

Chimpanzees (*Pan troglodytes*) Conceal Visual and Auditory Information From Others

Alicia P. Melis, Josep Call, and Michael Tomasello
Max Planck Institute for Evolutionary Anthropology

Chimpanzees (*Pan troglodytes*) competed with a human for food. The human sat inside a booth, with 1 piece of food to her left and 1 to her right, which she could retract from her chimpanzee competitor's reach as needed. In Experiment 1, chimpanzees could approach either side of the booth unseen but then had to reach through 1 of 2 tunnels (1 clear, 1 opaque) for the food. In Experiment 2, both tunnels were clear and the human was looking away, but 1 of the tunnels made a loud noise when it was opened. Chimpanzees preferentially reached through the opaque tunnel in the first study and the silent tunnel in the second, successfully concealing their taking of the food from the human competitor in both cases. These results suggest that chimpanzees can, in some circumstances, actively manipulate the visual and auditory perception of others by concealing information from them.

Keywords: deception, concealment, competition, *Pan troglodytes*, visual perspective, auditory perception

Many nonhuman primates as well as other animal species reliably follow the gaze direction of conspecifics and humans to external targets (Bugnyar, Stowe, & Heinrich, 2004; Emery, Lorinez, Perret, Oran, & Baker, 1997; Ferrari, Kohler, Fogassi, & Gallese, 2000; Kaminski, Riedel, Call, & Tomasello, 2005; Povinelli, Bierschwale, & Cech, 1999; Povinelli & Eddy, 1996a, 1996b, 1997; Tomasello, Call, & Hare, 1998; Tomasello, Hare, & Agnetta, 1999). Chimpanzees do not just look in the general direction of another's gaze, they actually follow the other's gaze direction to locations behind barriers and past distractors (Tomasello et al., 1999; see also Bräuer, Call, & Tomasello, 2005). If they do not find anything interesting in a human's line of sight, they often look back to the human and follow his or her gaze again (Call, Hare, & Tomasello, 1998), a behavior called *checking back*, which, in human infants, is considered evidence of understanding another's visual experience (Bates, 1979). However, some researchers have argued that following gaze direction does not indicate an understanding of the others' visual experience, and this is supported by results from some experimental paradigms, all cooperative or communicative in character, in which chimpanzees seemingly fail to understand what others see or do not understand the referential character of seeing (for reviews, see Call, Agnetta, & Tomasello, 2000; see Call & Tomasello, in press; Povinelli et al., 1999; Povinelli & Eddy, 1996b). However, new naturalistic experimental approaches have demonstrated that chimpanzees

know the content of what another sees, because individuals behave differently if a competitor does or does not see a contested food item (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; but see Karin-D'Arcy & Povinelli, 2002). If we accept that these studies, along with the gaze-following studies, indicate that chimpanzees have some understanding of what others can and cannot see, there is still the question of whether they are capable of actually manipulating what others see.

Numerous observations show that chimpanzees behave in ways that serve to deceive others (so-called tactical deception; de Waal, 1986; Whiten & Byrne, 1988). However, it is still controversial whether they engage in intentional deception (i.e., whether they have the specific goal to manipulate the visual or other psychological states of others). The most well-known experimental evidence is that of Woodruff & Premack (1979; see also Hirata & Matsuzawa, 2001; Menzel, 1974). In the study by Woodruff and Premack (1979), subjects took many trials to learn to withhold behavior (or in some cases produce misleading behavior) so that a competitor would not take the food that was potentially available to both of them. The large number of trials before successful performance raises the possibility that they learned the requisite contingencies associatively during the course of the experiment. Although the results of these previous studies show that chimpanzees use sophisticated strategies to deceive others, interpretations based on learning certain fixed contingencies or reacting to the dupe's behavior online cannot be ruled out.

A study by Hare, Call, and Tomasello (in press) showed that chimpanzees are able to use information about a competitor's visual state to conceal their approach to contested food, an ability that they did not acquire during the test. In this competitive paradigm, a human competitor placed pieces of food on two separate trays on either side of a booth and tried to prevent a chimpanzee subject from taking them (by retracting the tray), which he could do only if he could see the chimpanzee approaching. In the first experiment, the human looked at one piece of food and not at the other. In a second experiment, food was placed

Alicia P. Melis, Josep Call, and Michael Tomasello, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

We thank the Wolfgang Köhler Primate Research Center animal caretakers; David Buttelmann, Maria Graefenhain, and Victoria Wobber for their help with data collection and reliability coding; and Brian Hare and Daniel Stahl for their valuable comments on an earlier version of this article.

Correspondence concerning this article should be addressed to Alicia P. Melis, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103, Leipzig, Germany. E-mail: melis@eva.mpg.de

behind two barriers, one clear and one opaque. In both studies, chimpanzees preferentially went for the piece of food the human could not see or the ape could approach without being seen. However, a possible explanation in both of these cases is that chimpanzees might not be reasoning about what the competitor can see and may just be operating with the egocentric rule: "Avoid the food if the competitor's face is visible." In a third experiment, therefore, the clear barrier was replaced with a split barrier so that the chimpanzee had a choice between opaque barriers, both of which enabled it to avoid the face of the human. However, the split barrier enabled the human to see the lower part of the chimpanzee's body approaching, and so the food behind it, from a non-egocentric perspective, was unsafe. Once more, chimpanzees avoided the unsafe piece of food.

There is still one egocentric hypothesis that can explain chimpanzees' avoidance of the piece of food behind the split barrier, however. Because they could potentially see the lower part of the human's body as they approached on that side, they might have been operating with the rule: "Avoid seeing the human altogether." In the first of the current studies, therefore, we tested this hypothesis by presenting subjects with a situation in which they could not see the competitor on either side of the booth, but at the last moment the competitor could potentially see their arm reaching on one side (clear tunnel leading to food) but not on the other (opaque tunnel leading to food). To be successful, therefore, subjects had to imagine what the human could see from her perspective and reach through the opaque tunnel. It would be as though a subject hiding behind a large tree spied two pieces of food lying on the ground 30 cm beyond her reach on opposite sides of the tree. Although both pieces are fully visible to a potential competitor who is facing the tree 3 m away, a small bush contiguous to the left side of the tree creates a 25-cm natural barrier that ends right before the reward. Would the subject, without being able to see and monitor the competitor, choose to reach for the food on the left side (as opposed to the right side) because the barrier would conceal her reaching behavior?

