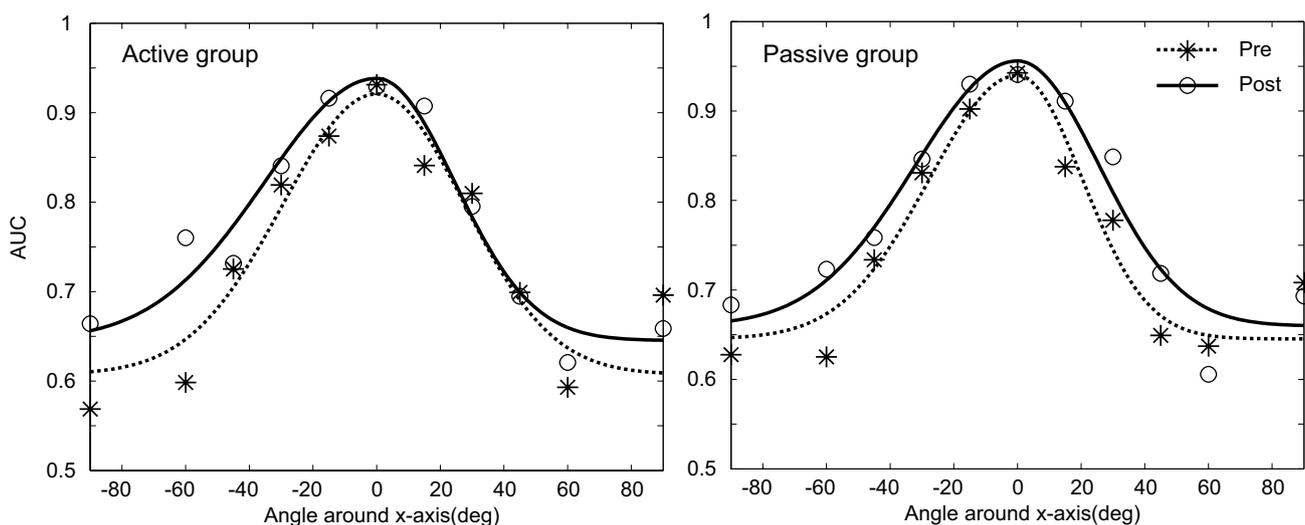

Fig. 4 AUCs for *x*-axis-rotated views. The left graph corresponds to the active group, the right graph corresponds to the passive group. "Pre" and "post" correspond to the results of the pre and post sessions, respectively
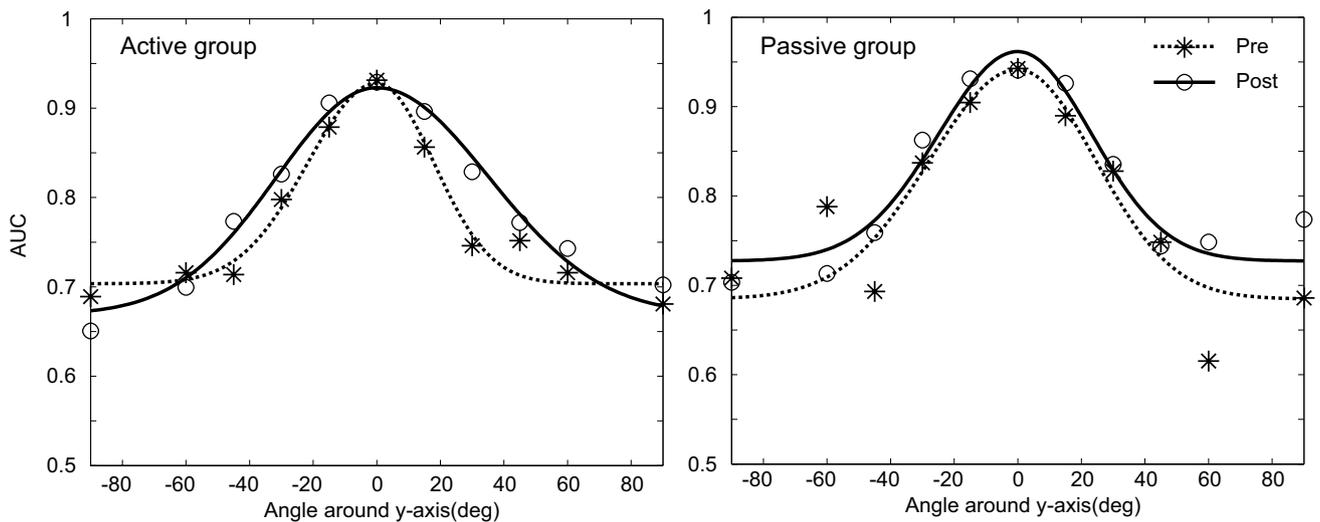
Fig. 5 AUCs for *y*-axis-rotated views. The left graph corresponds to the results of the active group, the right graph corresponds to the results of the passive group. "Pre" and "post" correspond to the results of the pre- and post-sessions, respectively

