Chimpanzees know that others make inferences

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If chimpanzees are faced with two opaque boards on a table, in the context of searching for a single piece of food, they do not choose the board lying flat (because if food was under there it would not be lying flat) but, rather, they choose the slanted one—presumably inferring that some unperceived food underneath is causing the slant. Here we demonstrate that chimpanzees know that other chimpanzees in the same situation will make a similar inference. In a back-and-forth foraging game, when their competitor had chosen before them, chimpanzees tended to avoid the slanted board on the assumption that the competitor had already chosen it. Chimpanzees can determine the inferences that a conspecific is likely to make and then adjust their competitive strategies accordingly.

social cognition | competition | theory of mind

Several primate species are capable of going beyond the information given to perception by making inferences about what is likely to be the case in unperceived situations (1, 2). For example, if chimpanzees are faced with two opaque boards on a table, in the context of searching for a single piece of food, they do not choose the one lying flat (because if food was under there it would not be lying flat), but rather they choose the slanted one—presumably inferring that some unperceived food underneath is causing the slant (3).

An interesting question is whether chimpanzees also know that others make inferences as well. In the past decade there has been much research on chimpanzees' so-called "theory of mind" (reviewed in ref. 4). The vast majority of this research concerns what chimpanzees know about the visual perception of others. For example, they know what others can and cannot see (5) and what others do and do not "know," in the sense of what others have seen in the past and so still can react to (6). They have more trouble predicting what another will do on the basis of a false belief about the world (again based on visual perception) (7). In one study, chimpanzees demonstrated an ability to determine what another individual could or could not hear, as they "stole" food from an inattentive human competitor with a silent rather than a noise-making method (8).

In the current study, we investigated whether chimpanzees could determine that another chimpanzee was guiding its actions not on the basis of visual or auditory perception but on the basis of inferences alone. This is a theoretically important question because Povinelli and Vonk (9), among others, have argued that when chimpanzees seemingly understand the visual perception of others, they are only reacting to overt orienting behaviors and the like. However, in the current study chimpanzees were faced with an individual in the slanted board situation from (3), who might or might not be making an inference about where the food was hidden—with no diagnostic orienting behaviors at all (the chimpanzee subject could not see the other individual making her choice).

General Methods

We adapted a methodology from a study of Kaminski et al. (7) In this study a chimpanzee subject watched while food was being hidden in one of three buckets, as did a conspecific competitor across the way, whom the subject could clearly see. So they both knew where that piece of food was hidden, and potentially that the other had that same information. In addition, a second piece of food was hidden in one of the other two buckets, but in this case only the subject (and not the competitor) could see which one. In a back-and-forth game, chimpanzees chose either of the two food-containing buckets randomly if they were given the three buckets to choose from straightaway. However, if instead the competitor was given the first choice, behind an occluder so that the subject could not see his choice, then when it was the subject's turn, she preferentially chose the bucket containing the food the competitor had not seen hidden. This strategy was presumably based on the knowledge that the competitor would choose the bucket where she had seen food hidden, so only the food in the other bucket was left.

In the current study chimpanzees played a similar back-and-forth game with a conspecific competitor. In a pre–test-phase pairs of chimpanzees learned a competitive game of food acquisition, in which they took turns choosing possible food locations. Then in the actual test, the subject watched while one piece of food was hidden under an opaque board (making it slant) and a second piece of food was hidden in a secret hole in the table such that a second opaque board could be placed over it and lie flat. The competitor across the way could not see this hiding process, and the subject could not see the competitor. Then the subject's view of the table was blocked by an occluder while the competitor was offered the boards to make her choice in private (Fig. 1).

After the competitor's choice, the two boards came back to the subject for her to choose (boards and competitor blocked from view). If the subject thought that the competitor had looked at the two boards and inferred that the food was under the slanted one, then, on her turn, she should prefer the flat board where there was still likely to be food. In a comparison condition, the subject simply chose first, in which case no thinking about the inferences of the other was needed (although if the subject thought she would get another turn, she should choose the slanted board because that was the one "at risk" from the competitor). Two other, nonsocial control conditions paralleled these two (i.e., subject chooses first, subject chooses last), but in this case there was no competitor present at all. This enabled us to assess the subjects' natural tendencies in the two main conditions in the absence of any social competition.

