

Chimpanzees' use of conspecific cues in matching-to-sample tasks: public information use in a fully automated testing environment

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Abstract Social animals have much to gain from observing and responding appropriately to the actions of their conspecific group members. This can in turn lead to the learning of novel behavior patterns (social learning) or to foraging, ranging, or social behavioral choices copied from fellow group members, which do not necessarily result in long-term learning, but at the time represent adaptive responses to environmental cues (public information use). In the current study, we developed a novel system for the study of public information use under fully automated conditions. We modified a classic single-subject laboratory paradigm—matching-to-sample (MTS)—and examined chimpanzees' ability to interpret and utilize cues provided by the behavior of a conspecific to solve the task. In Experiment 1, two subjects took turns on an identity MTS task, with one subject (the model) performing the first half of the trial and the other subject (the observer) completing the trial using the model's actions as discriminative cues. Both subjects performed above chance from the first session onwards. In Experiment 2, the subjects were tested on a symbolic version of the same MTS task, with one subject showing spontaneous transfer. Our study establishes a novel method for examining public information use within a highly controlled and automated setting.

Keywords Chimpanzee · Social cognition · Public information use · Matching-to-sample · Symbolic representation

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Introduction

Life in social groups affords animals the opportunity to perform adaptive behaviors by observing and responding appropriately to the actions of conspecifics. In broad terms, such responses to social information can lead to long-term changes in the observer's behavior, referred to as social learning, or to more ephemeral changes made in response to the behavior of fellow group members, through social eavesdropping or public information use (see Bonnie and Earley 2007 for a recent, extensive review). Important distinctions can thus be made between different kinds of social transmission processes that may vary greatly in their content, their underlying mechanisms, and their timescales. The social cognitive processes involved in, for example, the acquisition of group- or species-typical foraging techniques or anti-predatory responses are likely to be different from the processes underlying the utilization of social information in animals' choice of foraging patches, activity budgets, foci of attention, or behavior during inter-individual conflicts. While the former can be socially learned and thereafter individually retained without further need of social influence, the ongoing utilization of short-term social information requires observers to attend indefinitely and to respond flexibly to conspecific behavioral cues, which are subject to change over time.

For wild chimpanzees (*Pan troglodytes*), the contribution of social learning to the maintenance of community-specific cultures has recently become a major focus of interest (McGrew 2004; Whiten et al. 1999) with various field studies providing evidence suggestive of social influences on the acquisition of tool-using behaviors (Matsuzawa 1994; Biro et al. 2003; Lonsdorf 2006; Matsuzawa et al. 2011). As a complementary line of research, captive studies have examined social learning in chimpanzees

using observer–demonstrator pair designs (Hirata and Celli 2003; Hirata et al. 2009; Price et al. 2009) as well as more naturalistic open-group diffusion experiments (Hopper et al. 2007; Whiten et al. 2005, 2007).

In contrast to the aforementioned studies on long-term social learning, the short-term use of social information gained by chimpanzees from conspecifics has received less focused and unified attention. Examples from natural settings could include daily foraging or ranging choices based on the behavior of “leaders” within the group (Boesch 1991), attending to objects of interest as a result of alarm calls, food calls, or other forms of communication (Crockford and Boesch 2003) or participation in recurring social events that involve multiple “players”, such as conflict and reconciliation (Fraser and Aureli 2008). Laboratory experiments on chimpanzees’ social information use have, with a few exceptions, focused primarily on how subjects attend and respond to human rather than conspecific behavior (see Call and Tomasello 2008 for review). The rare exceptions include studies that used conspecific models for object-choice tasks (Itakura et al. 1999) and a series of food competition tasks among conspecifics (Hare et al. 2001). In the study of Itakura et al. (1999), observations of a conspecific model’s gaze cues, vocalizations, and body movements were shown, albeit with mixed results, to facilitate correct determinations about hidden-food locations. In the tasks of Hare et al. (2001), chimpanzees were shown in a competitive setting to take into account what a conspecific opponent could and could not see when deciding on a food item to approach.

A subset of social information use, we use the term “public information use” to refer to an animal’s use of cues gleaned in a social setting from the behavior of another individual, without any “deliberate” signalling on the latter’s part. This would exclude examples such as alarm and food calls, but include, among others, inadvertent gaze cues, foraging choices, and movement decisions. Furthermore, although in the behavioral ecology literature public information use generally refers to foraging contexts, and the evaluation, by the observer, of the quality of an environmental resource based on the perceived payoffs obtained by a model’s performance (Danchin et al. 2004; Coolen et al. 2005), we utilize a more inclusive definition. Ours is similar to that used by Valone (2007) who described a form of public information use reliant on observations of a model’s behavioral decisions rather than their performance rates. For our purposes, public information use can encompass any instance of an observer choosing between possible alternative actions (be they related to foraging, travel, habitat choice, or social interactions such as aggressive/affiliative encounters or mate selection) on the basis of having witnessed the choices or

actions of another and need not involve a direct or immediate evaluation of the quality of or payoff associated with such choices.