Table 1 Results of ANOVA performed on AUCs

	Sum of squares	Mean square	Mean square error	$df1$	$df2$	F	Partial η^2	p
Group	0.095	0.095	0.142	1	40	0.671	0.016	0.418
Axis	0.330	0.330	0.011	1	40	29.167	0.422	0.000**
Session	0.401	0.401	0.020	1	40	19.983	0.333	0.000**
View	16.833	1.683	0.015	10	400	114.748	0.742	0.000**
Group*axis	0.003	0.003	0.011	1	40	0.290	0.007	0.593
Group*session	0.001	0.001	0.020	1	40	0.061	0.002	0.806
Group*view	0.132	0.013	0.015	10	400	0.903	0.022	0.530
Axis*session	0.010	0.010	0.011	1	40	0.927	0.023	0.341
Axis*view	0.454	0.045	0.011	10	400	4.124	0.093	0.000**
Session*view	0.100	0.010	0.010	10	400	1.003	0.024	0.440
Group*axis*session	0.000	0.000	0.011	1	40	0.013	0.000	0.910
Group*axis*view	0.108	0.011	0.011	10	400	0.986	0.024	0.455
Group*session*view	0.073	0.007	0.010	10	400	0.738	0.018	0.688
Axis*session*view	0.596	0.060	0.010	10	400	6.062	0.132	0.000**
Group*axis*session*view	0.186	0.019	0.010	10	400	1.886	0.045	0.046*

(**$p < 0.01$, *$p < 0.05$)

effects. This revealed, for the active group, significant differences in the AUCs between the pre and post sessions at the $-90°$, $-60°$, and $15°$ views of the *x*-axis ($-90°$: $p = 0.002$; $-60°$: $p = 3.320 \times 10^{-7}$; $15°$: $p = 0.035$; we used the Holm method to conduct multiple comparisons) and, for the passive group, significant differences in the AUCs between the pre and post sessions at the $-60°$, $-45°$, $60°$, and $90°$ views of the *y*-axis ($-60°$: $p = 0.018$; $-45°$: $p = 0.037$; $60°$: $p = 0.00003$; $90°$: $p = 0.005$); however, for the passive group, at the $-60°$ view the effect was opposite to those at $-45°$, $60°$, and $90°$. We also observed a significant simple main

effect of session in the active and passive groups regarding the *x*-axis views, and in the passive group regarding the *y*-axis views [active group, *x*-axis: $F(1, 80) = 8.200$, $p = 0.005$; passive group, *x*-axis: $F(1, 80) = 9.306$, $p = 0.003$; passive group, *y*-axis: $F(1, 80) = 5.498$, $p = 0.022$]. Also, we observed in the passive group a non-significant but marginal interaction between session and view regarding the *x*-axis [$F(10, 800) = 1.824$, $p = 0.053$].

The values of sigma, estimated for each participant and averaged over the participants of each group, are shown in Fig. 6. We conducted a four-way ANOVA using the factors
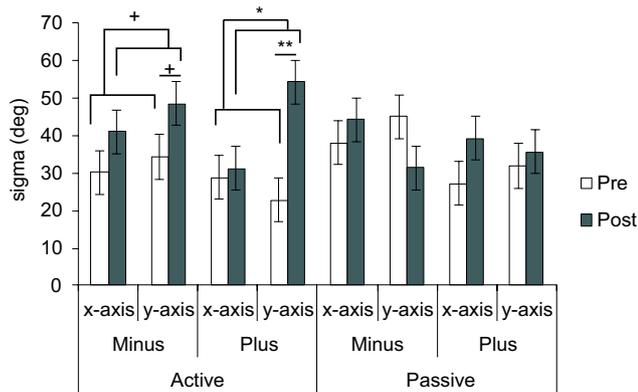
Fig. 6 Values of σs estimated in each session for each group. "Pre" and "post" correspond to the results of the pre- and post-sessions, respectively. For each participant's data, an asymmetric Gaussian function (see "Results" for details) was fitted, and optimized parameters were obtained. Error bars represent standard errors of estimated values. $**p < 0.01$, $*p < 0.05$, $+p < 0.1$