Results

In the two nonsocial conditions (Fig. 2) subjects chose the slanted board significantly above chance regardless of whether they chose first (paired-samples t test: $t_{11} = 4.54$, $P = 0.001$) or "last" (paired-samples t test: $t_{11} = 2.97$, $P = 0.013$); in these conditions "last" simply meant that the two boards had been pushed over to where the competitor would have been and then back to the subject. When there was a competitor present,

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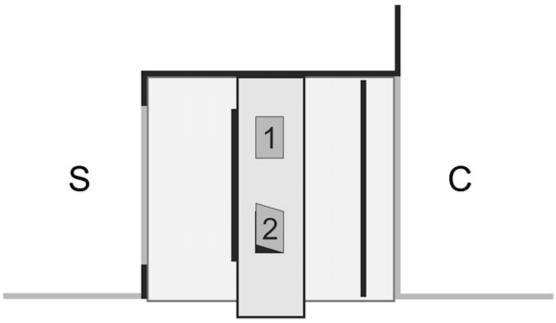

Fig. 1. Schematic view of the experimental setup. Subject S and competitor C are on opposite sides of the table. On the platform in the middle, board 1 covers the reward in the hole and board 2 covers the reward on top of the platform, acquiring a slant. C's view is blocked by the occluder, the view of S is blocked after the baiting by the sliding panel at the platform.

however, subjects made a sharp distinction between choosing first and choosing last. When subjects chose first, they selected the slanted board above chance, as they did in the nonsocial conditions (paired-samples t test: $t_{11} = 4.06$, $P = 0.002$), but when they chose last, after the competitor's choice, they chose the slanted board only around half the time (paired-samples t test: $t_{11} = 1.03$, $P = 0.33$) (Table S1).

A 2 × 2 ANOVA found a significant difference in the order-of-choice variable (subject first vs. subject last; $F_{1,10} = 13.83$, $P = 0.004$), and a trend in the interaction of the order-of-choice variable and the social variable (competitor present vs. nonsocial; $F_{1,10} = 4.36$, $P = 0.063$). Comparing order-of-choice within the competitor present condition revealed that subjects selected the slanted board more often when they chose first than when they chose last ($t_{11} = 3.35$, $P = 0.006$). No such difference was observed in the nonsocial condition ($t_{11} = 1.09$, $P = 0.30$). Comparing the social and nonsocial conditions within the order-of-choice variable revealed no difference when the subjects chose first ($t_{11} = -0.66$, $P = 0.52$). However, there was a trend that subjects chose the slanted board more often when choosing last in the nonsocial condition than in the social condition ($t_{11} = 2.06$, $P = 0.064$).

In terms of possible learning effects, the preference for the slanted board in the social condition remained unchanged between the first and last sessions in both choice orders ($t_{11} = -1.62$, $P = 0.13$ when subjects chose first and $t_{11} = 0.0$, $P = 1.0$ when subjects chose last), suggesting that the chimpanzees did not learn to respond to the situation in this way during the experiment. Comparing only the first and last trials of testing produced similar results (sign test, $P > 0.24$ in both cases). Note also that subjects who were competitors before they were subjects could not have learned anything useful during that first exposure because they were rewarded either for choosing the slanted board or else randomly (when no slanted board was present).

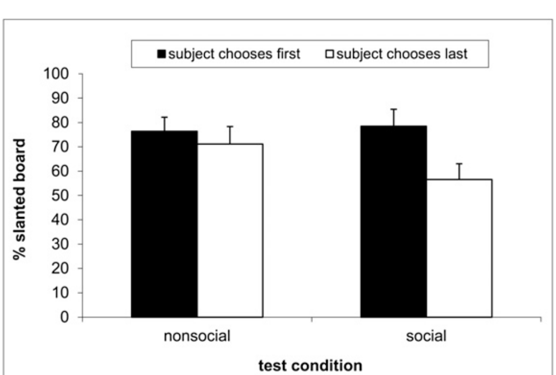

Fig. 2. Mean percentage of trials in which subjects selected the slanted board (± SEM; n = 12) in different conditions.

Discussion

Several studies have shown that chimpanzees know what others currently see, and what they saw just a few minutes before (and so now know about) (4). Here we demonstrated that chimpanzees also know that others go beyond direct perception and immediate memory to make inferences about nonperceived realities. In the current study subjects could not have been reacting to the behavior of the competitor (as they could not see her at the key points in the procedure), nor did they learn their best response during the test (and any influences from first being competitors in the social condition would have been the same for subjects choosing first or last in the test), thus obviating two key criticisms leveled at studies of animal social cognition in the past (10, 11). If we define thinking as going beyond the information given in perception to make inferences, we may conclude that not only is thinking not the exclusive province of human beings, but thinking about thinking is not either.

