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# Chimpanzees deceive a human competitor by hiding

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#### **Abstract**

There is little experimental evidence that any non-human species is capable of purposefully attempting to manipulate the psychological states of others deceptively (e.g., manipulating what another sees). We show here that chimpanzees, one of humans' two closest primate relatives, sometimes attempt to actively conceal things from others. Specifically, when competing with a human in three novel tests, eight chimpanzees, from their first trials, chose to approach a contested food item via a route hidden from the human's view (sometimes using a circuitous path to do so). These findings not only corroborate previous work showing that chimpanzees know what others can and cannot see, but also suggest that when competing for food chimpanzees are skillful at manipulating, to their own advantage, whether others can or cannot see them.

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#### 1. Introduction

Human beings sometimes attempt to deceive one another. Whereas various related but non-mentalistic phenomena such as bodily camouflage are widespread in the

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animal kingdom, intentional deception – in which one individual attempts to actively manipulate what another experiences cognitively – is considered by many to be a uniquely human cognitive ability (e.g., Cheney & Seyfarth, 1990; Hauser, 1997; Tomasello & Call, 1997).

While research on non-human primates has revealed a number of behaviors that function to deceive others (so-called "tactical deception", Whiten & Byrne, 1988), it remains unclear whether such cases also represent instances of intentional deception. For instance, subordinate primates refrain from giving food calls that might attract dominants to monopolizable food (Hauser, 1992, 1997; Hauser, Teixidor, Field, & Flaherty, 1993), learn to hide themselves from potential competitors (de Waal, 1998; Gygax, 2000; Kummer, Anzenberger, & Hemelrijk, 1996), and sometimes even actively lead approaching dominants away from the location of hidden food (Coussi-Korbel, 1994; Goodall, 1986; Hirata & Matsuzawa, 2001; Menzel, 1974). However, in each of these cases it is plausible that the animals are relying inflexibly on some invariant behavioral or contextual cue (Cheney & Seyfarth, 1990; Heyes, 1998; Ristau, 1991). For example, it is possible that subordinate primates simply learned during daily competition over food that they were more likely to obtain food if they refrained from behaving towards it in the presence of a dominant (Cheney & Seyfarth, 1990; Heyes, 1998).

Support for such a learning interpretation comes from experiments in which it took many dozens or even hundreds of trials for primates to learn to refrain from indicating the location of hidden food when an individual who did not share food was present (Anderson, Kuroshima, Kuwahata, Fujita, & Vick, 2001; Fujita, Kuroshima, & Masuda, 2002; Mitchell & Anderson, 1997; Woodruff & Premack, 1979). Most notably, Woodruff and Premack (1979) trained four chimpanzees to indicate the location of hidden food for humans, and then introduced two different experimenters. One experimenter shared the food with the subject if he found it while the second experimenter (wearing a mask) did not share the food with the subject if he found it. Only two of the chimpanzees eventually learned, after dozens of trials, to refrain from indicating the correct food location in the presence of the masked experimenter. Because it takes primates so long to master such skills and their newly acquired skills do not easily generalize to new settings, it is possible that in these studies primates base their decisions on invariant contextual or behavioral cues learned in each experimental setting (i.e., the chimpanzees of Woodruff & Premack, 1979 learned to use the mask as a discriminative cue to withhold signaling). It is based on findings such as these, that the majority of theorist have concluded that there is no solid experimental evidence demonstrating that non-human primates, or other animals, are capable of intentional deception (Hauser, 1997; Heyes, 1998; Povinelli, 2000; Ristau, 1991; Shettleworth, 1998; Tomasello & Call, 1997).

However, recent studies with one of humans' two closest primate relatives, the chimpanzee, suggest the possibility for a new test of the hypothesis that intentional deception is unique to humans. A powerful test might be possible since a recent series of experiments demonstrate that chimpanzees understand what other individuals can and cannot see – and in certain situations what they have and have not seen in the immediate past (Call, Agnetta, & Tomasello, 2000; Hare, Call, Agnetta, &

Tomasello, 2000; Hare, Call, & Tomasello, 2001; Tomasello, Hare, & Agnetta, 1999; Tomasello, Hare, & Fogleman, 2001). For example, subordinate chimpanzees prefer to retrieve food that is hidden behind an occluder and out of a dominant competitor's view rather than food that is visible to both – even if in each contest the subordinate must make her decision before seeing the dominant or the dominant behaving (Hare et al., 2000). In addition, subordinate chimpanzees are more likely to approach food if the dominant did not see than if the dominant did see the food hidden behind one of two opaque occluders (Hare et al., 2001). These findings suggest, in the right context (i.e., during natural food competition with conspecifics that does not involve using arbitrary cues such as masks to indicate deceitfulness), chimpanzees, like humans, might also demonstrate skill at actively and flexibly manipulating what others can and cannot see when it is to their benefit.