It is possible that chimpanzees know how to conceal certain information from others but only in the visual modality. However, if the underlying cognitive mechanisms involve a deeper understanding of others' perceptual states, then chimpanzees should show similar skills in other perceptual modalities. In a second study, therefore, we investigated whether chimpanzees also would manipulate what others hear when it was to their competitive advantage to do so. In this case, chimpanzees could approach either side of the booth unobserved by the human (because she was oriented away), but reaching for the piece of food on one side of the booth (but not the other) created a loud noise, which alerted the human, who then took the food. If chimpanzees avoided the noisy reach in this study as well as the clear tunnel in the first study, this would strongly support the hypothesis that chimpanzees know what others can and cannot perceive in a way that is not tied to any single perceptual modality and, further, that they are able to use this knowledge to actively manipulate what others perceive by concealing certain perceptual information from them.

Experiment 1

In this experiment, chimpanzees had to choose between reaching for food through an opaque tunnel, which shielded their reach-

ing from a human competitor's view, and a transparent one, which did not (thus enabling the human to see their reach in advance).

Method

Subjects

Subjects were 7 chimpanzees (*Pan troglodytes*; 4 females and 3 males) housed at the Wolfgang Koehler Primate Research Center in the Leipzig Zoo, Germany. They ranged in age from 4 to 10 years (Table 1). They lived in a stable group consisting of 18 individuals, and all 7 subjects had been raised by their mothers. They spent the day in a 4,000-m² outdoor area and a 400-m² indoor area, both of which have natural vegetation, climbing structures, trees, water streams, and various other natural features. At night they are in a series of sleeping rooms of approximately 47 m². The chimpanzees are fed various fruits, vegetables, and cereals several times per day. Subjects were tested individually in familiar testing rooms (16 m²) with a familiar experimenter. All subjects except the youngest one had participated 1 year before in the Hare et al. (in press) study. The subjects were never food deprived, and water was available at all times throughout the tests. Subjects could choose to stop participating at any time.

Apparatus

Subjects were tested individually in familiar testing rooms with a familiar experimenter. The apparatus consisted of a rectangular table placed into a rectangular testing booth. The booth had a frontal window (98 × 95 cm) and two Plexiglas panels (75 × 50 cm) on either side of the table. The panels had holes (10.5 × 7 cm) through which subjects could reach. Two transparent tunnels (25 × 25 × 21 cm) were fixed left and right in front of these holes on the table. Inside each tunnel, a transparent Plexiglas flap, which had to be pulled to open the tunnel, was attached 24 cm away from the Plexiglas panel. Food dishes were placed in the center of the table (on the inside edge of each tunnel) on sliding trays that could be pulled back by the experimenter. The food dishes were 30 cm away from the Plexiglas panels. Subjects had to reach their hands through the tunnels and pull the flap toward them before being able to reach the food on the dishes. A plastic tube (4 cm in diameter and 57 cm long) extended from the center of the table into the wire mesh underneath the front Plexiglas window. By pouring fruit juice into the tube, subjects were attracted to sit in front of the experimenter across the testing table behind the front window.

Procedure

The general procedure in all conditions was as follows: The experimenter attracted subjects to the center of the front window (and kept it

Table 1
Sex, Age, and Rearing History of Subjects^a

Name	Sex	Age ^c	Rearing history
Jahaga	Female	10	Mother
Fifi	Female	10	Mother
Riet ^b	Female	26	Nursery/peers
Sandra	Female	10	Mother
Truddy	Female	10	Mother
Frodo	Male	10	Mother
Robert ^b	Male	28	Nursery/peers
Patrick	Male	6	Mother
Brent	Male	4	Mother

^a All subjects except for Brent participated in the Hare et al. (in press) study.

^b Did not pass a motivational criterion and did not participate in the present study.

^c Age at Experiment 1 (in years).

there with juice) and then placed one piece of food on each food tray on the side of the table. As subjects finished drinking the juice and raised their head, they could see through the front window the baited dishes on the table and a certain type of experimental setup, depending on condition. The subjects had to reach through one of the tunnels and pull the flap toward themselves to obtain the food. If the subjects did not approach or did not make a choice for 40 s, the experimenter removed both pieces of food.

To introduce the general competition paradigm, all subjects participated in a series of warm-up motivation trials in which they competed with the experimenter in an easy task. When subjects raised their head after drinking the juice, they saw the experimenter oriented with head and body to one side of the booth and one of the tunnels. If subjects approached and reached for the piece of food that the experimenter was not oriented to, they were allowed to take the food piece, but if they approached to the experimenter's front side, the food was pulled away as soon as they started reaching with their hand through the tunnel. This procedure was repeated until they reached for the piece of food that the experimenter could not see (at her back) four times in a row. Only subjects that met this criterion within two sessions of 18 trials each participated further.

For the actual experiment, all three windows in the booth were covered with green opaque occluders; see Figure 1 (II). The approaching path to both sides of the booth was thus totally occluded. Subjects could see the experimenter and the apparatus only from the starting position in the center of the front window through a narrow gap (46 × 12 cm) that was left uncovered. There were two experimental conditions.

Hidden-visible reach condition. One of the reaching tunnels was covered with a gray opaque occluder and the other was left uncovered. The experimenter sat in her position and looked straight ahead during the entire

trial (see Figure 1A). If subjects reached through the opaque tunnel, they were allowed to take the piece of food; however, if they reached through the transparent tunnel, the experimenter pulled the tray back out of reach. In the previous study (Hare et al., in press), one of the subjects had shown an aversion for occluders (opaque barriers). Consequently, we slightly modified the apparatus for this subject (Truddy): Instead of concealing the reach by extending the arm through an opaque tunnel, this chimpanzee simply had to reach behind an occluding barrier (25 × 25 cm).