of group (active, passive), session (pre, post), direction (minus, plus), and axis (x-axis, y-axis) (Table 2). We predicted that there would be a significant interaction between the factors of group and session, a three-way interaction among the factors of group, session, and axis or direction, or a four-way interaction among group, session, axis, and direction. This ANOVA revealed no significant four-way interaction [$F (10, 40) = 0.997$, $p = 0.324$], but significant three-way interactions among group, axis, and session [$F (10, 40) = 6.271$, $p = 0.016$] and among axis, session, and direction [$F (1, 40) = 6.839$, $p = 0.013$]. Then, for every pair between the factors of group (active, passive) and direction

(minus, plus), we conducted a test for simple main effects. For the active group, in the minus direction, we observed a marginally significant simple main effect of session [$F (1, 80) = 3.520$, $p = 0.064$], and in the plus direction we observed a significant simple main effect of session [$F (1, 80) = 6.451$, $p = 0.013$] and a significant interaction between session and axis [$F (1, 80) = 8.573$, $p = 0.004$]. Meanwhile, for the passive group, in the minus direction we observed a significant interaction between session and axis [$F (1, 80) = 4.003$, $p = 0.049$], while in the plus direction we observed no significant main effect or interaction. For the minus directions of both the active and passive groups, in which we observed a significant interaction, we conducted post-hoc comparisons using the Holm method. As a result, we observed in the active group a marginally significant difference between the pre and post sessions regarding the sigma values for the minus direction of the y-axis ($p = 0.090$) and a significant difference between the pre and post sessions regarding the sigma values for the plus direction of the y-axis ($p = 0.0002$); there was no such significant difference in the passive group. Next, we focused on the asymmetry of the sigma values, conducting tests for simple main effects of direction. For the post session, we found for the active group a marginally significant simple main effect of direction regarding the x-axis [$F (1, 160) = 2.932$, $p = 0.089$], but no effect of direction regarding the y-axis; further, there was no such effect for the passive group for either the x- or y-axis.

To assess whether the time spent viewing certain object rotations during the learning task resulted in asymmetric facilitation, we examined the relative time that participants in the active group spent observing each view during this task (Fig. 7). The data for the relative time were divided into

Table 2 Results of ANOVA performed on sigma values

|	Sum of squares	Mean square	Mean square error	df1	df2	F	Partial η^2	p
Group	2.907	2.907	1422.771	1	40	0.002	0.000	0.964
Axis	732.283	732.283	1373.616	1	40	0.533	0.013	0.470
Session	5887.903	5887.903	1504.489	1	40	3.914	0.089	0.055+
Direction	2272.582	2272.582	329.553	1	40	6.896	0.147	0.012*
Group*axis	1427.818	1427.818	1373.616	1	40	1.039	0.025	0.314
Group*session	3383.604	3383.604	1504.489	1	40	2.249	0.053	0.142
Group*direction	81.714	81.714	329.553	1	40	0.248	0.006	0.621
Axis*session	22.860	22.860	766.558	1	40	0.030	0.001	0.864
Axis*direction	192.612	192.612	414.311	1	40	0.465	0.011	0.499
Session*direction	1351.336	1351.336	361.931	1	40	3.734	0.085	0.060+
Group*axis* session	4807.337	4807.337	766.558	1	40	6.271	0.136	0.016*
Group*axis* direction	2.248	2.248	414.311	1	40	0.005	0.000	0.942
Group*session* direction	271.823	271.823	361.931	1	40	0.751	0.018	0.391
Axis*session* direction	1820.088	1820.088	266.153	1	40	6.839	0.146	0.013*
Group*axis* session*direction	265.385	265.385	266.153	1	40	0.997	0.024	0.324