But there remains debate regarding whether these chimpanzee social problem solving behaviors might also be explained by an inflexible reliance on contextual or behavioral cues alone (Povinelli & Vonk, 2003; Tomasello, Call, & Hare, 2003a). Karin-Karin-D'Arcy and Povinelli (2002) suggest that the behavior of subordinates in Hare et al. (2000) represents inflexible preferences for approaching food near the safety of physical barriers during competition (although see Tomasello et al., 2003a, Tomasello, Call, & Hare, 2003b) and not an understanding of their occluding properties. Meanwhile, the previous findings of Povinelli and colleagues suggest that chimpanzees are extremely limited in their understanding of how others' visual perception actually works (i.e., they show little skill in using social cues related to others visual perception such as face direction in determining when someone can or cannot see them) (Povinelli, Bierschwale, & Cech, 1999; Povinelli & Eddy, 1996; Reaux, Theall, & Povinelli, 1999; Theall & Povinelli, 1999; however, see Leavens & Hopkins, 1998; Hostetter, Contera, & Hopkins, 2001; Kaminski, Call, & Tomasello, 2004; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2003 for contradictory evidence).

Therefore, in the current investigation we examine whether chimpanzees are not only capable of assessing when a competitor can and cannot see things, but also whether they use this same ability to intentionally manipulate another individual's visual information by concealing their approach toward contested food. In doing so, this investigation was designed to test the ability of the visual perspective-taking hypothesis of Hare et al. (2000, 2001) against that of the learned cues hypotheses of Povinelli and Eddy (1996) and Karin-Karin-D'Arcy and Povinelli (2002) in predicting the behavior of chimpanzees in solving several novel social problems.

Because chimpanzees perform most skillfully in competitive cognitive tasks (Hare, 2001; Hare & Tomasello, 2004), subjects competed against a human (E) who moved prized food items out of the subjects' reach when they attempted to retrieve them. Subjects' spontaneous behavior was measured in three novel experimental setups. In the first, subjects chose to either approach food that E's face was oriented toward or food that E's chest (but not face) was oriented toward. In the second, subjects chose to approach food either from behind a transparent barrier or from behind an opaque occluder as E faced the subject. In the third, subjects chose to approach from behind a barrier that occluded their approach either partially or fully as E faced

the subject. Unlike previous studies (i.e., Woodruff & Premack, 1979), this competitive paradigm did not require any behavioral shaping (i.e., training a new behavior) or communication in which the subject had to produce (or not) communicative signals – arguably a more difficult domain as it involves not just reading intentions but reading communicative intentions (Tomasello, 1999; Hare & Tomasello, 2004).

Thus, in the current experiment, the visual perspective-taking hypothesis predicts that subjects will spontaneously conceal their approach from their competitor by (1) avoiding food that E's face is oriented toward over food that E's chest is oriented toward (first experimental setup), (2) preferring to approach behind visual occluders over non-occluding barriers (second and third experimental setups), and (3) avoiding a direct approach to the food if a more indirect route might better conceal their intent to approach (first and second setups). Meanwhile, the learned cues hypothesis predicts that subjects' inflexible use and limited understanding of social cues related to visual perception (Povinelli, 2000; Povinelli & Eddy, 1996) and attraction to physical barriers (regardless of their occluding properties) during food competition (Karin-Karin-D'Arcy & Povinelli, 2002; Povinelli & Giambrone, 2001) will prohibit them from concealing their approach in any of these ways.

# 2. Method

# 2.1. Subjects

Eight chimpanzees participated and could stop participating at any time (see Table 1 for the sex, age, and rearing history of each subject). The chimpanzees live at the Wolfgang Köhler Primate Research Center (4533 m2) in the Leipzig Zoo, Germany. Water was available at all times throughout the experiment. All subjects were tested in a familiar testing room with a familiar experimenter.

# 2.2. Apparatus

A rectangular table was painted green and placed into a rectangular testing booth with three transparent Plexiglas sides (Fig. 1). The table  $(84 \times 32 \times 45)$  had sliding food dishes  $(12 \times 8 \times 2.5 \text{ cm})$  attached to either side which could travel 35 cm. In

Table 1	
Sex, age, and rearing history of participating chimpanzee subj	ects

Name	Sex	Age	Rearing history
Robert	Male	26	Human
Reit	Female	25	Human
Sandra	Female	9	Mother
Jahaga	Female	9	Mother
Frodo	Male	9	Mother
Fifi	Female	9	Mother
Truddy	Female	9	Mother
Patrick	Male	5	Mother