Nonsocial control. Everything was identical to the hidden-visible reach condition, except that the experimenter stood up and left the testing room after she baited the trays (see Figure 1B). Subjects were allowed to take both pieces of food. This condition tested for possible preferences for one or the other reaching tunnel independent of the presence of the competitor.

In addition, subjects participated in motivational trials, in which both tunnels remained uncovered but the experimenter sat orienting her face and body toward one of the tunnels and piece of food (see Figure 1C). Subjects were allowed to obtain the food reward if they reached through the tunnel behind the human competitor but not if they reached through the box to which the experimenter was oriented. These trials were introduced to measure subjects' motivation to compete and subjects' performance in an easier task, which they were already skilled at before starting the actual test.

Design

Subjects received two test sessions (one per day) of 27 trials each, organized into nine trios presented sequentially (Brent, because of his age,

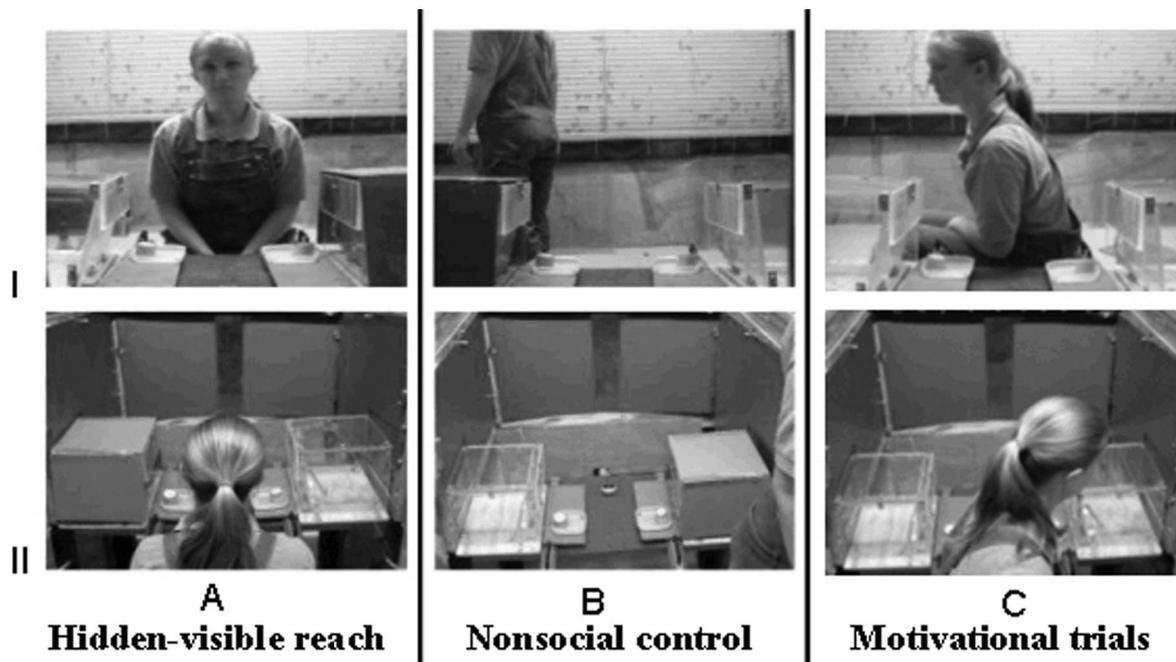


Figure 1. Experimental setup of Experiment 1. In this experiment, all three windows in the booth were covered with occluders. Subjects could see the experimenter and the apparatus only from the starting position in the center of the front window through a narrow gap that was left uncovered. Subjects had to choose the side of the booth that allowed them to conceal from the human competitor the reaching of the food. A. Hidden-visible reach: One of the tunnels is occluded, the experimenter looks straight ahead. B. Nonsocial control: One of the tunnels is occluded, the experimenter stands up and leaves the room. C. Motivational trials: Both tunnels are clear, the experimenter is oriented with her back to one of the tunnels. I = subjects' perspective; II = experimenter's perspective.

received four sessions). Each trio consisted of one trial of each of the experimental conditions: hidden-visible reach and nonsocial control and one motivation trial randomly ordered (see Figure 1). Each condition was counterbalanced for the number of times each manipulation (type of tunnel or the experimenter's body and head orientation) appeared on the left or the right side of the booth. Subjects thus received a total of 18 trials in each condition across the two sessions.

Scoring and Analysis

All trials were videotaped by three video cameras. Alicia P. Melis coded from video whether subjects approached, within 40 s, one of the windows and reached through the tunnel on the left or right side of the booth to obtain the food. The beginning of a trial was defined as the moment in which the subject lifted the head for the first time after drinking the juice. Twenty percent of the trials were blind-coded by a second coder. Interobserver reliability was 97% for location of reach (Cohen's $\kappa = 0.95$). Because subjects did not approach or make a choice in some trials, results were analyzed using proportions. We compared subjects' preference to reach through the opaque tunnel in the presence and absence of the competitor using a paired t test. We also compared subjects' preference for the opaque tunnel to that expected by chance (50%) using a one-sample t test. Because we had directional predictions (based on previous studies showing that chimpanzees understand what others can and cannot see; see discussion early in this article), all the p values reported are, unless otherwise specified, one-tailed. Finally, we assessed learning effects by comparing subjects' preference for the opaque tunnel within the first nine trials with that in the last nine trials using a paired t test. Effect sizes were calculated using Cohen's d (Cohen, 1988); means and 95% confidence intervals (CIs) are presented.