In order to obtain the kind of easily interpretable results that represent the major benefit of controlled laboratory tests, the behavior of models needs to be consistently predictable and reliable (hence the frequent use of human demonstrators in captive studies). Though absent for chimpanzees, prior studies on rats (Hake et al. 1983), pigeons (Millard 1979; Epstein et al. 1980), and macaques (Mason and Hollis 1962; Fushimi 1990) have benefitted from the use of experimental settings in which a conspecific model’s behavior was brought under the control of the experimenter, thereby serving as a systematically controlled discriminative cue for a second animal’s subsequent choice behavior. Fushimi (1990) showed that in such a setting, an observer monkey could, after multiple sessions of exposure to a task, learn to use the key-pressing behavior of a model conspecific as a discriminative cue. Similarly, a study by Subiaul et al. (2004) demonstrated that macaques’ learning of a pictorial sequence task was facilitated by prior visual exposure to a conspecific expert completing the same task in an adjacent experimental booth.

A greater understanding of chimpanzee public information use and its underlying mechanisms would benefit from utilization of the behavioral discrimination experimental methods mentioned above. Our aim was therefore to create a system for the study of public information use in which the behavior of chimpanzee models would be under the experimenter’s tight control, through the use of a highly automated testing environment. Furthermore, we were interested additionally in the underlying mechanisms of public information use. Explanations of how chimpanzees perceive and interpret conspecific behavior range from low-level theories of local or stimulus enhancement, in which observers direct their attention toward objects or locations that are near to models or being acted upon by them (Povinelli et al. 1997; Thorndike 1898) to more complex symbol-like utilization of social information as a referential phenomenon (i.e., use of vocalizations or gestures as references to distant target objects or locations; Boesch 1991; Leavens et al. 2004). We therefore designed an experimental setup to test public information use by chimpanzees with a focus on elucidating the levels at which social information is processed.

Our paradigm was comprised of a matching-to-sample (MTS) task performed sequentially by two subjects, a model and an observer, situated at two interconnected touch-panel stations. Input from both subjects was necessary to complete a single MTS trial, with one subject (the model) performing the first half of the trial and the other (the observer) completing the trial using the model’s actions as discriminative cues.

In comparison with the traditional object choice or gaze-following paradigms, our setup offers several key advantages for examining cognition underlying the comprehension of social information. First, in object choice experiments, the targets of the model's behavior are solid objects or locations in space, whereas in our setup they were represented by stimuli on the model's touch-panel monitor and could be recast on the observer's touch panel as either identical stimuli choices or as their corresponding symbols. In this way, local enhancement could be controlled for by presenting the stimuli at random locations on separate monitors, and stimulus enhancement could be controlled for by presenting observers with symbols whose physical characteristics (color and shape) were different from the corresponding stimuli being acted upon by the model. Finally, the common practice of using human models in object choice experiments has been criticized as a possible limitation that may have confounded the results of prior studies (Itakura et al. 1999), and a study by Hattori et al. (2010) using eye-tracking hardware showed that chimpanzees track the gaze of conspecifics but not of humans, which suggests that conspecific models are preferable to humans for discrimination of social information. In our setup, a conspecific model provides inadvertent social information without any human intervention or participation in the task.

Experiment 1: effects of local cues on identity matching-to-sample

The purpose of Experiment 1 was twofold. First, we aimed to determine whether or not chimpanzees could complete a computerized identity matching-to-sample task by using a conspecific model's behavior as a discriminative cue. Our secondary goal was to determine whether there was a saliency effect of local enhancement on their matching performance.

Methods

Subjects

Two chimpanzees, named Ai and Ayumu, participated in the experiment. Ai was a 31-year-old female and Ayumu was her 8-year-old son, raised since birth by Ai. Both had extensive prior experience with matching-to-sample tasks on touch-sensitive monitors; however, they were naïve to the two-touch-panel setup employed in this study. The participants lived in a social group with 11 other chimpanzees in a semi-natural enriched enclosure at the Primate Research Institute of Kyoto University (Matsuzawa 2003). They were not deprived of food at any time during the

present study. The use of the chimpanzees during the experimental period adhered to the *Guide for the Care and Use of Laboratory Primates* (2002) of the Primate Research Institute of Kyoto University.