($*p < 0.05$, $+p < 0.1$)
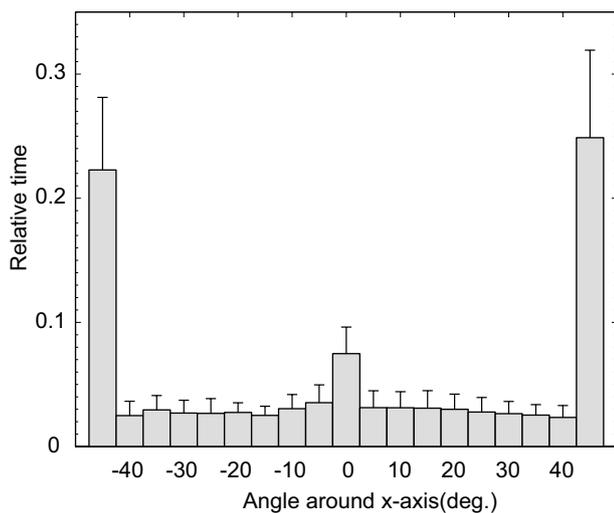
Fig. 7 Relative time spent observing each view by participants in the active group during the learning task, averaged over five objects and based on a 0° view of each object. The horizontal axis represents the angle around the *x*-axis from the 0° view of each object. Error bars represent standard deviations across participants

19 bins ($< -42.5°$, $-42.5°$ to $-37.5°$, …, $37.5°$ to $42.5°$, $> 42.5°$) and averaged over 20 participants (data from one participant could not be obtained as a result of an error in the experiment program). Figure 7 shows that all participants spent most time observing views in the range of $< -42.5°$ and $> 42.5°$. To examine whether there was a difference between the relative times spent on the plus and minus rotation views, a paired *t*-test was performed on relative time spent observing views in the range of $-2.5°$ to $-45°$ and $2.5°$ to $45°$. Consequently, no significant difference was found at the level of $p < 0.05$, although there was a trend that the view durations of rotations in the plus direction of the *x*-axis were longer ($p = 0.06$); this *plus* direction does not correspond to that for which facilitation was observed.

After the experiment, each participant in the active group was interviewed regarding the direction, away (ulnar deviation) or toward (radial deviation), they found easiest to rotate their right hand. As a result, 19 of 21 participants reported that it was easier to rotate their hand away (determined by a one-tailed binomial test to be significant, $p = 0.0001$). This direction corresponded to the minus direction in *x*-axis rotation.

Discussion

In the present study, we hypothesized that biomechanical constraints regarding hand rotation affect the view-matching process during object recognition. To verify this hypothesis, a learning task involving active exploration of novel 3-D objects was conducted, with view-generalization ranges (i.e.,

estimated σs obtained by fitting an asymmetric Gaussian function to AUCs) and the AUCs for each view (a view-wise analysis) being compared before and after (Sasaoka et al. 2010).

For views of rotations around the *x*-axis, in the post-session asymmetry of the view-generalization range between the plus and minus directions was only observed in the active group (Fig. 6). This indicates that, after the learning task, the view-generalization performance became direction-dependent for views involving rotation around the *x*-axis, which corresponded to the axis around which participants could manually rotate objects during the learning task. In the active group, view-wise analyses also showed that the effect of session was view-dependent, and significant facilitative effects were observed at $-90°$, $-60°$, and $15°$ views. In the passive group, however, there were no significant view-dependent facilitative effects. These observations are consistent with the results of Gaussian fitting. Thus, these results suggest that active exploration enhances asymmetric view generalization. For the passive group, we observed through the view-wise analysis some significant facilitation regarding *y*-axis rotation views; however, this facilitation would not contribute to sufficient expansion of the sigma values to indicate facilitation of the generalization range. For instance, at the 60° *y*-axis rotation view, the AUC value of the pre-session was located below the fitted curve, resulting in non-significant expansion regardless of the view-wise facilitation.

