Relative contributions of goal representation and kinematic information to self-monitoring by chimpanzees and humans

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ABSTRACT

It is important to monitor feedback related to the intended result of an action while executing that action. This monitoring process occurs hierarchically; that is, sensorimotor processing occurs at a lower level, and conceptual representation of action goals occurs at a higher level. Although the hierarchical nature of self-monitoring may derive from the evolutionary history of humans, little is known about this cognitive process in non-human primates. This study showed that the relative contributions of kinematic information and goal representations to self-monitoring differ for chimpanzees and humans. Both species performed aiming actions whereby participants moved a cursor to hit targets. Additionally, a distractor cursor was presented simultaneously, and participants discriminated the cursor under their control from the cursor not under their control. The results showed that chimpanzees found it difficult to determine whether they were controlling the distractor when it moved toward the target, even though the distractor's kinematics and the participant's actions were dissociated. In contrast, humans performed efficiently regardless of any overlap between the presumptive and observed goals of the action. Our results suggest that goal representation, rather than motor kinematics, is the primary source of information for self-monitoring in chimpanzees, whereas humans efficiently integrate both dimensions of information. Our results are consistent with evidence showing species differences during imitation of others’ actions, and suggest that humans have evolved the cognitive capacity to monitor motor kinematics in a more flexible manner than have chimpanzees.

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1. Introduction

It is particularly important to monitor the actual results of an action and compare them with the intended results to achieve efficient execution of the action. This monitoring process is important not only for novel motor learning or online motor corrections (Imamizu, 2010; Wolpert & Ghahramani, 2000) but also to build a sense of self-agency, which is the sense of being the author of one’s own actions and of initiating and controlling those actions (Gallagher, 2000).

Recent studies have shown that a monitoring process, in which the predicted results of a voluntary action are compared with its actual results, occurs hierarchically at different cognitive processing stages (Sato, 2009; Synofzik, Vosgerau, & Newen, 2008). This process relies on different types of information, such as motor kinematics at lower levels of processing (Blakemore, Frith, & Wolpert, 1999; Sato & Yasuda, 2005; Tsakiris, Haggard, Franck, Mainey, & Sirigu, 2005) or conceptual representations of action goals at higher levels of processing (Linser & Goschke, 2007; Wegner & Wheatley, 1999).

This hierarchical nature of the self-monitoring process may be derived from the evolutionary history of humans; however, few systematic studies have investigated the self-monitoring process in non-human primates (Couchman, 2011; Eliades & Wang, 2008; Kaneko & Tomonaga,
understanding of the evolutionary origins of the way humans and other primates would extend current knowledge about agency; that is, chimpanzees can judge whether actions are self-caused or externally caused by monitoring predicted states and experiencing actual feedback (Kaneko & Tomonaga, 2011). Although examining similarities between non-humans and humans is useful for understanding evolution, dissimilarities must also be considered (Premack, 2007). The unique features of human versus chimpanzee cognitive processes remain to be elucidated in terms of both the action goal and the motor kinematic trajectory of the action.

The experiment involved four experimental conditions consisting of two within-participant factors: two levels of distractor action (goal-directed and goal-away) × two levels of the number of targets (single and multiple) and an additional two baseline conditions. Thus, a total of six conditions were included (Fig. 2). Four experimental conditions differed in terms of the occurrence of an overlap between the goal of the participant’s own action and the apparent/predicted goal of the distractor. The rationales for the conditions were as follows: Under the goal-directed/single-target condition, when the participant focused on the distractor cursor, its movement corresponded to the direction of the target the participants aimed to hit. Therefore, the goal of the participant’s own action and that of the observed action were congruent at the conceptual level even though the action kinematics involved dissociation. In contrast, the participant’s goal was less likely to be congruent with that of the distractor under the goal-directed/multiple-target condition (i.e., congruence would occur at a rate that was one-third of that under the single-target condition). Goal-away was a control condition, as the distractor did not move toward the target(s); therefore, no congruence between the participant’s intended goal and the distractor’s apparent goal was achieved under either the single or multiple conditions.

We measured the time taken to hit the first target by the self-cursor under each condition. This value included not only the time taken to discriminate the self-cursor from the distractor but also the time taken to hit the target. To isolate the time required to discriminate the cursor, we used additional baseline conditions under which the distractor was absent. We calculated the time to discriminate the cursor by subtracting the time required to hit the target under the baseline condition from that required during the goal-directed or goal-away trials.