Apparatus

Subjects were tested in an experimental booth (180 cm by 280 cm) with acrylic panels as walls on all sides (Fig. 1). Two 15-inch touch-sensitive monitors (Mitsubishi model TSD-FT157-MN) were embedded in adjacent walls of the booth. The first touch panel, referred to as the model station, was located on the western wall of the booth at a height of 100 cm. The second touch panel, referred to as the observer station, was located approximately 140 cm from the model station on the southern wall of the booth at a height of 40 cm. The stations were arranged such that a subject sitting at the observer station had a direct line of sight toward the model station. A third monitor, referred to as the hidden panel, was located outside the booth in front of the model station at a height of 5 cm. The hidden panel was arranged at an angle such that the model chimpanzee situated at the model station had direct visual access to it, while the subject situated at the observer station could not see it at all. Two universal feeders (Biomedica, BUF 310) delivered small apple pieces (8 mm cubes) into food trays located alongside the touch panels. Correct responses triggered a single apple piece to fall into the food tray accompanied by a chime sound, and incorrect responses resulted in a buzzer sound and no food being delivered. All experimental events involving the three panels and the two feeders were controlled by a single PC running a Visual Basic 6.0 program.

Stimuli

Stimuli consisted of 45 mm by 45 mm colored squares (red, yellow, or green). The stimuli appeared against a black background. A 20-mm-diameter empty white circle, displayed at the bottom of the screen, was used to signal the beginning of each trial.

Pre-training procedure

Use of the dual touch-panel setup constituted a novel situation for the chimpanzees. Their extensive prior exposure to touch-panel tasks had consisted solely of individualized tasks, in which they were required to pay attention to just the one monitor situated directly in front of them. In order to assess comprehension of another individual's behavior on an interconnected touch-panel screen, it was first necessary to train the subjects to look away from their own monitor (the observer's monitor) and toward the location of



Fig. 1 The experimental booth used in the study, showing the subjects at the two interconnected stations. Ai (*right*, at the model station) is in the process of touching the correct stimulus while Ayumu (*left*, at the observer station) watches her. The *hidden panel* is located outside the booth in front of the model station

the model individual's monitor (the locations of the observer and model's monitors are shown in Fig. 1).

This was accomplished through a series of pre-training tasks. In these tasks, subjects were located in front of the observer's monitor, and were required on each trial to watch a sample stimulus being presented on the distally located model's monitor, and then match the sample on the observer's monitor directly in front of them. In this way, the subjects learned that their responses were yoked to the appearance of the sample on the model's monitor.

Subjects activated a pre-training trial by pressing a circular self-start key on their touch panel, at which point a sample stimulus (a 45 mm square that was colored red, green, or yellow) appeared on the model's touch panel, located on the perpendicular western wall of the experimental booth at a distance of approximately 140 cm (Fig. 1). The sample stimulus on the model's monitor was then pressed by a human experimenter (in this case, the model's monitor was outside the booth behind a clear acrylic wall), or a conspecific chimpanzee, or it was automatically presented on the model's monitor for a brief duration (referred to as the computer-only condition.) In the case of the human and conspecific model conditions, the sample stimulus disappeared from the model's monitor upon being touched by the human or conspecific. In the computer-only condition, the stimulus remained on the model's monitor for a period of 3 s before disappearing automatically. Two choice alternatives, one identical to the sample and the other a differently colored square of the

same size, subsequently appeared on the observer's monitor, and subjects were required to match the sample for a food reward. Subjects were given five sessions consisting of 24 trials in each of the three conditions. The conditions were given in blocks, first with the human model, then computer-only, and last with the chimpanzee model. A criterion level was set such that the subjects had to perform above 90% on two consecutive sessions for each condition in order to progress to the subsequent task. Both subjects passed the criterion in all three conditions (Ai: 4, 4, and 2 sessions; Ayumu: 5, 3, and 4 sessions; human, computer-only, and conspecific conditions, respectively).

Experimental procedure

In the pre-training task, the subject in the observer role was required to match to a sample it had previously observed being presented on a second distal monitor. Although pre-training included conditions in which a touch to the sample on the second monitor was made by a human or conspecific, attention toward the model's touch was not a necessary component of the task, because only one stimulus was presented on the model's monitor and the subject could successfully complete the task by viewing the sample while ignoring the behavior of the model. In the post-training experimental phase, the complexity of the task was increased by adding a second, distracter stimulus to the model's monitor, so that the observer was required to determine the sample's identity by paying attention to which of the stimuli was pressed by the model. In this way, it was necessary for the observer to attend closely to the behavior of the conspecific model.