Furthermore, the direction to which the active group's asymmetric view generalization was observed in the post-session corresponded to ulnar deviation of the hand, which was the direction most participants (19 of 21) reported finding easiest to rotate their hand. These subjective reports are supported by many previous studies that measured the range of motion of the wrist joint. The most well-known source of the normal range of joint motion is the handbook of the American Academy of Orthopaedic Surgeons (1965), which reports that the ranges of ulnar and radial deviations are 30° and 20°, respectively. According to a review by Spilman and Pinkston (1969), 17 of 23 studies have reported that the range of motion of ulnar deviation is larger than that of radial deviation, four studies have reported that the ranges of ulnar and radial deviations are identical, and two studies have reported that ulnar deviation has a larger range than radial deviation when measured with the forearm supinated, but that the opposite is true when the forearm is pronated. Two studies (Moore 1965; Glanville and Kreezer 1937) that measured the range of motion when the hand is in a position midway between pronation and supination, as in the learning task of the present study, also reported that ulnar deviation has a larger range of motion than does radial deviation. This asymmetric range of joint motion can be explained by the

anatomical fact that during radial deviation the radial side of the carpal bones soon comes into contact with the styloid process of the radius, which restricts the range of deviation (Mansfield and Neumann 2014). In the present study, however, we only determined subjective ease of movement through interviewing the participants. Previous studies have reported that ulnar deviation is associated with less perceived stiffness than is radial deviation (Formica et al. 2012; Crisco et al. 2011); this accords with the subjective ease of movement reported by our participants, as well as anatomical facts. However, our results cannot lead to the conclusion that subjective ease of movement corresponds to the range of motion or the flexibility of the wrist joint, because we did not measure the participants' range of hand rotation, and it is possible that participants reported the direction they found easiest by considering the ease of movement up until they encountered the limit of their range of hand rotation. This issue should be addressed in future studies.

These observations suggest that the biomechanical constraints of the hand affect active-exploration-influenced view-matching, supporting our hypothesis. Sasaoka et al. (2010, Experiment four) also reported an asymmetric facilitative effect, but only in a condition in which participants actively explored y-axis rotation views using a turntable; in this condition, the facilitative effect was observed for the generalization of views of rotations in the ulnar-deviation direction (the minus direction of y-axis rotation) when the object was held from above by the right hand. Similar to Sasaoka et al.'s (2010) study, in which the rotational axis of the turntable was parallel to that of the stimuli, in the present study, the rotational axis of the control device was aligned with the stimuli displayed on the CRT monitor. In addition, participants could obtain 3-D information, as the stimuli were presented in a binocular stereo format. Active exploration of virtual objects through realistic rotation might enhance the effect of the biomechanical constraints of the hand, resulting in an asymmetric effect. In the present study, however, we could not observe a clear difference between the active and passive groups in this regard, unlike in Sasaoka et al. (2010). One possibility for this difference is that the stereoscopic presentation of the stimuli provided rich perceptual information (discussed later), resulting in a degree of facilitative effect, even during passive observation.

Analysis of the relative time spent during the learning task viewing the various rotations indicated that the participants spent more time on 0° and ± 45° views. This result replicated that reported by Sasaoka et al. (2010), in which a trackball was used for active exploration. More importantly, our result revealed that the participants had a tendency to spend more time observing rotations in the plus direction than in the minus direction, although no significant difference was observed in this regard. Accordingly, this asymmetry in estimated σs does not simply reflect how much time participants spent viewing each rotation.

Which mechanisms underlie the active-exploration-influenced asymmetric change in the generalization range observed in the post-session? In the present study, since different sets of stimuli were used for the learning and view-matching tasks, this change must have occurred in the matching process between input and stored views, not during the encoding process. This suggests that a view-transformation rule that was applicable to a category of paper-clip objects, not to a specific object, could have been learned during the learning task and used to generalize the novel views (Sasaoka et al. 2010). Tarr and Pinker (1989) suggested that the view-matching process in shape recognition comprises two subprocesses: (1) template matching, which involves storing multiple views of objects; and (2) transformation process, which involves mental rotation (multiple-views-plus-transformation (MVPT) theory). MVPT theory suggests that multiple views of objects are stored in the brain. When an input view closely resembles one of the stored views, the object can then be immediately recognized; however, when the similarity between the input and the stored views is insufficient to perform recognition through template-matching, transformation is used. These processes are related to the ventral and dorsal visual streams (Ungerleider and Mishkin 1982). In particular, the dorsal pathway is involved in visual processing of object-oriented actions (Goodale and Milner 1992), which implies that this pathway also plays an important role in hand–object interaction. However, previous neuropsychological studies have reported that the parietal cortex plays a crucial role in recognizing unconventional ("non-canonical") views of objects (Warrington and Taylor 1973; Warrington and James 1988), suggesting that the dorsal pathway is also involved in object recognition and, in particular, recognition of non-canonical views. Several neuroimaging studies have supported this view (Kosslyn et al. 1994; Sugio et al. 1999; Schendan and Stern 2007, 2008). Schendan and Stern (2007, 2008) provided neuroimaging evidence that supported MVPT theory, reporting that distinct brain networks are related to the recognition and categorization of canonical and non-canonical views of common objects; in particular, they reported that the occipito-parietal regions are involved in the transformation process of non-canonical views. These observations suggest that the two abovementioned processes, template matching and transformation, are associated with the visual information processes via the ventral and dorsal pathways in the brain, respectively. Further, in the present study, the view-wise facilitation observed regarding the x-axis-rotated views was mostly evident for views of rotations that greatly differed from that of the first stimulus; that is, views that differed from the stored views. Thus, our findings suggest