Results

A comparison between the test condition (hidden-visible reach) and the nonsocial control revealed that subjects preferred to reach through the opaque tunnel significantly more if the human competitor was present than if she was absent, paired $t(6) = 1.98$, $p = .047$, $d = 0.8$ (Figure 2). Furthermore, within the hidden-visible reach condition, subjects preferred to reach through the opaque tunnel significantly more as expected by chance, one-sample $t(6) = 2.25$, $p = .032$, $d = 0.9$, whereas they showed no such

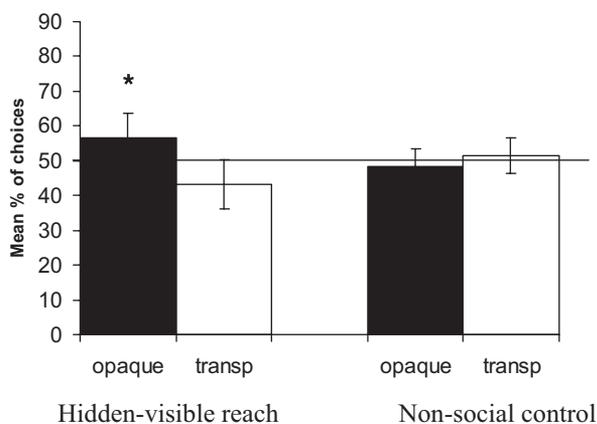


Figure 2. Mean percentage of reaches (\pm 95% confidence interval) into the different tunnels in the experimental conditions of Experiment 1 ($N = 7$). transp = transparent. $*p < .05$, one-sample t test and paired t test, one-tailed.

Table 2

Percentage of Trials in Which Subjects Chose the Opaque Tunnel in the Test and Control Conditions of Experiment 1

Name	Hidden-visible reach	Nonsocial control
Jahaga	50	50
Fifi	56	44
Truddy	44	50
Sandra	56	56
Frodo	59	50
Patrick	67	50
Brent	65	39
Mean*	57	48

* $p < .05$, one-sample t test and paired t test, one-tailed.

preference in the nonsocial control, $t(6) = 0.79$, $p = .23$, $d = 0.3$. Five of the 7 subjects reached more often through the opaque than through the transparent tunnel in the presence of the competitor, whereas only 1 showed such a preference in the absence of the competitor (Table 2). A learning analysis revealed no significant changes in subjects' performance in the first nine and last nine trials of the hidden-visible reach condition (first half vs. second half of the test session; percentage of reaches through opaque tunnel: $M_{\text{first trials}} = 52$, $SE = 4$, $CI = 43-60$; $M_{\text{last trials}} = 65$, $SE = 7$, $CI = 48-82$); paired $t(6) = 1.62$, $p = .16$, $d = 0.8$, two-tailed.

Discussion

Chimpanzees chose to reach for a piece of food through an opaque tunnel rather than through a clear tunnel in the presence of a human competitor, who would take the food for herself if she saw the reaching. They showed no such preference in a nonsocial control condition. Although the mean percentage of reaches through the opaque tunnel was not very high, it is important to note that we had a rather small number of chimpanzees and that the task itself was quite demanding (probably at the limit of what chimpanzees are capable of). The approach to both tunnels was occluded, so that once the chimpanzee left its starting position it could not see the human at all. This meant that to choose the appropriate tunnel, subjects had to, in some sense, imagine whether the human would or would not be able to see the reaching from her point of view, because from their perspective both sides of the booth were identical.

In addition, both pieces of food were in the open so that subjects could not rely on any kind of preference for food around barriers (Povinelli, Bering, & Giambone, 2000). By choosing the opaque tunnel, subjects were able to conceal just the initial reaching for the food, but this was enough to impede the experimenter from reacting in time. In preferentially choosing the opaque tunnel, subjects demonstrated that they were not operating with some egocentric rule of the type "If I cannot see the competitor I am safe," as they might have in the previous Hare et al. (in press) study. Although the mean number of reaches through the opaque tunnel was higher in the second half of the test, analyses showed that this change in performance was not statistically significant. The current findings, together with those from previous studies (e.g., Hare et al., 2000, 2001, in press; Tomasello et al., 1999), add to the growing body of evidence suggesting that chimpanzees can take the visual percep-

tive of others and, indeed, to some degree manipulate it (by concealing).

Experiment 2

In this experiment, chimpanzees had to choose between reaching for food through a silent tunnel or a noisy tunnel, in which case the distracted human competitor could hear and so react to by taking the food first.

Method

Subjects

Subjects were the same 7 chimpanzees that participated in Experiment 1. This experiment was conducted 12 months after Experiment 1.

Apparatus

The apparatus was the same as in Experiment 1 except that the flap in one tunnel was silent and the flap in the other was noisy. The silent flap consisted of a piece of transparent Plexiglas (16×19 cm) attached to one side of a square metal frame (21.5×23 cm), whereas the loud flap had, additionally, a thin metal blade (5×1.5 cm), which, when pulled, rattled against a metal-toothed piece fixed on the bottom part of the metal frame, making a loud noise. The loud flap was visually recognizable by a green line on the upper edge of the transparent Plexiglas (Figure 3A and B) and a different colored string to pull from. The flaps could be slid into the tunnels through a narrow opening (4.5 cm wide) on their upper part.

Procedure

Subjects were introduced to the apparatus with the new flaps by a cooperative (noncompetitive) human, Experimenter 2. In an initial introductory session consisting of 12 trials, both tunnels on the table contained loud flaps, and subjects were allowed (even encouraged) to take both pieces of food, one after the other. Then, in a second session, this same cooperative human presented subjects with the apparatus containing both types of flaps, one silent and one loud, for 10 trials to check whether subjects had a priori preference for one type of flap. Finally, on a different session, before starting the actual test, subjects were introduced to the competitive aspect of the task and the human competitor, Experimenter 1. During this introduction, both reaching tunnels had loud flaps. The competitive Experimenter 1 looked straight ahead at the subject and took the food away as soon as the subject approached one of the tunnels. Subjects

never obtained food in this introduction. To continue with the actual test, subjects had to refrain from approaching for 5 s in four of five consecutive trials, which all 7 subjects did within 11 trials. For the actual test, there were two experimental conditions.

Silent-loud reach condition. One of the reaching tunnels contained a silent flap and the other a loud flap. After centering the subject by pouring juice into the tube and baiting the food dishes, Experimenter 1 remained seated but bent her upper body toward the floor, sinking her head below the table (see Figure 3A). If subjects pulled from the silent flap, Experimenter 1 remained in her position looking to the floor, and they were able to take the piece of food. However, if subjects pulled the loud flap, Experimenter 1 raised up and pulled the food away.