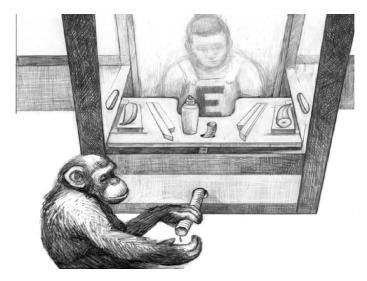


Fig. 1. The experimental apparatus showing the experimental room, the testing booth, experimenter, and subject (in addition, the placement of the food table, the sliding food trays, the hand holes in the two Plexiglas windows for the subject to reach through, and the juice tube are also visible. *Note*. The tube only protruded from the booth a few centimeters and could not be held by the subject. Therefore, subjects always drank out of the juice tube using their mouth forcing them to sit facing the experimenter).

addition, a plastic tube (4 cm in diameter and 57 cm long) extended 31 cm from underneath the table top into the wire mesh below the table and at the front of the testing booth (98  $\times$  95 cm). Fruit juice could be poured through the tube to attract the subjects to sit in front of the center glass window (83  $\times$  48 cm) across the table from the experimenter. In the booth on either side of the table were Plexiglas testing windows (75  $\times$  50 cm) that each had small oval holes cut into them (10  $\times$  5 cm) which subjects could reach their fingers through to obtain food from the food dishes when pushed within reach of the subject.

#### 2.3. Procedure

#### 2.3.1. Introduction

The subjects had never been tested with the apparatus, general testing procedure, or competitive humans (i.e., human caretakers almost exclusively share food altruistically). Therefore, to acquaint the subjects to the apparatus and procedure, they first received four non-competitive introduction trials. E attracted the subject to sit across the table from him, behind the center window, by pouring juice for the subject through the juice tube which she could drink with her mouth. Once the subject was sitting behind the center window drinking juice, pieces of banana were placed on both food dishes and pushed within reach of the subject (Fig. 1). Subjects quickly learned that they could obtain both pieces of banana by reaching through the oval hand holes in the Plexiglas testing windows on either side of the table.

Second, E changed his behavior and began to compete with the subject. The procedure was the same as the initial non-competitive trials with the exception that E

pulled the food out of the subject's reach if they attempted to approach the food (E always stared straight ahead). In addition, if the subject refrained from approaching for over 5 s then the food was removed. In this way the subjects would understand that E, like their group mates, no longer was willing to share prized food (i.e., banana pieces) with them. To help assure that subjects understood that E was now a competitor like their group mates, this competitive introduction procedure was repeated until either: (1) the subject refrained from approaching for four out of five consecutive trials or (2) they received 36 warm-up trials.

#### 2.3.2. Test sessions

Once each subject had been introduced to the new apparatus, general procedure, and competitive E, subjects were tested in three different tests each with its own experimental setup. Each test consisted of three different conditions, all of which followed the same general testing procedure used in the introduction. Two conditions in each test were experimental while the third was a non-social control designed to measure subject's baseline behavior with the apparatus but without the experimenter. Subjects were rewarded differently in each of the three types of conditions within a test session. Once the subject was sitting across the testing table from E, drinking juice with their mouth and E had pushed the food within reach of the hand holes, the following conditions and rewarding were used for each of the three sessions.

2.3.2.1. Test 1: Body orientation (Fig. 2). Face and chest condition. E oriented his face and chest towards one of the two pieces of food, with his back turned to the other. If subjects approached, they were allowed to retrieve the piece of food behind the experimenter, but the food was removed if the subjects approached the food E's face and chest were oriented toward.

Face versus chest condition. E oriented his face toward one of the food dishes while orienting his chest toward the other piece of food. Regardless of which piece of food the subject approached, E removed the food.

*Non-social control.* E immediately left the testing room allowing the subject to obtain both pieces of food.

2.3.2.2. Test 2: Occluder (Fig. 3). Face and chest condition. Same as in Session 1.

Occluder condition. A plastic occluder  $(74 \times 50 \text{ cm})$  was placed over one of the choice windows between trials. The occluder also had a hole  $(10 \times 5 \text{ cm})$  allowing subjects to reach through the hand hole in Plexiglas window to obtain the food. Regardless of which piece of food the subject approach, E removed the food while staring straight ahead.

*Non-social control*. The occluder was placed on one of the Plexiglas windows and E left, thus allowing the subject to retrieve both pieces of food.