that the observed asymmetric change in view generalization occurred in the dorsal pathway during the view-matching process.

Previous brain-imaging studies have shown that motor-related areas become active when motor imagery is required to perform a mental-rotation task (Kosslyn et al. 2001; Wraga et al. 2003; de Lange et al. 2005; Sasaoka et al. 2014). For instance, in Kosslyn et al. (2001) participants performed a mental-rotation task involving 3-D block patterns, and it was found that the group who had familiarized themselves with the real block patterns by rotating them using their hand showed activation of the primary motor area, while the group who merely observed the block patterns being rotated by exogenous forces did not. Zacks (2008) suggested that when a mental-rotation task involves updating coupled object- and effector-based reference frames, the motor regions are activated. In the present study, it is possible that active exploration using the hand created a tight coupling between these reference frames. This is underpinned by the observation of a biomechanical-constraint-dependent asymmetric facilitative effect on view generalization. Previous findings that the biomechanical constraints of the hand modulate the performances of hand-laterality judgments regarding rotated hand drawings (Sekiyama 1982; Parsons 1987, 1994) also support this view. The present results, therefore, suggest that the participants in the active group used tightly coupled object- and effector-based reference frames acquired through active exploration, in contrast to the members of the passive group, who performed no such active exploration. Such coupled reference frames would have facilitated motor simulation of the rotated objects during the view-matching task, and were supported by the asymmetric effect present for the x-axis-rotated views that was consistent with the biomechanical constraints of hand rotation.

Active exploration of x-axis-rotated views also resulted in facilitated view-generalization for views of objects rotated around the y-axis, an axis around which participants did not rotate the objects in the learning task. This effect was evident in the expansion in estimated σs, but no significant main effect of session or interaction between session and view was observed in the AUC. Sasaoka et al. (2010) reported a limited effect in this regard, in that active exploration of x-axis-rotated views facilitated matching of y-axis-rotated views although, again, no significant or asymmetric expansion in the estimated σs was observed. One possible reason for this inconsistency is that the more realistic object rotation used in the present study compared to that in the previous study may have, to some degree, enhanced the view-matching process of the orthogonal-axis-rotated views. The active exploration, in which the participants rotated objects realistically, could have created a tight coupling between object- and effector-based reference frames, resulting in the acquiring of object representations associated with the hand.

In the present study, the facilitation effect was observed for views of the objects rotated in the ulnar-deviation direction if the objects had been held from below by the right hand. When an individual wishes to observe changes in an object as it rotates on its y-axis, generally he/she would hold the object from below to avoid obscuring their view of the object with his/her hand and/or arm. However, in Sasaoka et al. (2010; Experiment 4), active exploration of y-axis-rotated views using a turntable was found to only result in an expansion in the view-generalization range for the minus direction of y-axis rotation, which corresponds to ulnar deviation when the object is held from above by the right hand. In their study, the rotational axis of the turntable was parallel to that of the stimuli, but not identical, resulting in an indirect association between the hand and stimuli. Thus, the results of Sasaoka et al. (2010) can be interpreted as follows: embodied representations created through rotating a turntable (i.e., rotating with a tool that resembles holding an object from above by the hand) enhance the facilitative effect for rotations in the ulnar-deviation direction if the object were being held from above. It is possible that the present result was caused by the coupled movement between ulnar deviation and flexion motion. It has previously been demonstrated that ulnar deviation is naturally coupled with flexion motion, which is known as "dart-thrower motion" (Formica et al. 2012). In our study, the direction to which asymmetric facilitation was observed for the y-axis-rotated views corresponds to flexion motion. Thus, this asymmetry observed regarding the y-axis rotation could have resulted from the flexion motion being implicitly coupled with the ulnar deviation used to rotate the handle.