2. Experiment 1

Chimpanzee and human participants performed a cursor-discrimination task in which they had to move a cursor to hit a target while ignoring a visually identical distractor cursor (Fig. 1, see also Movie S1). The task display was divided into two sides, and each side contained the target(s) and either the self-cursor or the distractor. Participants could control the cursor to hit the target(s) using a trackball device. The distractor cursor was moved by a pre-defined algorithm and directed toward the target(s). Thus, participants were required to discriminate the self-cursor from the distractor cursor so that they could actively control the former and hit the target(s) while ignoring the latter. The action of the distractor was determined by pre-recording an action that was performed by the participant in the past. Thus, the physical-movement properties of the cursor actions (e.g., velocity) were comparable to those of the distractor. It was not possible to distinguish between the self-cursor and the distractor based solely on the appearance of the cursors, but it was possible to do so by monitoring the intended action and the actual result in terms of both the action goal and the motor kinematic trajectory of the action.

2.1. Methods

2.1.1. Participants

Six chimpanzees (Pan troglodytes; mean age, 20 years; standard deviation [SD] = 10.1; one male and five females) at the Primate Research Institute of Kyoto University, Japan and eight humans (mean age, 21.4 years; SD = 3.0; two males and six females) participated in the experiment. The human participants were naïve with respect to the purpose and hypothesis of the experiment. The care and use of chimpanzees complied with the Guide for the Care and Use of Laboratory Primates (2002) of the Primate Use of Laboratory Primates (2002).
The human study was approved by an institutional ethics committee. All human participants had normal or corrected-to-normal vision.

2.1.2. Apparatus

The participants were tested in an experimental booth (160 × 180 × 210 cm) with acrylic panel walls. A 17-in. LCD touch-panel monitor (Gunze AV10226N02W) was used to present the stimuli. A 12-cm diameter trackball (Sanwa H55-0300-SET) was attached 34 cm below the monitor. Viewing distance was approximately 35 cm. The visual angle between the center of the monitor and the trackball was approximately 50°. This configuration prevented participants from viewing the monitor and the trackball simultaneously. Small fruit rewards were delivered to the chimpanzee participants via a universal feeder (Biomedica, BUF-310).

2.1.3. Procedure

Both humans and chimpanzees received pre-training before the main experiment to become familiarized with the experimental setting (details are described in another section below).

The main part of the experiment consisted of path-recording trials and test blocks. In the path-recording trials, the distractor cursor was not presented, and changes in the locations of cursor and target were recorded for later use as distractors in the test trials. A test block consisted of 32 trials for each of six conditions (192 trials in total; goal-directed, goal-away, and baseline single and multiple). Two additional baseline conditions (with no distractor presented) differed at the level of target number (single and multiple). The four experimental conditions differed in terms of the occurrence of an overlap between the goal of the participant’s own action and the predicted goal of the distractor. Under the single-target/goal-directed condition, if the participant focused on the distractor cursor (right cursor in this figure), the target they intended to hit corresponded to the trajectory of the distractor-cursor movement. Thus, under this condition, the goal associated with the participant’s own action and that associated with the observed action were congruent. In contrast, congruence between the participant’s goal and the apparent goal of the distractor was less likely to occur under the multiple-target/goal-directed condition (i.e., a one-third probability of congruence existed under the single-target condition).
targets). The order of trial type was pseudo-randomly counterbalanced within each block. Each chimpanzee completed eight blocks plus path-recording trials interspersed among the test blocks. Human participants performed 96 path-recording trials and then moved to one test block.

No specific instructions about how to perform the task were given to the human participants. As with the chimpanzees, human participants were required to learn the task by trial and error.

2.1.4. Path-recording trial

Participants initiated a trial by touching the start key (68 x 18 mm) shown at the bottom-center of the display. Then, a single 150 x 150-mm window appeared at the center of the display. This window contained the three targets (filled green rectangle, 5 x 5 mm) and a self-cursor (7-mm diameter, white filled circle). In this path-recording trial, no distractor stimuli were presented. The locations of the cursor and the targets were randomly chosen from 16 candidate locations, consisting of a 4 x 4-grid with a cell size of 30 x 30 mm.

The participant's task was to hit the target with the cursor. Participants could control the self-cursors by manipulating the trackball device. Once the cursor hit the target, that target disappeared and reappeared at a different location, while the cursor and other targets remained at the same positions. A trial was completed when the participant hit the target three times with the cursor. It did not matter which target the participant hit (i.e., hitting the same target at three different locations or hitting three different targets). A chime sounded to signal successful completion of a trial, and the chimpanzee participants were rewarded with a small piece of fruit.