2.3.2.3. Test 3: Split occluder (Fig. 4). Double occluder condition. Two occluders were placed on the same side of table. One of these occluders covered one of the Plexiglas windows  $(74 \times 50 \text{ cm})$  while the other barrier  $(71.5 \times 50 \text{ cm})$  was placed upright on the table. The subject was allowed to retrieve food from behind the occluders, while

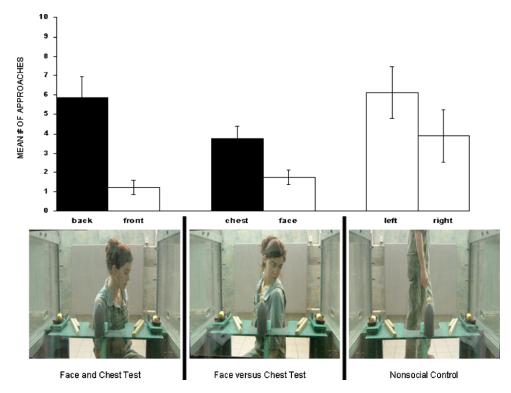


Fig. 2. A picture of experimental manipulations used in the Test 1 and the mean number of approaches within each of the three test conditions (note: the two social cues in the two social tests were presented on the right side (as in pictures) in half of trials and on the left side in the other half of trials).

food was moved out of reach if the subject approached the unoccluded Plexiglas window (E stared straight ahead).

Split occluder condition. A barrier was placed on either side of the table. Each side had barriers that equalled half the occluding surface area of the barriers used in Double Occluder condition. One barrier  $(72 \times 50 \text{ cm})$  was placed on one side of the table and acted as an occluder. Meanwhile, two barriers (each  $72 \times 25 \text{ cm}$ ), that were each half the size of the occluder, were placed on the other side of the table. One of the two smaller barriers was attached to the Plexiglas window at eye level while the other was placed on the table. In addition, regardless of which piece of food the subject approached, E removed the food and stared straight ahead.

*Non-social control*. The barriers were positioned as in the Split Occluder condition. In this condition E left allowing the subject to obtain both pieces of food.

# 2.4. Design

Each test was completed on a separate day, in the order 1–3, and all followed the same general design. Each test session contained two introduction trials (to

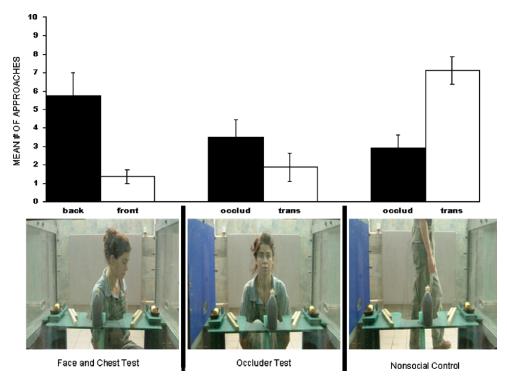


Fig. 3. A picture of experimental manipulations used in Test 2 and the mean number of approaches within each of the three test conditions.

remind subjects before starting that, unlike usual, E was a competitor) and 10 trials of each of the different conditions (30 total trials). The conditions were counterbalanced across subjects using two different orders with half of the subjects receiving each of the two orders in each test. Within each test session the conditions were presented to each subject in a mixed order in 10 sets of three trials. Each set of three trials contained one of each type of trial being tested in that session (trials were counterbalanced to assure that subjects had the opportunity to be rewarded regularly for hiding so that their motivation for competing against E might be maintained across the entire session). Each condition was counterbalanced for the side on which each manipulation was administered (e.g., in the face and chest condition E oriented both toward the food on the left and the right for half of the trials, etc.).

Finally, as a supplemental control, after all three of the test sessions were completed, all subjects were tested in an additional control condition in which barriers were present but did not occlude E's view of the subject's approach to either food dish. As in the Split Occluder condition, an opaque barrier was placed on either side of the testing table. One barrier  $(35 \times 25 \text{ cm})$  was half the size of the other  $(72 \times 25 \text{ cm})$ , but neither barrier was large enough to act as a visual occluder. The procedure was identical to the previous tests with the exception that subjects were rewarded for approaching behind the larger of the two non-occluding barriers. Each subject

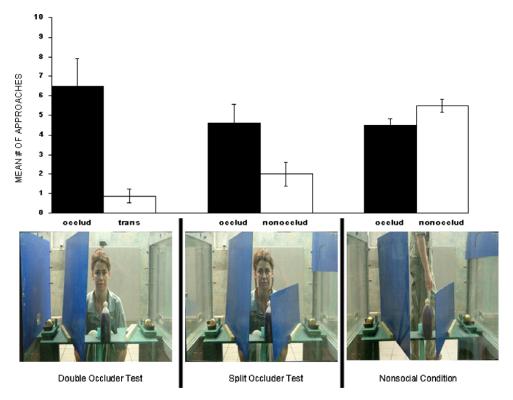


Fig. 4. A picture of experimental manipulations used in Test 3 and the mean number of approaches within each of the three test conditions.

participated in a test session of 10 consecutive trials with the placement of the barriers (left or right) being counterbalanced within and between subjects. This supplemental control is designed to test if subjects prefer larger barriers, regardless of their occluding properties, while competing with E.