Nonsocial control. Everything was identical to the silent-loud reach condition except that at the moment in which Experimenter 1 finished pouring the juice and baiting the food dishes she stood up and left the testing room (see Figure 3B). Subjects could potentially obtain both pieces of food.

In the motivation trials, both tunnels had silent flaps and Experimenter 1 sat oriented to the front but with the head turned toward one tunnel (see Figure 3C). If subjects approached and reached through the box that Experimenter 1 could not see, they were allowed to take the food piece, but if they approached and reached through the box to which Experimenter 1's head was oriented, she pulled the food away from them. These trials were introduced to measure subjects' motivation to compete and performance in a task, which, as established in a previous study (Hare et al., in press), subjects are skilled at.

Design

Subjects received three test sessions (one per day) of 18 trials each, organized into six trios consisting of one trial in the silent-loud reach condition, one in the nonsocial control, and one motivation trial, randomly ordered. Each condition was counterbalanced for the number of times each manipulation (silent vs. loud flap or the experimenter's head orientation) appeared on the left or the right side of the booth. Subjects thus received a total of 18 trials in each condition across the three sessions.

Scoring and Analysis

Scoring and analyses were identical to those of Experiment 1. Interobserver reliability was excellent (Cohen's $\kappa = 0.94$).

Results

In the baseline session with a cooperative experimenter (Experimenter 2), subjects showed no significant preference for choosing

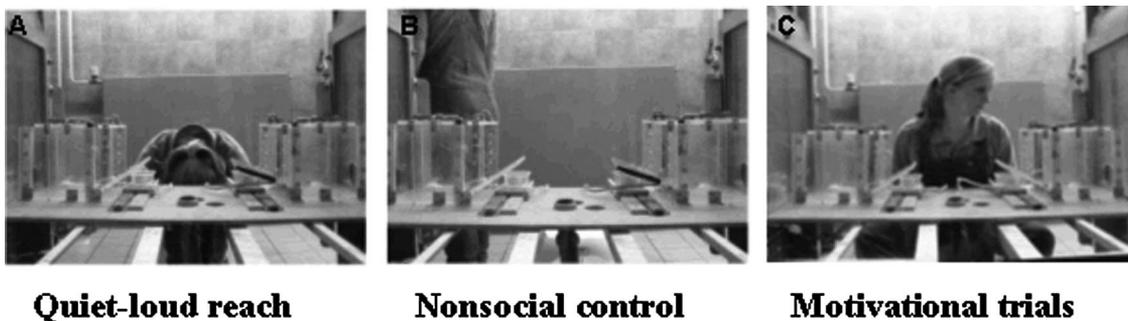


Figure 3. Experimental setup of Experiment 2. All three windows in the booth were transparent. A. Silent-loud reach: One of the flaps (with colored edge and string) is noisy, the experimenter cannot see (looks to the floor). B. Nonsocial control: One of the flaps (with colored edge and string) is noisy, the experimenter stands up and leaves. C. Motivational trials: Both tunnels are silent, the experimenter looks to one of them.

the noisy or silent flap, one-sample $t(6) = 0.50, p = .60, d = 0.2$, two-tailed. The comparison between the test condition and the nonsocial control showed no significant differences, paired $t(6) = 0.77, p = .23, d = 0.2$. A within-condition analysis showed that subjects did not preferentially pull from the silent flap in the test condition, one-sample $t(6) = 0.52, p = .30, d = 0.2$, nor was there any preference for one or the other type of flap in the nonsocial control condition, $t(6) = 0.54, p = .30, d = 0.2$.

Unlike Experiment 1, however, motivation to compete varied considerably across sessions, and in some cases subjects seemed disinclined to compete. We, therefore, performed a second set of analyses focusing only on sessions in which subjects obtained at least 80% correct choices in the motivation trials. Analysis of this subset of trials indicated that subjects pulled the silent flap significantly more often when Experimenter 1 was present in the silent-loud reach experimental conditions than when she was gone in the nonsocial control condition, paired $t(6) = 3.46, p = .006, d = 0.8$ (Figure 4). Moreover, subjects showed a tendency to prefer the silent flap compared to chance levels (50%) within the experimental condition, one-sample $t(6) = 1.75, p = .065, d = 0.7$, whereas they showed no such preference in the nonsocial control, $t(6) = 1.0, p = .17, d = 0.3$. At an individual level, 5 of the 7 subjects reached more often through the silent than through the noisy tunnel in the presence of the competitor, whereas only 1 showed such a preference in the absence of the competitor (Table 3). Once again, a learning analysis revealed no significant changes in subjects' performance in the first nine and last nine trials of the test condition (percentage of reaches through silent tunnel: $M_{\text{first trials}} = 46, SE = 5, CI = 33\text{--}60; M_{\text{last trials}} = 58, SE = 12, CI = 30\text{--}87$); paired $t(6) = 1.14, p = .30, d = 0.5$, two-tailed.

Discussion

In sessions in which chimpanzees were hiding from the human competitor in the motivation trials (by choosing the tunnel that the experimenter was not looking at), they were also avoiding the noisy flap in the experimental condition but not avoiding it in the nonsocial control condition. These results suggest that chimpanzees are able to assess not only what others can and cannot see but

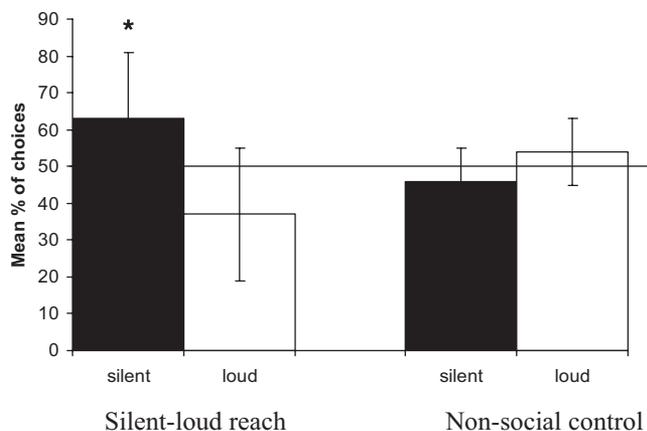


Figure 4. Mean percentage of reaches ($\pm 95\%$ confidence interval) into the different tunnels in the experimental and control conditions of Experiment 2 ($N = 7$). $*p < .05$, paired t test, one-tailed.