2.1.5. Test trials

Test trials were comprised of two within-participants factors; two levels of distractor action (goal-directed and goal-away) and two levels of the number of targets (single and multiple); an additional two baseline conditions were also included. Thus, a total of six conditions were included (Fig. 2).

The flow of each trial was the same as the path-recording trials, except that the task display was divided into two and the distractors were presented on one side (Fig. 1). One side contained the target(s) and the self-cursor, while the other presented the distractor cursor and the target(s) under the goal-directed or goal-away condition. In baseline trials, no object was presented on the distractor side. The sides of the self- and distractor cursors were counterbalanced in a pseudo-random order across trials.

Under the goal-directed and goal-away conditions, the distractor cursor was presented on the other side of the display at the same moment as the self-cursor appeared. Once the participant began to manipulate the trackball, the distractor also started to move. In each trial, the action of the distractor was pre-recorded during one of the path-recording trials. The distractor cursor also moved toward the target and sometimes hit a target. At such times, the target disappeared and reappeared at a different location, as in the case of the self-cursor; however, a successful hit by the distractor was irrelevant to the completion of the task. Because the distractor action was pre-recorded, it lasted for the time needed to hit the three targets in the original path-recording trial. During the test trial, if the distractor action reached the maximum duration of the original recorded trial, the distractor cursor stopped moving and disappeared. This was also irrelevant to the completion of the task. Note that events occurring on the distractor side were independent from those occurring on the self-cursor side, with the exception of the onset of the distractor and its movement.

The location of the target on the distractor side was also derived from the path-recording trials, and the replay regime of target locations differed according to the test condition. Under the multiple-target/goal-directed condition, the actions of the cursor and target on the distractor side were the same as those in the original path-recording trial. Note that three targets were always presented during the path-recording trials. Under the single-target/goal-directed condition, the actions of the cursor were the same as those in the original path-recording trial, but only a single target, which was hit by the cursor in the original trial (three different locations for three hits), was shown. Under the multiple-target/goal-away condition and the single-target/goal-away condition, the actions of the distractor were the same as those in the original path-recording trial, but the target locations were completely novel. In these trials, the target appeared at a location that the cursor did not pass by during the original trials; thus, the cursor did not move toward the new target location. The multiple-target/goal-away condition and the single-target/goal-away condition differed in the number of target presentations.

2.1.6. Analysis

Cursor-discrimination time was calculated by subtracting the median time to hitting the target by the self-cursor under the baseline condition from that under the goal-directed or goal-away condition in each block for each participant. The calculations for single- and multiple-target tests were performed using different baseline conditions: single-target tests were calculated for single-target baseline conditions, and multiple-target tests were calculated for multiple-targets baseline conditions (Fig. 2). This procedure was followed because it was easier to hit the targets under the multiple-target than under the single-target condition. Thus, we used multiple- and single-target baseline conditions to appropriately calculate the cursor-discrimination times for the respective tests.

2.1.7. Pre-training

All chimpanzees had experienced manipulating the trackball before the study. Before the main experiment, we briefly checked to determine that the chimpanzees were able to transfer their manipulation skill to the current stimulus display. The chimpanzees completed an aiming task, in which they moved the cursor to hit a target using the trackball. This training trial was exactly the same as the baseline trials in which the distractor was absent. When participants completed >80% of a sequence of 48 trials within 10 s each, they progressed to the main
experiments. All chimpanzees required a single set of 48 trials to fulfill this criterion.

Human participants were naïve with respect to the purpose and hypothesis of the experiment, but some had had previous experience with the trackball apparatus. Regardless of past experience, each completed 96 training trials.

2.2. Results and discussion

2.2.1. Effect of goal overlap on cursor discrimination

Chimpanzees took longer to discriminate the cursor when the goal of the distractor was more likely to overlap with that of the intended target than when goal overlap was less likely to occur. In contrast, human participants did not show this effect (Fig. 3 and Fig. S1). We conducted a mixed-model two-way analysis of variance (ANOVA), with participant as a random factor and number of targets and distractor action as fixed factors, for each species.

A significant interaction was found between number of targets and distractor action in chimpanzees \((F(1,5) = 21.07, \ p = .006, \ \eta^2 = .81)\). The chimpanzees required more time to discriminate the cursor under the single-target condition, in which goal overlap was more likely to occur, than under the multiple-target condition, in which goal overlap was less likely to occur \((t(5) = 4.5, \ p = .007)\). However, when the distractor did not move toward the target (control condition), no difference was observed between single- and multiple-target conditions \((t(5) = 0.4, \ p = .684)\). The main effects of both distractor action and number of targets were significant \((F(1,5) = 14.24, \ p = .013, \ \eta^2 = .74 \text{ for distractor action}; \ F(1,5) = 18.17, \ p = .008, \ \eta^2 = .78 \text{ for number-of-targets})\). These main effects appeared to be due to the presence of an interaction and to the higher value under the single-target/goal-directed condition.