Methods

Subjects. We tested 12 juvenile and adolescent chimpanzees (eight female and four male; mean age, 11.8 y, range, 6–17 y) socially housed at the Wolfgang Köhler Primate Research Center. Subjects in the social condition were tested with a competitor in the opposite cage, whereas in the nonsocial condition they faced no competitor. Individuals were tested one after another, each competitor becoming the next test subject.

Apparatus. A platform (80 × 20 cm) resting on a table was placed between two opposite cages. Depending on the condition, the platform was solid or had a hole on one side. The experimenter (E) could slide the platform back and forth between the cages and chimpanzees could see and access the platform from each side only through a mesh panel. Visual access to the platform could be blocked for the subject by a sliding panel that when was flush against the mesh allowed her to slide it to one side to access the opposite side of the platform. Two opaque boards (15 × 10 cm) were used to cover food.

Procedure. Before the test, subjects were required to pass two prerequisites. In prerequisite 1, two rewards (pellets or banana slices) were put under two identical opaque cups on opposite sides of the solid platform. The platform was slid to the competitor's cage (empty in the nonsocial condition) who selected one cup by poking her finger through the mesh on that side. The platform was then slid to the subject's side where she could get the remaining piece if she chose correctly. This session enabled subjects in the social condition to experience competition with their partners (or the lack of competition in the nonsocial condition). Subjects received prerequisite 2 if they selected the baited cup in at least 10 of 12 trials that formed a session. All subjects passed prerequisite 1 in the first session.

In prerequisite 2, no competitor was present; one reward was deposited on one side of the platform, and the sliding panel was installed. Then the platform was flush against the mesh so that the subject could slide the panel aside to access the reward. After completing six such trials, subjects received 12 additional trials per session in which the platform with the hole was used and the view from the (empty) competitor's cage was blocked by a plastic occluder. Subjects witnessed one reward being placed either inside the hole or on the platform's opposite side. E covered the reward with a board, which acquired a slant (the open side facing the subject) when placed against the nonholed reward. The second board was put on the opposite side to the existing board. Upon completing the baiting, which always began on E's far side, the subject's view of the entire setup was blocked by first inserting the panel and then moving the occluder from the competitor's side to the subject's side. E slid the platform to the competitor's side and back to the subject's side, placing the occluder back to the competitor's side. Now the subject could choose by sliding the panel. Passing this condition ensured that subjects were able to remember the food location after their view was blocked for several seconds between baiting and choice. The side of the hole alternated and the side of the food was randomized and counterbalanced, with the stipulation that it could not be the same in more than three successive trials. Criterion was reached by choosing the baited side in at least 10 out of 12 trials in two consecutive sessions. On average, subjects passed prerequiste 2 after 6.5 sessions (SD, 7.6; median, 4.5).

All subjects received both the social and nonsocial conditions with half of the subjects being tested in the social condition first. Each session of the test conditions (four sessions per subject) began with a six-trial warm-up that was identical to prerequisite 1 except that the subject and competitor randomly alternated in selecting first. Upon completing these trials, the competitor's view was blocked by an opaque occluder, the solid platform was replaced by the platform with the hole and testing proper (12 trials per session) began. The subject was ignorant whether the competitor knew there was a hole in the platform. In the social condition the subject witnessed E baiting the platform on both sides and placing the boards on each reward while the occluder blocked the view from the competitor's cage. After inserting the sliding panel, the platform was either slid first to the competitor or the subject. The subject did not see the boards on the platform behind the panel and could choose one side by moving the panel to the other side as learned in prerequisite 2. The competitor saw the platform and the boards directly while choosing and did so by poking her finger through the mesh on one side. Both were rewarded according to which side they chose, when there was no food on that side, they did not receive a reward. If the competitor chose the side of the hole and there was food in it, the hole was not revealed by lifting the board but she received a reward directly from E. Upon choosing and getting the reward, it was the partner's turn to select one side while the occluder always blocked the view of the chimpanzee who was not choosing (Movie S1). In the nonsocial condition the procedure was identical except that the competitor's cage was empty at all times.

All trials were videotaped and choices were unambiguous because the subject had to move the sliding panel toward one side to make her choice. The side of the hole and the order of choice was randomized and counterbalanced, with the stipulation that they could not be the same in more than three successive trials.

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