Table 3
Percentage of Trials in Which Subjects Chose the Silent Tunnel in the Test and Control Conditions of Experiment 2

Name	Silent-loud reach	Nonsocial control
Jahaga	67	50
Fifi	33	33
Truddy	67	58
Sandra	83	50
Frodo	83	50
Patrick	67	50
Brent	40	33
Mean*	63	46

Note. The data are based on the subset of sessions in which subjects performed well in the motivational trials (see Results section).

* $p < .05$, paired t test, one-tailed.

also what others can and cannot hear, and they can use this knowledge to avoid being detected. However, there was an increase in subjects' choice of the correct tunnel throughout both Experiments 1 and 2. Although the change was not statistically significant, it is possible that the data set was simply not powerful enough to detect such an increase. This implies that subjects may have just learned to associate the visual (and auditory) cues provided with the loss of the reward without any true understanding of how the competitor's visual and auditory perception affected the behavior of taking the food away. Experiment 3 tested this alternative explanation.

Experiment 3

Experiment 3 investigated whether subjects in the previous experiments had just learned to associate a particular visually marked tunnel (and noise) with a loss of reward because of the human's behavior. The contingencies in this experiment were highly similar to those in Experiment 2: Choice of one visually discriminable tunnel (marked) led to a noise and loss of food, whereas the other (unmarked) did not. What differed was that the noise was produced arbitrarily (but contingently) right after the flap was opened, so that it could not have caused the humans' alerting reaction.

Method

Subjects

Subjects were the same 7 chimpanzees that participated in Experiments 1 and 2. This experiment was conducted 3.5 months after Experiment 2.

Apparatus

The apparatus was the same as in Experiment 2. For this experiment only silent flaps were used. The flap that led to a noise and loss of food was marked by putting a plastic red square sign (12×8 cm) on the side of the tunnel facing the subject. This mirrored the mark of the loud flap from Experiment 2. The auditory cue was a low-pitched sound from a toy cell phone, and it was played in the testing room through a walkie-talkie.

Procedure

The procedure was almost identical to that from Experiment 2. Subjects first received an introductory session to the marked tunnel and the new

sound by a cooperative human (12 trials in which both tunnels were marked and led to a noise, but subjects were allowed, even encouraged, to take both pieces of food, one after the other). Then subjects participated in a baseline session to rule out a priori preference for one of the tunnels (10 trials with the apparatus containing both types of tunnels: marked–noisy, unmarked–silent). After that, they were introduced to the competitive context (as in Experiment 2) by Experimenter 1, and the testing phase began with several conditions.

Marked–unmarked tunnel condition. One of the tunnels had the red square sign on the side of the box facing the subject (marked), whereas the other remained transparent (unmarked). Experimenter 1 remained seated but bent her upper body toward the floor, sinking her head below the table. If subjects pulled from the unmarked flap, Experimenter 1 remained in her position looking to the floor, and they were able to take the piece of food. However, if subjects pulled from the flap in the marked tunnel, Experimenter 1 rose up and pulled the food away. Immediately afterward, they heard the cell phone sound.

Nonsocial control. This was identical to the previous condition except that when the experimenter finished pouring the juice and baiting the food dishes, she stood up and left the testing room. Subjects could potentially obtain both pieces of food. As in the previous condition, after pulling from the flap in the marked tunnel, subjects heard the cell phone sound.

Motivational trials were identical to those in Experiment 2. During the test phase, Experimenter 2 remained outside the testing room watching the test online through a monitor connected to the video cameras. Experimenter 2 informed Experimenter 1 by walkie-talkie (just by knocking briefly on it) whether subjects reached through the marked tunnel so that Experimenter 1 could react pulling the food away. The cell phone sound was played through the walkie-talkie, so that subjects could hear it in the presence and absence of the experimenter.

Design

As in Experiment 2, subjects received three test sessions (one per day) of 18 trials each, organized into six trios consisting of one trial of each type (marked–unmarked tunnel, nonsocial control, and motivation trial).

Scoring and Analysis

We used the same analyses as in Experiment 2. Interobserver reliability was excellent (Cohen's $\kappa = 1.00$).

Results and Discussion

In the baseline session with the cooperative experimenter, subjects showed no significant preference for reaching through one or the other tunnel (marked vs. unmarked), one-sample $t(6) = 1.0$, $p = .36$, $d = 0.4$, two-tailed. There were no significant differences between the test condition and the nonsocial control, paired $t(6) = 0.78$, $p = .23$, $d = 0.4$. A within-trial analysis showed that subjects did not preferentially reach through the unmarked–silent tunnel in the experimental condition, one-sample $t(6) = -2.50$, $p = .97$, $d = -0.9$. There was also no preference for one or the other type of tunnel in the nonsocial control condition, $t(6) = 1.0$, $p = .18$, $d = 0.4$. The same results are found when only those sessions in which subjects were most motivated were included. Finally, a learning analysis revealed no significant changes in subjects' performance in the first nine and last nine trials of the silent–loud reach experimental condition (percentage of reaches through unmarked–silent tunnel: $M_{\text{first trials}} = 45$, $SE = 4$; $CI = 36\text{--}54$; $M_{\text{last trials}} = 42$, $SE = 8$, $CI = 24\text{--}62$); paired $t(6) = 0.23$, $p = .82$, $d = 0.04$, two-tailed.

Subjects were unable to learn the association between a visually and acoustically distinguishable tunnel and the loss of the reward. Crucially, the visual cue on the incorrect tunnel, which was comparable to the one present in the previous experiment, could have helped the subject learn about the unsuitability of that tunnel even before the production of any auditory cues. The conclusion is thus that the contingencies in Experiment 3 were not of a type that would enable subjects to solve the problem by only associating the cues available with certain outcomes.