In humans, a significant main effect was observed only for distractor action \((F(1,7) = 14.24, \ p = .013, \ \eta^2 = .74)\), but neither the main effect of number of targets \((F(1,7) = 0.29, \ p = .61, \ \eta^2 = .04)\) nor the interaction was significant \((F(1,7) = 0.02, \ p = .89, \ \eta^2 = .003)\). This means that the number of targets did not affect cursor discrimination among human participants. The significant main effect of distractor action indicated that humans discriminated the cursor faster under the goal-away compared with under the goal-directed condition.

These results suggest that (in)congruence with the goal rather than motor kinematics was the primary cue used by chimpanzees for discriminating cursors; this is evident in the longer duration when goals overlapped (single-target condition) compared with when they did not (multiple-target condition). It should also be noted that the number of targets did not affect the time needed for cursor discrimination when the distractor was not directed at the target (goal-away condition). This suggests that the number of targets per se did not affect chimpanzees’ performance, whereas the congruence between the goal of the chimpanzees and the apparent goal of the distractor was a main factor in the performance of chimpanzees. On the other hand, the absence of both a main effect of the number of targets and the interaction in humans suggests that humans were able to efficiently discriminate the cursors solely based on kinematic information, even when the goals overlapped.

Notably, the absence of the goal-congruency effect in humans cannot have been due to a floor effect because cursor discrimination by humans was faster under the goal-away than under the goal-directed condition. The main effect of distractor action also indicated that humans utilized, at least to some extent, the (in)congruence of the goal representation to discriminate between the cursors. Thus, humans efficiently integrated both dimensions of goal representation and kinetic information to discriminate between the cursors.

2.2.2. Shift of attention in chimpanzees

We analyzed the distribution of the time taken to hit the target to further characterize the chimpanzees’ performance (Fig. 4). The data produced gamma distributions, which are commonly observed for response times, under the goal-away conditions involving both multiple and single targets. However, the distributions showed two peaks under the goal-directed condition. We performed a regression analysis using a finite gamma mixed distribution model for each individual (Benaglia, Chauveau, Hunter, & Young, 2009). Models including two gamma components (Akaike information criterion [AIC] across-participants mean = 802, SD = 50.7) were a better fit than was a model...
with a single gamma distribution (AIC, across-participants mean = 883, SD = 97.0), except for one chimpanzee’s performance under the goal-directed/multi-target condition (single gamma component, AIC = 823; two gamma components, AIC = 828). Trials that fit in the first peak of the distribution can be interpreted as trials in which participants initially focused on the self-cursor, whereas trials that fit in the second peak were trials in which participants focused on the distractor cursor first. Therefore, participants may have focused on one of the sides of the monitor first and then switched their focus to the other side when they recognized that the cursor on that side was not under their control. Interestingly, the relationship between the first and second peaks differed under the multiple- and single-target conditions. The second peak under the single-target condition was higher than that under the multiple-target condition, indicating that goal overlap delayed the shift of attention from the distractor cursor to the self-cursor.

This result indicates that the distractor under the single-target condition, in which the goal of the participant and that of distractor overlapped, captured the chimpanzees’ attention more strongly than did the distractor under the multiple-target condition, in which goal overlap was less likely to occur. Thus, the results support the view that (in)congruency of the goal rather than kinematic information was the primary source for self-motoring in chimpanzees.

The results for human participants are presented in histogram form in Fig. 5. The wider distribution under the goal-directed than under the goal-away condition seemed to result from the mixture of two gamma components; however, the dual peaks were not so salient. Model fitting showed that a single gamma distribution fit better (AICs for across participants; mean = 62.6, SD = 15.5) than a mixed distribution (AICs for across participants; mean = 66.5, SD = 13.3). Thus, analyses used for the chimpanzees could not be used for the human participants.