The task procedure is shown in Fig. 2. The observer initiated each trial by pressing an empty white circle, whereupon an identical white circle appeared on the model's monitor. After touching the white circle, a sample stimulus then appeared in the center of the hidden monitor, which was visible only to the model (see Fig. 1), for a period of 3 s. After 3 s, two choice alternatives appeared on the model's monitor. The model was required to match-to-sample. Both choice alternatives on the model's monitor (the sample and the distracter) disappeared simultaneously from the model's monitor when either was touched by the model. If the model matched the sample from the hidden monitor correctly, a chime sounded, a reward was dispensed to the model, and the trial proceeded. This was referred to as a valid trial. If the model matched incorrectly, a buzzer sounded, no food was dispensed, and the trial terminated prematurely. This was referred to as an invalid trial. On valid trials, after the model touched the sample and the stimuli disappeared from the model's monitor, the same two choice alternatives appeared on the observer's monitor. The observer was required to touch the

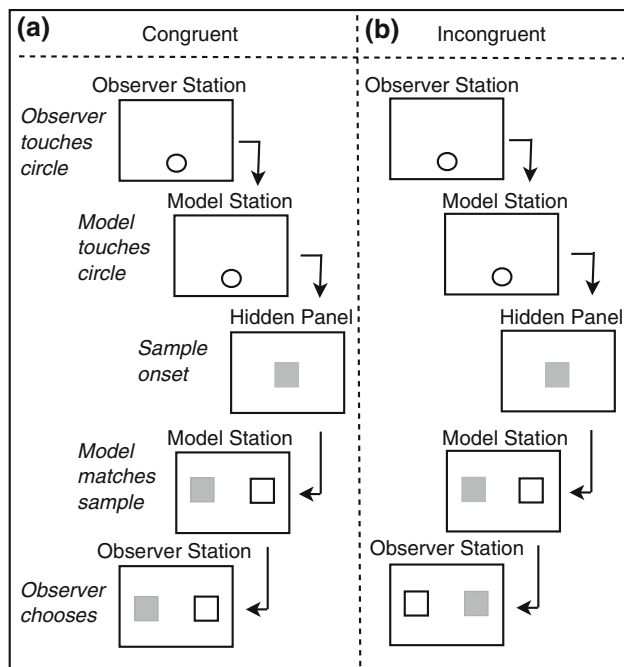


Fig. 2 Schematic diagram illustrating trials of the identity MTS task. The condition shown is for the *left/right* stimuli placement, in both **a** congruent and **b** incongruent configurations

sample that it had seen the model touch beforehand. Upon a successful match, a chime sounded and a food reward was delivered to the observer's food tray. Upon an incorrect match, a buzzer sounded and no food reward was delivered. Accuracy was measured as the percentage of correct valid trials completed by the observer.

The subjects completed three conditions that differed from each other in the placement of the stimuli on the two touch panels. Each condition was comprised of five sessions of 48 trials. Two sessions were conducted each day, and the subjects alternated roles as model and observer by switching places after the first session. The first condition had choice stimuli placed on the left and right side of the monitors. The second condition had the choice stimuli placed on the top and bottom of the monitors. For both the first and second condition, trials were divided into two categories: congruent and incongruent. On congruent trials, the locations of the sample and distracter stimuli were presented at the same location on both the model and the observer's touch panels. On incongruent trials, the locations of the sample and distracter stimuli were reversed between the model's touch panel and the observer's touch panel. Congruent and incongruent trials were presented in random order during each session of the first two conditions. The third condition had the choice stimuli placed at random locations on both of the touch panels. It was hypothesized that if local enhancement cues are salient to observers, then performance should be better on congruent

trials versus incongruent or random placement trials, because the observer would be paying attention to the specific motor action of the model toward a relative location on the touch panel.

Results

Learning

Learning data are shown in Fig. 3a. For the first block of sessions, comprised of left/right stimulus placements, there was a significant positive correlation for subject Ayumu between percentage of correct responses and session number (Pearson's correlation, Ayumu: $r = 0.951$, $N = 5$, $P = 0.013$, two-tailed). Ayumu did not show within-block learning effects for the remaining two conditions (top/bottom placement and random placement), and Ai showed no within-block learning effects for any of the three conditions; however, Ai showed a significant learning effect across sessions of all three blocks combined ($r = 0.659$, $N = 15$, $P = 0.008$, two-tailed). Somewhat surprisingly, the performance of both subjects was above chance level already in the first block of sessions, which suggests that their ability to use the model's behavior as a cue may have been spontaneous. This is supported by the fact that, although during pre-training the subjects had prior exposure to a similar situation in which a model touched the sample, there the sample appeared without a distracter stimulus alongside it, and hence observers did not need to pay attention to the model's choice as a discriminative cue; only in Experiment 1 was the discriminative cue for the first time provided exclusively by the model's behavior.