# 2.5. Scoring and analysis

All trials were coded from video for whether subjects approached (moved within reaching distance of food) within the 30 s trial of one of the pieces of food (left or right). All of the experimental trials were also coded for whether the subject approached on the side where it was most difficult for E to see her. This means a trial was scored as hiding when: Face and Chest – the subject approached from behind E's back; Face versus Chest – the subject approached towards E's chest; Occluder – the subject approached behind the occluder; Double Occluder – the subject approached behind the two occluders; Split Occluder – the subject approached behind the solid occluder. In addition, all trials were coded for whether the approach was direct (Fig. 5: subjects first reduced the distance between themselves and the food) or indirect (Fig. 5: subjects first distanced themselves from the food 1–3 m before reducing the distance between themselves and the food). Twenty percent of trials were coded by a second coder who was blind

to the condition. Interobserver reliability was 99.7% for approaches, with a Cohen's  $\kappa$  of .98 and 97.9% for the type of approach with a Cohen's  $\kappa$  of .86.

To test the predictions of the competing hypotheses, we planned to analyze subjects' approach behavior in several ways. Within each condition a paired t-test was used to compare the number of trials subjects, as a group, hid their approach or did not (percentage of approaches are presented in all figures because of differences in the number of trials in which subjects chose to approach at all during each session). In addition, to assess individual hiding preferences each subject's combined hiding preference in all six social conditions was compared to chance (each subject generally approached too infrequently in each session to provide sufficient power for reliable assessment of individual preferences in each of the six social conditions separately). Finally, we examined whether as a group, subjects approached indirectly more often in the experimental than control condition in each test using a one-way ANOVA and paired comparisons (Fischer LSD test corrected for multiple planned comparisons). Because this experiment was designed to test the directional predictions of the visual perspective-taking hypothesis against the null predictions of the contextual and learned cues hypothesis, all statistics were one tailed unless otherwise noted.

In order to assess if subjects came to the experiment with an understanding of how to hide from E's view, or if they learned to do so during the experiment, we conducted three tests of learning. First, within each test session we looked to see if subjects' approach behavior changed across the session. The group's approach preferences in the social conditions of each session were compared using (1) trials 1–3 compared to trials 4–6, and (2) the first 10 trials to the last 10 trials using paired *t*-tests (multiple

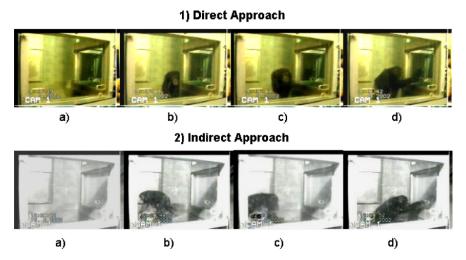


Fig. 5. An illustration of a subject's (1) direct approach and (2) indirect approach to the left of the experimenter. When approaching directly subjects: (1a) sat at the juice tube out of the camera's view, (1b) look directly around the corner of the test booth, (1c) approached directly around the corner of the test booth, (1d) and reached for the food. When approaching indirectly subjects: (2a) sat at the juice tube out of view of the camera, (2b) distanced themselves from the food and experimenter, (2c) returned out of view of the experimenter (notice occluded window), (2d) and reached for the food.

tests were not corrected since such tests favor finding evidence of learning). Second, we tested to see if subjects approached and hid more in the conditions where they were rewarded than those in which they were not using a paired *t*-test. Third, we also examined subjects' first approach behavior. This was done by comparing the groups' preferred direction of approach in the first trial of the two experimental conditions in each test. For the first two learning analysis we had no directional prediction since during a test session subjects might have increased hiding due to rewarding or decreased hiding due to a loss of motivation. The third analysis was one tailed since the visual perspective-taking hypothesis makes the directional prediction that subjects will hide within trials.

#### 3. Results

In the introduction session seven of the eight subjects met the criteria and quickly refrained from approaching (mean 13 trials; range 2–25 trials). One subject (Truddy) continued approaching throughout the 36-trial session, but because the introduction was only designed to introduce the subjects to the competitive E (not act as a criterion for participation or as a behavior shaping procedure) this subject also participated in all subsequent tests (she concealed her approach in a majority of trials in five of the six experimental tests).