### 2.2.3. Effect of manipulation accuracy

The species difference we observed may have been caused by the degree of precision with which the participant could manipulate the trackball. If the chimpanzees had limited skill manipulating the trackball device, it may have forced them to ignore the detailed kinematics when discriminating between the cursors. Here, we addressed this issue. To determine the accuracy of trackball manipulation, we calculated manipulation efficiency (i.e., the direct distance from the initial cursor location to the target was divided by the actual trajectory to reach the target; Fig. S2). That is, a straight trajectory toward the target resulted in values close to one, whereas the value decreased toward zero for trajectories with increasing imprecision. Efficiency was calculated for the baseline trials in which the distractor was not presented. The results revealed that human participants were more precise in their manipulation than were chimpanzees (chimpanzees, $M = 0.65$, $SD = 0.10$; humans, $M = 0.79$, $SD = 0.08$; $t(12) = 2.89$, $p = 0.01$). Therefore, we conducted a follow-up experiment with eight naive human participants (mean age, 20.6 years; $SD = 1.6$; four males and four females) and introduced distortion into the contingency between the manipulation and the cursor action to decrease manipulation accuracy down to the performance level of the chimpanzees. The cursor action was rotated clockwise or counterclockwise by a particular number of degrees. For example, if a participant manipulated the trackball such that the cursor should have moved in a vertical upward direction without distortion, the cursor actually moved in a $30^\circ$ right angle relative to the vertical axis as a result of

![Fig. 4. Shift of attention from distractor cursor to self-cursor in chimpanzees. Histograms show the number of trials (vertical axis) as a function of time taken to hit the target (horizontal axis) under all four conditions. The red vertical line indicates the mean response time under the baseline condition across participants. The distribution of response times under the goal-directed condition is characterized by two peaks. The first peak reflects trials in which participants initially focused on the self-cursor, whereas the second peak reflects trials in which participants focused initially on the distractor cursor. The second peak under the single-target condition was higher than that under the multiple-target condition, indicating that goal overlap delayed the shift of attention from the distractor cursor to the self-cursor.](image-url)
the distortion. The magnitude of the distortion angle changed over time and followed a sine curve function from negative to positive with a 2-second cycle. The maximum amplitude was adjusted for each participant (36.8°, SD = 10.1). Under these conditions, manipulation efficiency of the trackball was equalized (humans under the distortion condition, M = 0.68, SD = 0.05; chimpanzees, M = 0.65, SD = 0.10; t(12) = 0.76, p = 0.46). However, cursor discrimination in humans under the distortion condition showed the same tendency as that demonstrated without distortion (Fig. S2d, F(1,7) = 0.24, p = .64, ηp² = .03 for the main effect of number of targets; F(1,7) = 4.38, p = .007, ηp² = .39 for the main effect of distractor action; F(1,7) = 0.96, p = .36, ηp² = .12 for one-way interaction). Human participants performed consistently with respect to cursor discrimination regardless of the probability of goal overlap (Fig. 3). Therefore, the species difference observed in previous experiments could not be attributed to a difference in manipulation accuracy.

2.2.4. Summary

The results of Experiment 1 showed that chimpanzees had more difficulty discriminating between cursors when goals overlapped than when goal overlap was less likely to occur. Further analysis showed that the distractor captured the chimpanzee’s attention more strongly under the single-target condition, when goals overlapped, than under the multiple-target condition, when goal overlap was less likely to occur. These goal-overlap effects were not observed in humans. Our overall results suggest that goal representation was the primary cue used by chimpanzees to discriminate between cursors and that monitoring of prediction and feedback at the level of motor kinematics contributed less to cursor discrimination. However, humans efficiently utilized both dimensions of information. We also confirmed that the species difference we observed could not be attributed to a difference in the extent of how precisely the participants could manipulate the trackball.

3. Experiment 2

The species difference in the goal-overlap effect may have been caused by the use of qualitatively different task strategies by chimpanzees and humans rather than by a difference in the relative importance of goal-related versus kinematic information in self-monitoring. The chimpanzee results may be explained by the following strategy: In each trial, participants first focused on one-half of the display and tried to hit one of the targets in that half. If the cursor in that half did not move toward the target they intended to hit, then the participants switched their attention to the other half (i.e., participants monitored the dissociation between the intended and the estimated goal of the observed cursor to efficiently execute the action, “goal efficiency monitoring”). However, human participants may have used a different strategy, based on categorical representation of self-efficiency: participants may have first tried to detect which cursor they could control and then attempted to hit the target. If this strategy were followed, the number of targets would not have affected cursor discrimination (i.e., a “self–other labeling” strategy).

Different eye-movement patterns would be predicted if the species followed these different task strategies. That is, if a self–other labeling strategy were used, participants...
would be expected to fixate on the cursor at the beginning of a trial, whereas if goal-efficiency monitoring were used, participants would be expected to fixate on the target. Additionally, different patterns would not have been observed when the self–other distinction was not required (the baseline condition) or during the later part of the trial, in which participants had already discriminated between the cursors. Thus, we measured the eye movements of participants while they performed identical tasks to investigate whether the different effects of goal overlap were due to qualitatively different task strategies between species or to a difference in the relative importance of goal-related versus kinematic information in self-monitoring.