Local enhancement effects

The placement of the stimuli in congruent versus incongruent configurations had no significant effect on the performance of either subject (Fig. 3b). Furthermore, both subjects performed with higher accuracy (although not significantly so) in the random condition than in the congruent and incongruent trials of the first two conditions; however, this may have been due to an expertise effect because the random condition block was conducted after the other two conditions were completed.

Discussion

Experiment 1 confirmed that chimpanzees are able to use conspecific behavior as a discriminative cue in a computerized matching-to-sample task. Both subjects spontaneously performed above chance level during the first block of sessions, and one of the two subjects, Ai, remained above chance level throughout all three blocks. This result

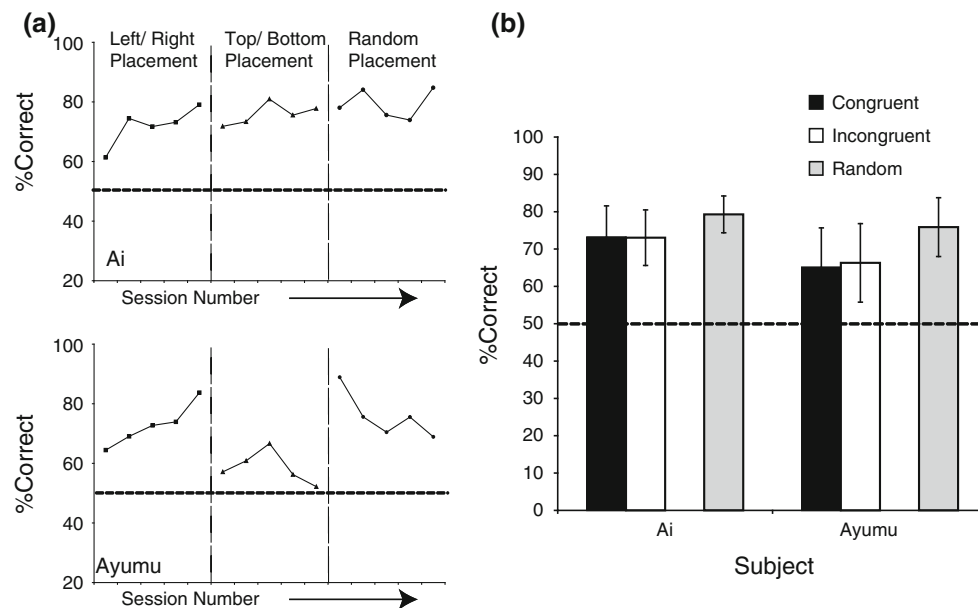


Fig. 3 **a** Learning data and **b** accuracy for the identity MTS task. The bars located at 50% correct on the y-axis indicate chance level. Error bars represent standard deviation

constitutes the first case of spontaneous public information use among conspecific chimpanzees in a fully automated laboratory setting. Furthermore, it was demonstrated that local enhancement cues had a negligible effect on the observer's matching performance. It should be noted that the subjects had, throughout their experimental history, been trained to match to sample based on color and not location, and therefore would not necessarily be expected to show local enhancement effects. Nonetheless, since the social setting in which the present experiment was conducted was entirely novel to the chimpanzees, we could not rule out a priori that they would not default to local enhancement to solve the task. The absence of local enhancement effects suggests that the physical characteristics of the stimuli themselves—in this case color—had a greater saliency to the subjects than the position of a stimulus relative to the distracter or the location on the touch screen toward which the model's motor movements were directed.

Experiment 2: transfer of social cue comprehension to a symbolic task

In experiment 1, chimpanzees' performance on an identity matching task was shown not to be influenced by local enhancement effects of stimuli placement. These results leave open the possibility that the subjects might have paid attention strictly to the physical properties of the stimulus being touched, i.e., the color of the sample stimulus. Such a finding does not rule out the possibility

that chimpanzees relied on stimulus enhancement as the mechanism for completing the task. In experiment 2, stimulus enhancement was controlled for by adding a symbolic element to the task procedure. We hypothesized that if an observer could complete the task by pressing a symbol corresponding to the sample stimulus being touched by the model, then stimulus enhancement alone could not serve as an explanation for their performance because the symbol does not share any of the physical characteristics (color and shape) of the sample being touched by the model. Transfer of the subjects' matching ability demonstrated in Experiment 1 to a novel symbolic task would therefore show that their public information use does not rely entirely on low-level mechanisms of local and stimulus enhancement.

Methods

Subjects, apparatus, and stimuli

Subjects and experimental apparatus were identical to Experiment 1. Stimuli consisted of three 45 mm by 45 mm colored squares (red, green, and yellow), as well as three Chinese ideograms (kanji) that had meanings corresponding to the colors. The kanji characters were roughly the same size as the color squares.