In Test 1: Body Orientation, as a group, subjects avoided approaching the food that E was watching in both the Face and Chest condition, [t(7) = 3.87, p = 0.003], and in the Face versus Chest condition, [t(7) = 2.65, p = 0.017]. As a group, subjects did not have a significant preference for approaching one side of the booth or the other in the Non-social control condition (Fig. 2).

In Test 2: Occluder, as a group, subjects again had a preference for avoiding the food E was watching in the Face and Chest condition [t(7) = 3.38, p = 0.006], replicating the results from the first test. In the Occluder condition, as a group, subjects did not have an overall preference for approaching behind either the opaque occluder or the transparent barrier [t(7) = 1.31, p = NS] (Fig. 3). However, this result is explained by the fact that some subjects had a strong aversion to the occluder regardless of whether E was present or not – as revealed in the Non-social control in which overall subjects preferred to approach behind the transparent barrier [t(7) = 2.86, p = 0.012, two tailed].

Because of this unexpected preference for the transparent barrier in the Non-social control, we ran additional analysis of this test to examine more closely if subjects used the occluder to hide. First, a two-way ANOVA (condition × barrier type) was used to compare subjects' approach behavior in the Occluder condition to that in the Non-social control. There was a significant effect of condition [F(1,7) = 16.66, p = 0.005] and a significant condition × barrier type interaction [F(2,21) = 15.234, p = 0.006], with subjects avoiding the transparent barrier significantly more in the Occluder condition than in the Non-social control. Second, we also examined the first trials within the Occluder test and Non-social control conditions. Subjects had a significant preference for approaching behind the occluder in the first trial they

approached in the Occluder condition but not in the Non-social control [Sign Test, p < 0.05]. Finally, after removing the two subjects who had significant individual preferences for the transparent barrier in the Non-social control (both individuals approached behind the transparent barrier in all 10 trials, p < 0.002, binomial probability, two tailed), we found that the remaining six subjects did have an overall preference for hiding behind the occluder in the Occluder condition (T = 19, N = 6, p < 0.045, Wilcoxon Sign Rank test).

In Test 3: Split Occluder subjects preferred to approach behind the visual occluder both in the Double Occluder condition [t(7) = 3.56, p = 0.005], and in the Split Occluder condition [t(7) = 3.59, p = 0.005]. Subjects had no preference for either of the different types of barriers within the Non-social control (Fig. 4).

Table 2 presents the percentage of trials in which each subject hid in the six different social conditions (percentages were used because subjects did not always approach in every trial). With one exception (Robert), all subjects hid their approach in over two-thirds of trials in at least five of the six social conditions (this was the case in all conditions for three subjects). In addition, half of the subjects hid their approach in a majority of trials (i.e., over half) in all six social conditions.

Table 2 also presents the percentage of trials in which each subject hid when all six social conditions are combined. All but one subject (Robert) hid from their competitor at above chance levels (curiously, Robert, the only adult male tested, initially hid in each test session, but then seemed to switch strategies and instead displayed in sight of the male experimenter or begged for the food using a food begging gesture before attempting to retrieve the visible food much in the way that male chimpanzees do in the wild when trying to obtain prized food such as meat from one another).

Table 2
Percentage of trials in which subjects hid from the experimenter in each of the six social conditions and all six social conditions combined

Subject	Condition					Total	
	Test 1: body orientation		Test 2: occluder		Test 3: split occluder		
	Face and chest	Face versus chest	Face and chest	Occluder	Double occluder	Split occluder	
Robert	40	50	100	25	0	100	52.5
Reit	100	75	50	100	100	100	87.5*
Sandra	71	67	67	100	100	70	79.1***
Jahaga	90	75	80	80	100	90	85.6***
Frodo	100	83	100	70	100	60	85.5***
Fifi	80	33	80	75	80	67	69.2**
Truddy	80	75	90	14	67	75	66.7*
Patrick	90	75	67	100	90	56	79.5***
Total	81.4	66.7	79.2	70.5	79.6	77	
1st trial	6	6	5	7	6	7	

Symbols indicate significant overall hiding preference (binomial probability: p < 0.05, \*\*p < 0.01, \*\*\*p < 0.01). Bold type represents conditions in which subjects hid on their first trial in which they approached. Also shown is the number of subjects that hid in the first trials across conditions.

With respect to the use of indirect approaches, analyses revealed that in the experimental conditions of Test 1, six of eight subjects approached indirectly in one or more trials (a mean of 15% of experimental trials), whereas no subject approached indirectly in the Non-social control. The conditions thus differed from one another in the number of indirect approaches  $[F(2,21)=3.63,\,p=0.044]$ , with both of the experimental conditions in Test 1 having more indirect approaches than the Non-social control (p<0.05 in both cases, Fischer LSD). In Test 2, five of eight subjects approached indirectly in one or more trials of the Experimental conditions (a mean of 16% of experimental trials), whereas no subject approached indirectly in the Non-social control. This difference in indirect approaches neared significance  $[F(2,21)=2.65,\,p=0.094]$ , with the Occluder condition having significantly more indirect approaches than the Non-social control (p<0.05, Fischer LSD). Subjects never used an indirect approach in Test 3 in which it would have served no purpose (likewise, in the introduction only one subject approached indirectly only one time, <1% of trials).