General Discussion

In the presence of a human competitor, chimpanzees preferentially reached through an opaque tunnel (Experiment 1) or a silent tunnel (Experiment 2). In the absence of a competitor, chimpanzees showed no such preference for any of the tunnels. These results support the hypothesis that chimpanzees are sensitive to what others see and hear and, moreover, are able to conceal certain types of information from them.

Although there was a nonsignificant increase in subjects' choice of the correct tunnel throughout both experiments, the data set may not have been powerful enough to reveal learning effects. To investigate whether subjects could learn to use visual or auditory cues to solve the task during the course of the experiment, subjects participated in a third experiment. We provided them with cues that had contingencies comparable to those used in previous experiments but that lacked the causal structure of the earlier cues. The results indicated that subjects were unable to use such arbitrary discriminative cues to obtain the food from the human competitor. A similar control was conducted in the previous study by Hare et al. (in press). In that case, the goal was to rule out the hypothesis that subjects simply had a preference for larger visual barriers (without any understanding of their occluding features). Subjects were rewarded for going behind the largest visual barrier of two possible barriers (although none of them actually occluded the subjects' approach). Once again, subjects did not learn to go behind the larger, but nonoccluding, barrier. If chimpanzees were just associating contextual cues with certain behavioral outcomes in the first two experiments, they should have been able to learn to use cues provided in these control conditions.

Of course, it remains possible that chimpanzees might have a predisposition to learn certain stimuli and not others. However, this is a difficult position to take, because the main difference between the stimuli that they can learn and those that they cannot is directly related to the effects that the stimuli have on others' perception. The cues' contingencies in the control experiment were almost identical to those used in the experiment; the main differences between the two types of cues (correctly used vs. nonlearnable) were causally related to the competitors' perception.

The current results add to a growing body of research suggesting that chimpanzees understand something of the psychological states of others (Call, 2003; Tomasello, Call & Hare, 2003a, 2003b). Most clearly, chimpanzees know what others see. They follow others' gaze, even around barriers (Tomasello et al., 1999); they check back when nothing interesting is there (Call et al., 1998); and when competing they know which objects others can and cannot see (Hare et al., 2000, 2001). Together with the findings of Hare et al. (in press), the current results support the hypothesis that

chimpanzees are sensitive to what others see, and they can conceal certain types of information from them.

The current study also shows that chimpanzees can avoid producing auditory cues in order to outwit competitors. This finding is consistent with that of other researchers, who have reported such observations as (a) subordinate chimpanzees suppress vocalizations in mating contexts (Hauser, 1990; de Waal, 1986); (b) chimpanzees on border patrol avoid making noises that might alert their neighbors to their presence (Watts & Mitani, 2001) and occasionally adults may even try to suppress the noises and vocalizations made by others (Goodall, 1986; de Waal, 1982); (c) males hunting for monkeys in their home range periphery often remain more silent than they normally would (Boesch & Boesch-Achermann, 2000); and (d) subordinates refrain from producing food calls that might attract dominants when they encounter monopolizable food resources (Brosnan & de Waal, 2003; Hauser, Teixidor, Field, & Flaherty, 1993). The current experimental results thus support these observations and, at the same time, especially given the results of the third control experiment and the lack of a learning effect during the first two experiments, suggest that the mechanism involved is not associative learning but something more deeply cognitive.

Alternatively, one might imagine some history of reinforcement contingencies experienced by these individuals that enabled them to perform well in the experiment. In fact, our subjects participated in a similar experimental set up 1 year earlier (Hare et al., in press), and so it might be argued that some learning carried over from this experience. However, in that study, there was no differential reinforcement, there were no tunnels, and there were also no signs of learning. The use of noise in our Experiment 2 is clearly unique for these individuals; indeed, in the Hare et al. (in press) study 1 year before, they could be as noisy as they wanted with no adverse consequences. Occasionally, in previous experiments, when reaching for the food that the experimenter could not see, the apparatus made some noise. Nevertheless, subjects were still able to obtain the food. Therefore, if anything, subjects had had experience with human competitors from whom they could steal the food even when they were being loud. Therefore, to the best of our knowledge, our subjects had had no previous experience in reaching through opaque and clear tunnels or through noisy and silent tunnels. In addition, it seems highly unlikely that our subjects had had experience stealing food from a competitor whom they could not even partially see and whose behavior could not be monitored during the ongoing transgression (as in Experiment 1).

Thus, one must posit that these chimpanzees had had similar previous experiences in reaching for food behind certain kinds of barriers or in certain noise-making situations in the presence of dominant individuals in the past, and they have now generalized that learning to the current situation. Note, however, that generalization should occur not across a single dimension but across multiple dimensions as a result of the complex nature of the stimuli involved. Furthermore, there is now converging evidence from a large number of studies demonstrating that chimpanzees know what others see (Call & Tomasello, in press); thus, to be consistent with an association learning explanation, one would have to hypothesize specific learning histories and generalization mechanisms to account for each of those cases as well, including ones that would account for subjects' failure to learn in our third control experiment and in Hare et al.'s (in press) control. Given the many

differences in the different experiments, the number of post hoc hypothetical learning contingencies posited as responsible is going to have to be very large.

Another issue with attributing these results to a stimulus generalization mechanism is that it becomes functionally identical to a mechanism that reasons about the perceptual states of others, for such a stimulus generalization mechanism must allow individuals to perform successfully across many different and novel contexts but only operate when the cues provided are causally relevant to the perceptual states of others. Furthermore, because a system that reasons about mental states uses information about behavior to generate inferences about the role of psychological states in producing behaviors (Povinelli & Vonk, 2003, 2004), every mentalistic interpretation can be substituted by a behavioral account. It will always be possible to attribute subjects' ability to predict others' behavior to a generalization mechanism that relates perceptual regularities to future behaviors (Povinelli & Vonk, 2003, 2004). Thus, the problem with this debate is that it is nearly impossible to solve empirically: All the results coming from experiments with an ecologically valid design can always be interpreted by means of a behavioral account (for a discussion of this topic, see Povinelli & Vonk, 2003, 2004; Tomasello et al., 2003a, 2003b).