Procedure

Both subjects had prior exposure to symbolic matching-to-sample tasks involving the same stimuli (colors and

corresponding kanji characters) used in Experiment 2 and had acquired the correspondence between the different classes of stimuli while being trained individually (e.g., Matsuno et al. 2004; Sousa and Matsuzawa 2001). To determine whether they retained their competence at symbolic matching-to-sample and to determine their baseline performance for identity MTS as well as symbolic MTS, the subjects were given an individual (non-social) task identical to these previous studies. For this purpose, the subjects completed identity MTS and symbolic MTS tasks while they were alone in the booth. Each trial was initiated by the subject's touch to an empty white circle displayed at the bottom of the screen. After touching the start key, the sample stimulus (color or kanji character) appeared at a random location of the screen. Upon touching the sample, the sample stimulus disappeared and two choice alternatives appeared on the screen at random locations. The subject was required to select the alternative that matched the sample. The subjects completed 12 sessions of identity matching-to-sample (6 color-to-color and 6 kanji-to-kanji) and 12 sessions of symbolic matching to sample (6 color-to-kanji and 6 kanji-to-color). Sessions consisted of 48 trials each, and were completed in blocks, with symbolic sessions following identity sessions. Both subjects performed above chance level (binomial test, $P < 0.01$) in all sessions for both the identity and the symbolic conditions, which confirmed that they were proficient at symbolic matching-to-sample (Fig. 5b).

In addition to the individual task, subjects subsequently completed a social task in Experiment 2 that was similar to that of Experiment 1, with the addition of a symbolic matching element. Participants completed two kinds of matching-to-sample tasks: identity MTS and symbolic MTS (Fig. 4). For identity MTS, the choice alternatives were of the same category as the sample (color sample to color alternatives or kanji sample to kanji alternatives), and for symbolic MTS, the choice alternatives were of the opposite category from the sample (color sample to kanji alternatives or kanji sample to color alternatives). In the social task, 12 of the sessions involved identity MTS and the other 12 involved symbolic MTS. The sessions of symbolic and identity MTS were conducted on alternate days. The two subjects alternated roles as model and observer by switching places after each session in a given day. All trials were videotaped from multiple angles, and for a random sampling of 8 sessions (4 per subject, 2 of which were identity tasks and the other 2 symbolic tasks), looking behavior on each trial of the observer subject toward the model screen at the time of the model's touch to the sample was independently coded by two viewers. Ai looked at the model's touch to the sample on 98% of identity trials and 100% of symbolic trials, and Ayumu looked at the model's touch to the sample on 97% of

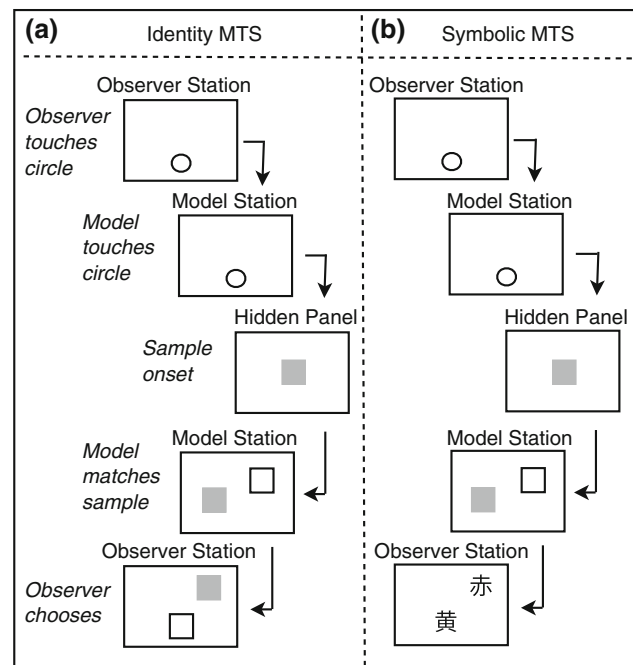


Fig. 4 Schematic diagram illustrating the social cue conditions for **a** identity and **b** symbolic MTS tasks

identity trials and 98% of symbolic trials, and the reliability between the two coders was 98%.