Learning analyses revealed no evidence that subjects increased the frequency of hiding in the social conditions within any test when the first three social trials are compared to next three social trials within each test [Test 1: t(7) = 0.71, p = 0.49; Test 2: t(6) = 1.76, p = 0.87; Test 3: t(4) = 1, p = 0.37, two tailed]. Likewise, there was no evidence for learning when the first 10 social trials within each test were compared to the last 10 social trials of the same test [Test 1: t(7) = 0.38, p = 0.72; Test 2: t(7) = 0.62, p = 0.74; Test 3: t(7) = 0.35, p = 0.74, two tailed]. Comparison between all three rewarded and all three unrewarded conditions reveals that subjects were more likely to approach in the rewarded conditions T = 2.91, N = 7, p = 0.023, two tailed (mean:  $21.6 \pm 3.3$  SEM approaches in rewarded conditions and  $17.5 \pm 2.7$  SEM approaches in unrewarded conditions)]. In addition, subjects demonstrated a tendency to hide more frequently in the rewarded conditions T = 2.29, N = 7, p = 0.056, two tailed (hiding in  $78.8\% \pm 6.5$  SEM of rewarded) and  $65.9\% \pm 5.5$  SEM of unrewarded conditions). However, a two-way ANOVA (type of rewarding x trial block) revealed no effect of or interaction between the rewarding scheme (rewarded and non-rewarded trials) and the trial block (first half of social trials and second half of social trials).

Table 2 also presents the conditions in which each subject hid the first time they approached in each of the six social conditions (hiding on a first trial is indicated by underlining the overall hiding percentage in each condition). Overall, subjects had a preference for hiding in the first trial of each experimental test (T=36, N=8, p=0.005, Wilcoxon Sign Rank test). In all three sessions, subjects had a preference for hiding in both of their first experimental trials [Session 1: T=17.5, N=6, p<0.051; Session 2: T=10, N=4, p<0.023; Session 3: T=15, N=5, p<0.013; Wilcoxon Sign Rank test] and a one-way ANOVA revealed no difference between the number of times subjects hid on their first trial in each session (post hoc tests also reveal no significant differences between hiding in the first trial of any two sessions). All subjects hid in at least four of six social conditions on their first trial with five subjects hiding on their first trial in five of six social conditions. Finally, in the supplemental control condition completed after all the other sessions, subjects, as a

group, did not have a preference for approaching the larger barrier (rewarded) or the smaller barrier (unrewarded) on their first trial or over the entire session [t(7) = 1.51, p = NS] with only three of eight subjects approaching behind the larger barrier (rewarded) in more trials than the smaller barrier (unrewarded).

#### 4. Discussion

The results of these experiments demonstrate that chimpanzees can flexibly use knowledge of what a competitor can and cannot see to develop active, deceptive strategies for concealing their approach to contested food – and they do this from the very first trials in several novel situations. First, contrary to the conclusions of Povinelli and colleagues (Povinelli et al., 1999; Povinelli & Eddy, 1996; Reaux et al., 1999; Theall & Povinelli, 1999) based on studies using a different methodology, chimpanzees in the current experiment spontaneously avoided food that the experimenter was watching, as indicated by gaze direction, and instead approached food that he was not watching, even when the majority of his body (including his arms and hands which can physically remove food from the subjects reach) was oriented in this same direction. Second, contrary to the conclusions of Karin-Karin-D'Arcy and Povinelli (2002) and consistent with those of Hare et al. (2000, 2001), subjects in the current experiment preferred to approach food behind various visual occluders while refraining from approaching food behind non-occluding transparent or opaque barriers. In addition, in the supplemental control session when subjects were forced to choose between two non-occluding barriers, they did not prefer to approach food near the larger of the two non-occluding barriers even though they were rewarded for doing so.

However, perhaps the most striking aspect of subject's behavior was their exclusive use of indirect approaches when initially distancing themselves from the food could potentially aid in concealing their later approach towards the food. Subjects only used indirect approaches if the experimenter was able to see them distance themselves from the food, but subsequently could not see them approach the food after positioning themselves behind the experimenter or an occluder (Test 1 and 2). Meanwhile, subjects did not use indirect approaches if the positioning of the occluders prevented the experimenter from seeing them distance themselves from the food (Test 3), or they could easily be seen approaching after distancing themselves from the food (introduction). This indirect approach behavior is striking because it suggests the possibility that subjects not only understood it was important to be hidden from their competitor's view while approaching contested food, but that they also understood that in some cases it was useful to hide their attempt to hide. These results are thus consistent with the predictions of the visual perspective-taking hypothesis, while providing little, if any, support for the predictions of the learned cues hypothesis (i.e., subjects have learned to react to a set of invariant perceptual regularities).