The fact is that, whatever chimpanzees are reasoning about, a large number of studies are demonstrating similar skills in many different situations and now maybe even in two sensory modalities. In addition, low-level interpretations such as simple associative learning during or before the test cannot easily and fully explain these results.

We thus believe that the current findings, together with those of Hare et al. (in press) and others (Flombaum & Santos, 2005; Hare et al., 2000, 2001, see also Shillito, Shumaker, Gallup, & Beck, 2005), demonstrate that chimpanzees have some understanding of what others can see and, moreover, that they know how to use this knowledge to conceal visual information from them. Additionally, the current study provides evidence that this ability may extend to the auditory domain, suggesting that the underlying mechanism is not tied to any one sensory modality. Instead, it appears to involve a broader understanding of others' perceptual states. This does not mean, of course, that chimpanzees understand all kinds of psychological states and are capable of all forms of deception. There are other psychological states, such as thoughts and beliefs, that chimpanzees may not understand and other forms of deception, such as active misleading or lying, that may only be possible for *Homo sapiens*.

References

- Bates, E. (1979). *The emergence of symbols: Cognition and communication in infancy*. New York: Academic Press.
- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest*. Oxford, UK: Oxford University Press.
- Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology, 119*, 145–154.
- Brosnan, S. F., & de Waal, F. B. M. (2003). Regulation of vocal output by chimpanzees finding food in the presence or absence of an audience. *Evolution of Communication, 4*, 211–224.
- Bugnyar, T., Stowe, M., & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the*

- Royal Society of London: *Series B. Biological Sciences*, 271, 1331–1336.
- Call, J. (2003). Beyond learning fixed rules and social cues: Abstraction in the social arena. *Philosophical Transactions of the Royal Society of London: Series B. Biological sciences*, 358, 1189–1196.
- Call, J., Agnetta, B., & Tomasello, M. (2000). Social cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, 3, 23–34.
- Call, J., Hare, B. A., & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal Cognition*, 1, 89–99.
- Call, J., & Tomasello, M. (2005). What chimpanzees know about seeing revisited: An explanation of the third kind. In N. Eilan, C. Hoerl, T. McCormack, & J. Roessler (Eds.), *Issues in joint attention*. (pp. 234–253). Oxford, UK: Oxford University Press.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: Erlbaum.
- de Waal, F. B. M. (1986). Deception in the natural communication of chimpanzees. In R. W. Mitchell & N. S. Thompson (Eds.), *Deception: Perspectives on human and nonhuman deceit* (pp. 221–244). Albany, NY: State University of New York Press.
- de Waal, F. B. M. (1982). *Chimpanzee politics*. London: Jonathan Cape.
- Emery, N., Lorinez, E., Perret, D., Oran, M., & Baker, C. (1997). Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 111, 286–293.
- Ferrari, P. F., Kohler, E., Fogassi, L., & Gallese, V. (2000). The ability to follow eye gaze and its emergence during development in macaque monkeys. *Proceedings of the National Academy of Sciences, USA*, 97, 13997–14002.
- Flombaum, J. I., & Santos, L. R. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, 15, 447–452.
- Goodall, J. (1986). *The chimpanzee of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59, 771–785.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61, 139–151.
- Hare, B., Call, J., & Tomasello, M. (in press). Chimpanzees deceive a human competitor by hiding. *Cognition*.
- Hauser, M. D. (1990). Do female chimpanzee copulation calls incite male-male competition? *Animal Behaviour*, 39, 596–597.
- Hauser, M. D., Teixidor, P., Field, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: Effects of food quantity and divisibility. *Animal Behaviour*, 45, 817–819.
- Hirata, S., & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition*, 4, 285–295.
- Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats (*Capra hircus*) follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, 69, 11–18.
- Karin-D'Arcy, M., & Povinelli, D. J. (2002). Do chimpanzees know what each other see? A closer look. *International Journal of Comparative Psychology*, 15, 21–54.
- Menzel, E. W. (1974). A group of young chimpanzees in a one-acre field: Leadership and communication. In A. M. Schrier & F. Stollnitz (Eds.), *Behavior of nonhuman primates* (pp. 83–153). New York: Academic Press.
- Povinelli, D. J., Bering, J. M., & Giambrone, S. (2000). Toward a science of other minds: Escaping the argument by analogy. *Cognitive Science*, 24, 509–541.
- Povinelli, D. J., Bierschwale, D. T., & Cech, C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, 17, 37–70.
- Povinelli, D. J., & Eddy, T. J. (1996a). Factors influencing young chimpanzees' recognition of attention. *Journal of Comparative Psychology*, 110, 336–345.
- Povinelli, D. J., & Eddy, T. J. (1996b). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, 61, 1–152.
- Povinelli, D. J., & Eddy, T. J. (1997). Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology*, 15, 213–222.
- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Sciences*, 7, 157–160.
- Povinelli, D. J., & Vonk, J. (2004). We don't need a microscope to explore the chimpanzee mind. *Mind and Language*, 19, 1–28.
- Shillito, D. J., Shumaker, R. W., Gallup, G. G., & Beck, B. B. (2005). Understanding visual barriers: Evidence for Level 1 perspective taking in an orang-utan, *Pongo pygmaeus*. *Animal Behaviour*, 69, 679–687.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55, 1063–1069.
- Tomasello, M., Call, J., & Hare, B. (2003a). Chimpanzees understand psychological states—The question is which ones and to what extent. *Trends in Cognitive Sciences*, 7, 153–156.
- Tomasello, M., Call, J., & Hare, B. (2003b). Chimpanzees versus humans: It's not that simple. *Trends in Cognitive Sciences*, 7, 239–240.
- Tomasello, M., Hare, B., & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour*, 58, 769–777.
- Watts, D., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters among wild chimpanzees. *Behaviour*, 138, 299–327.
- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, 11, 233–273.
- Woodruff, G., & Premack, D. (1979). Intentional communication in the chimpanzee: The development of deception. *Cognition*, 7, 332–362.

Received August 8, 2005

Revision received November 10, 2005

Accepted November 29, 2005 ■