Results

As shown in Fig. 5a, one of the two subjects, Ai, performed the social cue symbolic MTS above chance level on the first session of her exposure to it (binomial test, $P < 0.01$), which suggests that her ability to discriminate the behavior of the model was not based solely on reinforcement learning. A comparison between symbolic and identity social tasks was possible due to parity in the models' performances, based on the number of valid versus invalid trials for the respective tasks. We found no significant difference for either model in the number of valid versus invalid trials between tasks. Ai's performance in the observer role (Fig. 5a) was above chance level (binomial test, $P < 0.05$.) on both tasks (identity MTS and symbolic MTS) in both cue conditions (individual and social). For further statistical analysis, we applied the arcsine transformation to percentage correct values for each subject to satisfy the assumptions of parametric analysis. In a two (cue type) by two (task type) ANOVA of Ai's performance, the main effect of cue type was significant ($F(1, 11) = 439.763$, $P < 0.001$), and the main effect of task type was significant ($F(1, 11) = 158.813$, $P < 0.001$). Further inspection of the results showed that Ai's accuracy was higher for individual than for social cues, and on identity compared to symbolic tasks. There was a

significant interaction between cue and task type ($F(1, 11) = 9.449, P = 0.011$). This interaction is displayed in Fig. 5b, showing that Ai's performance on symbolic matching was disrupted more by the social cue than the individual cue, and that this effect of cue type was reduced for the identity matching task.

Ayumu's performance (Fig. 5b) was above chance level ($P < 0.05$, binomial test) in all but one treatment (symbolic task with social cue). In a two-by-two ANOVA of Ayumu's performance (see details above for Ai), the main effect of cue type (individual, social) was significant ($F(1, 11) = 374.520, P < 0.001$) and the main effect of task type (identity, symbolic) was also significant ($F(1, 11) = 135.638, P < 0.001$). Much like Ai, Ayumu scored better performance under the individual cue condition compared to the social cue condition, and under identity compared to symbolic matching. However, unlike in the case of Ai, there was no significant interaction between cue condition and matching task type ($F(1, 11) = 0.426, P = 0.527$); in other words, the degree of decrement in performance during the symbolic version of the task was comparable across the social and individual cue conditions.

Discussion

Experiment 2 examined the ability of the subjects to associate the target of a conspecific's touch with a

symbolically related stimulus (the social cue symbolic MTS condition). One of the subjects, Ai, was able to perform above chance level on this task and she did so spontaneously already in the first session of being exposed to it. Such a finding rules out the possibility that her ability to use a conspecific's behavior as a discriminative cue was based on stimulus enhancement, because the kanji characters and the color stimuli did not share any of the same physical properties. Furthermore, her ability upon first exposure to symbolically match the target of the model's touch also suggests that expertise was not responsible for her success. To explain Ai's success, we propose a possible alternative mechanism, *semantic enhancement*, whereby a model's behavior directed toward a stimulus allows the observer to recall previously learned (in our case arbitrary) associative properties of the target stimulus. The other subject, Ayumu, performed at chance level for the same task, and it cannot therefore be ruled out that he might have been relying on stimulus enhancement in order to successfully complete the task in the identity condition.

General discussion

Public information use, or the ability to respond adaptively to specific properties of or changes in conspecific behavior, plays a central role in the social lives of many animal

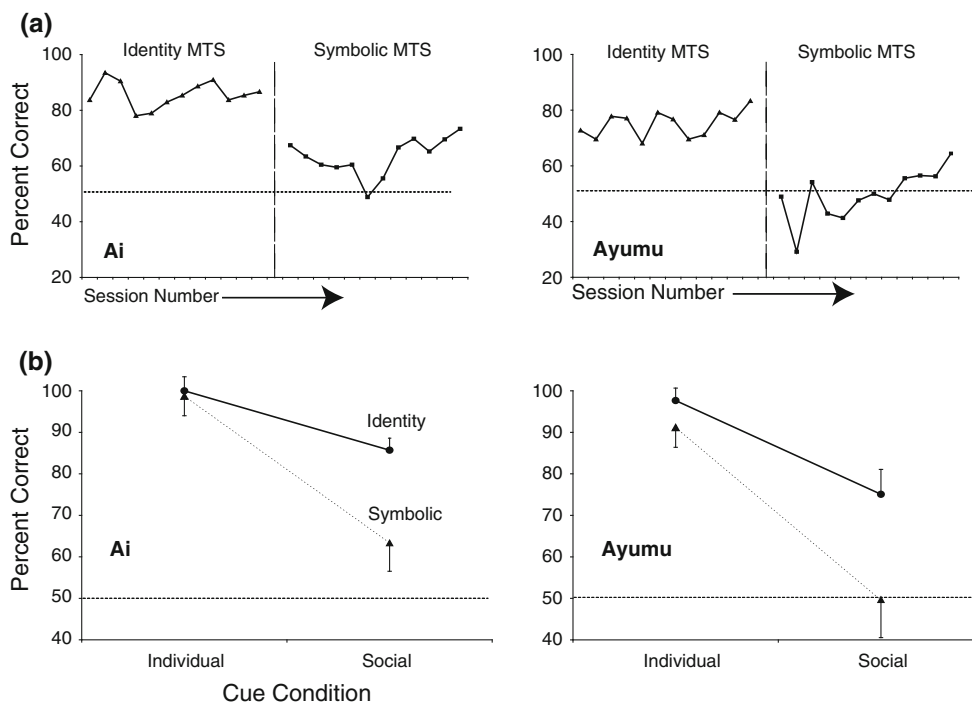


Fig. 5 **a** Learning data during the social cue conditions for identity and symbolic tasks. **b** Accuracy in identity and symbolic MTS tasks for the two cueing conditions. Ai's data are shown on the left and