3.1. Methods

3.1.1. Participants

Five of the six chimpanzees who participated in Experiment 1 took part in this experiment. One chimpanzee did not participate due to difficulty in controlling his posture for stable eye tracking. Eight new human participants (mean age, 19.3 years; SD = 1.6; one male and seven females) took part in this experiment.

3.1.2. Apparatus

Gaze behavior was measured with a TX120 eye tracker (Tobii, Danderyd Sweden) recording at 60 Hz. This device was designed for studying human infants and has recently been applied to studying apes (Kano & Tomonaga, 2009). The viewing distance was changed from that in Experiment 1 and was approximately 60 cm. This was due to the need to place the eye tracker between the display and the participant as well as due to the requirements of the eye-tracking device. In the first experiment, humans used exactly the same apparatus as did the chimpanzees, whereas in the second eye-tracking experiment humans were tested in an arrangement dedicated to human experiments. The spatial configurations of the trackball, eye tracker, and display remained consistent with those used by chimpanzees.

3.1.3. Procedures

The experimental procedures were almost identical to those used in Experiment 1 except for minor changes regarding eye tracking. First, the process of touching the start stimulus was removed. Instead, a small open circle was presented at the center of a display with a black background at the beginning of the trial. The cursor (a white filled circle) was also presented at a pseudo-randomly chosen location on the display. Each participant initiated the trial when the cursor was moved to the open circle, and the participant's head was kept stable at the appropriate position to reliably track eye gaze. Second, the validity of eye tracking was monitored online, and the trial was terminated if eye tracking was unstable. If the eye tracker lost the gaze position for >20% of the total duration at any point during a trial, that trial was stopped with a buzzer alarm sound and then initiated again from the start stimuli. The remainder of the procedure was the same as that followed in the initial experiment.

Estimates of eye-tracking error were made on each day for each participant before starting the main part of the experiment. During the error estimation procedure, one small rectangle was presented on the display for the participants to look at. (No reward contingency was provided for looking at the rectangle. They spontaneously looked at the rectangle as the only stimulus was on the display.) We calculated eye-tracking errors as the distance between the estimated fixation point and the small rectangle at which participants were supposed to look. Tracking errors were <0.5° of visual angle in each species (the average error across participants was 0.3° in chimpanzees and 0.39° in humans at a viewing distance of 600 mm.) Lost eye-tracking data represented 2.7% of data from chimpanzees and 3.0% of data from humans.

3.2. Results and discussion

The results of the time for cursor discrimination were consistent with those obtained in Experiment 1 (Fig. S3). The interaction between number of targets and distractor action ($F(1, 4) = 21.46, p = .010, \eta^2_g = .84$), and the main effect of number of targets were significant ($F(1, 4) = 21.50, p = .010, \eta^2_g = .84$) in chimpanzees. The main effect of distractor action tended toward significance but did not reach this level ($F(1, 4) = 7.0, p = .057, \eta^2_g = .64$). This differed from the results of Experiment 1. However, the absence of this main effect did not alter our main conclusion with respect to the significant effect of the interaction and may have been due to the use of fewer subjects in Experiment 2. A significant main effect of distractor action ($F(1, 7) = 9.12, p = .019, \eta^2_g = .57$) but not number of targets ($F(1, 7) = .61, p = .46, \eta^2_g = .08$) was observed in humans. Importantly, the interaction between number of targets and distractor action was not significant ($F(1, 7) = .089, p = .38, \eta^2_g = .11$). Thus, the species difference observed in Experiment 1 was replicated here; that is, goal overlap was associated with impaired cursor discrimination in chimpanzees but not in humans.

We calculated the distance between each eye fixation and stimulus (i.e., cursor or target). A shorter distance indicated that participants looked directly at a given stimulus, whereas a higher value indicated that participants did not look at the stimulus or used peripheral vision. The distance was calculated between the gaze position and the nearest cursor or target irrespective of whether the latter was on the distractor side or the self-side. The results show that the mean distance between fixation and target was shorter in chimpanzees than in humans, whereas the distance between fixation and cursor was shorter in humans than in chimpanzees. This tendency was consistent from the beginning to the end of a trial regardless of the absence or presence of the distractor (Fig. 6 and Fig. S4). A mixed-model two-way ANOVA (with species, distractor presence, and objects as fixed factors and participants as random factors nested in species) revealed an interaction between species and object ($F(1, 11) = 38.7, p < .001, \eta^2_g = .78$). Chimpanzees fixated on the target significantly more closely than did humans ($t(24) = 4.63, p < .001$), whereas humans fixated on the cursors significantly more closely than did chimpanzees ($t(24) = 4.02, p < .001$). These trends.
were observed under the conditions with and without distractors, which is reflected by the lack of any significant interactions between species and distractor ($F(1,11) = 0.1$, $p = .74$, $\eta^2 = .01$) or among species, distractor, and object ($F(1,11) = 0.2$, $p = .64$, $\eta^2 = .02$).