One alternative account of these results would be that the observed advantage of active exploration resulted from differences between the active and passive groups regarding perceptual factors, such as attention and predictability of movement. Differences in attention between active and passive groups were examined in an experiment by Meijer and Van der Lubbe (2011), in which the attentional difference between the active and passive groups was controlled; they consequently reported that the advantage of active exploration is not based on differences in attention between the active and passive groups. Also, the difference in predictability between the groups was examined by Sasaoka et al. (2010, Experiment three) using an experimental paradigm similar to that used in the present study. In the experiment, participants observed an object rotating at a constant speed (the speed was determined based on typical data for active exploration) within the same range as the active exploration. Consequently, no significant facilitation was observed.

Related to this issue, there is additional evidence that speaks against the motor simulation account of our results. Vannuscorps and Caramazza (2015, 2016) reported that individuals born without upper limbs show the same

biomechanical biases as typically developed individuals in action recognition and hand-laterality-judgment tasks. Their findings imply that perceptual experience, rather than motor experience, should be responsible for the observed effects of biomechanical constraints. This, in turn, again raises a possibility that the observed advantage of active exploration could be due to some differences in perceptual experience between the active and passive groups during the learning task. However, we argue against such a purely perceptual account for a few reasons. First, since we used novel 3-D paper-clip objects as stimuli, the perceptual familiarity of the object views was controlled between the active and passive groups. Next, the observed sequences of object rotations during the learning task were also matched between the active and passive groups: a participant in the passive group observed a replay of the active exploration of an object by a participant in the active group. Finally, and crucially, asymmetric view generalization for the active group is hard to predict from perceptual experience alone, because we found no significant difference in the viewing duration between the plus and minus object rotations during the learning task. All told, our results argue for a significant role of motor experience in recognition of external objects.

Moreover, Vannuscorps and Caramazza (2015) do not deny the existence of motoric simulation itself. They pointed out that hand-laterality judgment can be viewed as involving two processes: an initial perceptual analysis of the hand shape and its later verification process. The latter is an implicit simulation of the hand posture and orientation; motor disorders interfere with the verification process, which in turn affects participants' performance. Thus, their finding does not contradict our results. In this study, we observed a facilitative effect of active exploration when participants were required to match views of the object at a greatly different rotation to that shown in the first stimulus. According to MVPT theory, the matching of views of the object at a similar rotation to that shown the first stimulus was conducted using 2-D template matching; that is, matching of pure perceptual information. We observed a degree of facilitation effect caused by passive observation, but no asymmetric facilitation in sigma values; this supports the notion that both perceptual and motoric processes play a role in object recognition. This produces another possible interpretation of the result that active exploration of x-axis-rotated views facilitates the view-generalization process for orthogonal-axis-rotated views. That is, it is possible that the view-generalization process, facilitated by observation of views of rotations around the same axis, differs from that for orthogonal-axis rotation. For the y-axis-rotated views (Fig. 5, left), for instance, a facilitative, but not significant, effect in the AUC was most evident for the 30° view, but not for the views at greatly different rotations to the 0° view. It could be assumed that this facilitation occurred in the

view-matching process through template matching, not mental rotation, resulting in the difference in facilitation between the x-axis and y-axis rotations. This possibility could be examined by neuroimaging. For instance, it can be postulated that view-matching for views close to the stored view is based on template matching, which is associated with the ventral pathway, whereas that for views greatly different from the stored views is based on mental rotation, which is associated with the dorsal pathway. By investigating networks involving these view-matching processes, the mechanism of active-exploration-influenced facilitation can be clarified in greater detail.

Conclusion

The present study demonstrated that the ease of hand rotation, influenced by biomechanical constraints, affects object recognition, which was previously considered a process based mainly on visual information. The dependency on biomechanical constraints observed in the present study suggests that motor simulation of the hand is involved in the view-matching process during object recognition, which supports the theory that embodiment occurs during object recognition.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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