Ayumu's on the right. The bars located at 50% correct on the y-axis indicate chance level. Error bars represent standard deviation

species, including chimpanzees. The current study examined one aspect of public information use—the ability to discriminate the target object of a conspecific’s behavior—in order to determine the possible importance of local or stimulus enhancement in the chimpanzee’s processing of social information. Both subjects were able to use a conspecific model’s behavior as a discriminative cue in the absence of local enhancement cues (random placement condition) during Experiment 1, and congruent versus incongruent stimuli placements also had no significant difference on performance. Moving beyond stimulus enhancement (Experiment 2), one of the subjects spontaneously performed above chance level in a symbolic task in which the target of the model’s touch did not share any physical characteristics with the correct stimuli, thereby showing that her discrimination of the model’s behavior was not only based on the appearance of the target stimuli. The other subject’s performance did not rise above chance level on the same task, and therefore stimulus enhancement could not be ruled out as a possible factor contributing to his success on the identity task from Experiment 1.

Both subjects displayed significantly lower matching performance on the symbolic MTS tasks than on identity MTS tasks in both cue conditions, individual and social. One subject, Ayumu, showed a robust understanding of symbolic associations during the individual MTS task, but was unable to transfer such understanding to the social cue condition, in which he performed at chance level. The other subject, Ai, showed a significant interactive decrease in performance between cue conditions. Together, these findings might suggest the presence of a compound effect on task difficulty resulting from the combination of (1) discriminating the target of a conspecific’s behavior and (2) associating it with a symbolically related stimulus. However, the observed interaction found in Ai’s performance could also have been due to her greater expertise on the identity versus symbolic tasks resulting from her prior exposure to the social identity task in Experiment 1.

The current study demonstrated that chimpanzees’ public information use in the context of a social cue discrimination task is not limited to low-level mechanisms of local and stimulus enhancement. Such a finding is consistent with Subiaul et al. (2004) study, in which “cognitive imitation”, as opposed to local and stimulus enhancement, was inferred as an explanation for rhesus macaques’ ability to learn complex behavioral rules facilitated by observation of a conspecific model. However, unlike the task employed by Subiaul et al. (2004), which focused on social learning, the matching-to-sample procedure in the current study allowed us to focus on public information use by requiring the subjects to continually pay attention to the model’s behavior, as the latter changed from trial to trial. Interpreting another’s behavior, and not simply a reliance on

stimulus and local enhancement, was evident in the performance of one subject, Ai, in this study. As an alternative to local and stimulus enhancement effects, we propose a novel explanation, *semantic enhancement*, as the possible mechanism responsible for Ai’s successful performance in the social symbolic cue task. Similar to cognitive imitation (albeit referring to a case-by-case reliance on a model’s behavior based on some previously learnt rule rather than the social learning of the rule itself), semantic enhancement would require the observer to interpret a model’s actions using cognitive rules and respond appropriately based on properties associated with the model’s target stimulus that are not perceptually present in the observer’s target. For Ai, semantic enhancement might have allowed the model’s actions to draw her attention toward the correct target (entirely different in appearance to the model’s target) via symbolic associative rules acquired through prior learning.

Finally, it is also worth noting that the subject Ai, who was the mother of Ayumu, performed on the social conditions within our task with better accuracy than her son. Given what previous field and laboratory studies have revealed about information transfer and the acquisition of socially learned behaviors in chimpanzees (Biro et al. 2003; Hirata and Celli 2003; Lonsdorf 2006)—where offspring attend closely to their mother’s behavior but not vice versa—this is somewhat surprising. In the current study, it was shown that the mother, Ai, was better at responding appropriately to the behavior of her offspring than the reverse situation. However, due to our small sample size (comprised of a single mother-offspring pair), it is not possible to draw any strong conclusions about the role of social relationships in modulating the direction and strength of social information flow in chimpanzees. Future studies using a more diverse set of participant pairs may help elucidate how social relations determine the way public information flows through chimpanzee social groups.

In sum, our study established a fully automated testing environment to examine social information transfer between a pair of chimpanzees and showed that subjects were responsive to conspecific behavior directed toward touch-sensitive monitors. We suggest that the use of interconnected touch-panel stations may provide many opportunities for future research on socio-cognitive processes not only in chimpanzees but a variety of other primate and non-primate subjects.

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