We were concerned about the possibility that participants might completely separate the task into two phases, the self-cursor discrimination phase and the aiming action, rendering goal overlap between the distractor and participants’ own actions impossible due to the absence of an aiming goal during the process of discriminating the cursor. Under this circumstance, the number of targets would not have affected performance. Moreover, the absence of a goal-congruency effect in humans may have been due to their adoption of this strategy. According to our gaze results, both humans and chimpanzees did not substantially change their task strategy with vs. without cursor discrimination. These results indicate that humans did not completely separate the aiming action from cursor discrimination. Indeed, they performed the discrimination and aiming actions simultaneously. Thus, the absence of a goal-congruency effect in humans cannot be explained by qualitatively different task strategies. Instead, we found a consistent difference in the degree to which each species directed its gaze to kinematics versus to goals irrespective of the inclusion of a distractor. Humans selectively attended to kinematics more than did chimpanzees, and chimpanzee selectively attended to goals more than did humans. These trends were consistent with the results of Experiment 1, which showed a species difference in the relative importance of kinematics and goal representation for self-monitoring. The monitoring of aimed actions and actual feedback is involved not only in cursor discrimination but also in action execution itself; thus, gaze bias can occur either with or without a distractor cursor.

In summary, we investigated the possibility that the species difference in the goal-overlap effect may be due to qualitatively different task strategies applied by chimpanzees and humans (i.e., “goal-efficiency monitoring” or “self–other labeling”). The gaze-behavior results indicate that a qualitative difference in task strategy is unlikely to explain the species difference in the effect of goal overlap on self-monitoring. Therefore, the difference in the goal-overlap effect likely occurred due to the different relative importance placed by the two species on goal representation and kinematic information in the process of self-monitoring.

4. General discussion

The current study investigated the relative contributions of goal representation and kinematic information to self-monitoring of chimpanzees and humans under a novel situation in which differences between events that resulted from the participants’ own actions and events that were caused externally were ambiguous. We found that the predicted state and actual feedback were monitored by chimpanzees at the conceptual level involving goal representation and used as the primary cues for guiding their attention to the proper action target. In contrast, human participants efficiently monitored the discrepancy between their own kinematic input and the observed kinematics, even when the apparent goals of the distractor movement and their own intentions overlapped. We also confirmed that these species differences could not be explained by a difference in manipulation accuracy. Additionally, we demonstrated that the difference in the goal-overlap effect could not be attributed to a qualitative difference in the task strategies used by chimpanzees and humans. Overall, our results suggest that chimpanzees rely primarily on goal representations and rely less on motor kinematics, whereas humans efficiently integrate both dimensions of information in self-monitoring.

Our results are consistent with those of studies showing a species difference in imitation. Chimpanzees

Fig. 6. Fixation position relative to cursor and target. Mean distance between each fixation point and stimulus across participants. Error bars indicate 95% confidence intervals. Baseline conditions (which did not include distractors) are shown in the left panel, and the experimental conditions (with distractors) are shown in the right panel. Lower values indicate that the participant looked at the object directly, whereas higher values indicate that the participant did not look at the object or used peripheral vision. Chimpanzees tended to look at the goal of the action more than did humans regardless of the presence/absence of a distractor.
emulate the goal of others’ motor actions but rarely imitate detailed motor actions (Myowa-Yamakoshi & Matsuzawa, 1999, 2000; Tomasello et al., 1987), whereas humans both emulate and imitate. Emulation (imitation of a goal) may be an efficient strategy when the imitator can readily predict the goal of others’ actions. However, when the observed action is entirely novel to the imitator, meaning that its goal or purpose is difficult to predict, then the imitator would need to pay attention to the kinematic properties of the action itself. Our results showing relatively poor motor kinematic contributions to self-monitoring suggest that chimpanzees’ failure to imitate motor actions may derive from difficulty with paying attention to the details of their own motor kinematics in the service of executing actions.

It would be counter-intuitive to claim that chimpanzees are insensitive to their own motor kinematics with respect to self-monitoring. Indeed, chimpanzees have very sophisticated and acrobatic repertoires of actions, such as brachiation. Thus, it is hard to imagine that such actions do not rely on sensitivity to a mismatch between a planned consequence and feedback about their own actions at the level of motor kinematics. These contradictory views may be reconciled by considering the hierarchical nature of the process by which one’s own actions are monitored.

Several studies have demonstrated the distinctive features of planning an action goal and performing the actual motor action. The monitoring of processes at the sensorimotor level operates outside of conscious recognition and invokes the conscious mode only when automatic and implicit processes fail (Norman & Shallice, 1986; Willingham, 1998). For example, humans’ reports about the kinematic properties of their own bodies are inaccurate (Knoblich & Kircher, 2004; Musseler & Sutter, 2009). The presence of online motor control does not disturb performance on a simultaneous-attention task (Liu, Chua, & Enns, 2008). Online kinematic correction occurs during target displacement even when the target is not consciously visible (Goodale, Pelisson, & Prablanc, 1986; Pelisson, Prablanc, Goodale, & Jeannerod, 1986). Kinematic corrections related to target displacement during a reaching action occur spontaneously, and humans often fail to intentionally inhibit them (Pisella et al., 2000). These experiments demonstrated that online motor control occurs via a special sensorimotor system and is controlled outside of the attentional system. Only after the mismatch between motor estimation and feedback reaches a certain threshold, do we become aware of it.

According to this view, one may hypothesize that the species difference we observed in the current study reflects a difference in the extent to which implicit motor information can be explicitly recognized. We showed that the monitoring processes for conceptual goal representations are equally important to both humans and chimpanzees. However, the monitoring of motor kinematics was less important in guiding a chimpanzee’s attention to the proper action target (self-cursor). This raises the possibility that implicit motor monitoring hardly reaches explicit recognition in chimpanzees. This view is also supported by neurocognitive and neuroanatomical studies. Neurocognitive studies have determined that the prefrontal cortex is involved in the conscious/explicit monitoring of actions but not in the monitoring that occurs at the level of implicit sensorimotor processing. For example, Slachevsky et al. (2001) showed that patients with prefrontal deficits are less aware of the mismatch between the results of planned action and distorted feedback. Human imaging studies have shown that the mismatch between motor intention and feedback activates primarily the right dorsolateral prefrontal cortex (Fink et al., 1999). An anatomical comparison between the brains of humans and chimpanzees suggests that the prefrontal region is one of the most enlarged and elaborated regions in the cortex of members of the human lineage (Rilling & Insel, 1999; Sakai et al., 2011; Schoenemann, Sheehan, & Glotzer, 2005). These two different lines of studies support our interpretation that the species would differ in the extent to which implicit motor information could emerge into explicit recognition. However, our interpretation depends on the assumption that the cursor discrimination in the current study required an explicit monitoring mode, whereas the execution of the aiming action (trackball manipulation) was sufficiently controlled by implicit sensorimotor monitoring processes. As a limitation of this study, we could not empirically determine to what extent implicit versus explicit monitoring was involved in different aspects (cursor discrimination and aiming action) of our current task. Thus, it would be worthwhile to develop a task that allows separate investigations of the implicit and explicit modes of self-monitoring.

Another possibility is that the chimpanzees did not monitor kinematic information on either the implicit or the explicit level. Although chimpanzees may rely on kinematic information to monitor the movement of their own limbs (which allows for their sophisticated motor actions, such as brachiation), this does not necessarily mean that they also monitor the action of external objects (such as in tool-using behaviors). Flexible and sophisticated tool use is a hallmark of humans. It is possible that the species differences demonstrated in this experiment are related to the cognitive processes specific to the tool-using context. It should be noted that this argument does not suggest that our results were due to the inferior ability of chimpanzees to manipulate the trackball. The important element in self-monitoring is the extent to which individuals can predict the effects of their own actions. In this sense, our chimpanzees were already familiar with the experimental setting and were skilled in manipulating our devices. Furthermore, the results of the distortion experiments ruled out the possibility that the species difference found by this study was attributable to deficiencies in the ability to manipulate the trackball (Fig. S2).

In summary, the current results revealed differences in the relative contributions of kinematics and goal representation during self-monitoring by chimpanzees and humans. Chimpanzees relied primarily on goal representations and less on kinematic information. In contrast, humans efficiently utilized both types of information. These findings suggest that humans may have evolved the ability to manage kinematic information in a more flexible manner and provide unique insights into the evolution of the way in which we recognize our own actions.
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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2012.07.006.

References


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