Meanwhile, while the subjects' approach behavior is consistent with the predictions of the visual perspective-taking hypothesis, the design of the current

experiment makes it difficult to account for such results by proposing a task specific behavior reading or learning hypotheses (e.g., Heyes, 1993, 1998). While the Face versus Chest condition (Test 1) demonstrates that chimpanzees can take advantage of a relatively subtle behavioral cue such as gaze direction in assessing whether a competitor will see them, subjects did not rely solely on such behavioral cues when hiding. Throughout the second and third tests – the Occluder, Double Occluder, and Split Occluder conditions – the experimenter always faced directly forward (remaining motionless until subjects made a choice), yet subjects still spontaneously used the barriers to conceal their approach. Moreover, it is also difficult to argue that subjects' preferences represent a set of simple contingencies learned within the experiment. First, subjects showed their hiding preferences in the first trial of both experimental conditions within each of the three tests. Second, subjects maintained their initial hiding preferences throughout the session in the Face versus Chest condition, Occluder condition (see additional analysis), and Split Occluder condition, even though subjects were never successful in obtaining food in these unrewarded conditions. Third, there was no evidence that subjects rapidly increased their hiding response in the first six trials of each test or that they more gradually increased their hiding by the second half of each test. Finally, although subjects approached and hid more in the rewarded conditions than in the non-rewarded conditions, there is no evidence that subjects' level of hiding in the rewarded and unrewarded conditions changed relative to each other across the first and second half of the experiment (i.e., this is contrary to a within-session learning hypothesis that predicts that in the second half of the experiment subjects hiding will decrease in the unrewarded conditions while increasing in the rewarded condition). Further the fact that the subjects hid slightly more in the rewarded conditions is easily explainable by the fact that the choices in those conditions were intentionally designed to be less ambiguous than the unrewarded conditions (i.e., to maintain motivation). As an example, the biggest difference between a rewarded and unrewarded condition in hiding is in Test 1 where subjects hid 15% more in the Face and Chest condition than in the Face versus Chest condition. However, in the Face and Chest condition the subjects likely hid more simply because the experimenter in this condition both could not see one of the food pieces and had to turn around to remove this same piece of food (see Fig. 2). Meanwhile in the Face versus Chest condition the subject had to choose between hiding from view or avoiding the food that was easier for the experimenter to remove – making the choice more ambiguous regardless of rewarding. Therefore, overall there is little reason to believe that the rewarding scheme caused the subjects' spontaneous hiding preferences to change significantly during the relatively short experimental sessions. Instead, it seems most plausible to conclude that subjects flexibly generalized previous cognitive skills in solving all of the novel social problems with which they were presented in the current experiment – arguably representing a successful case of triangulation (Heyes, 1993, 1998).

However, there is one specific egocentric hypothesis that must be addressed in relation to the current results. It might be suggested that throughout ontogeny and into adulthood chimpanzees simply learn that contested food is best obtained when a path is taken to food that prevents them from seeing their competitor's face

as they approach. This would mean that subjects in the current experiment hid behind visual occluders not because they understood the experimenter could not see them, but instead because they knew if they went behind the occluder they could not see the experimenter. At first this might seem to be a useful candidate explanation for the current results, but details of the experimental design, the subject's behavior, and previous findings make such an explanation seem implausible.

First, the Split Occluder condition directly addresses this alternative hypothesis. Recall in this condition that one piece of food was behind a solid barrier while the other was behind a split barrier (one on the testing table and the other at eye level: see Fig. 4). Therefore, in both cases subjects could potentially hide the experimenter's face from their own view as they retrieved the food, and so in this condition the 'avoid face' hypothesis predicts no preference in subjects' approaches. Yet subjects preferred to steal the food from behind the solid barrier, not the split barrier, consistent with the idea that they understood the human could see them behind the split barrier even if they could position themselves so as not to see the human's face. Second, in the Face versus Chest condition, the human experimenter's face (including eyes) and body were always visible regardless of which testing window subjects approached (see Fig. 2). Therefore, the experimenter was completely visible to the subjects regardless of which direction subjects approached, yet they preferred to avoid the food at which the experimenter was gazing (and they could not only rely on the rule, "do not approach when the eyes of another are directed towards food" since gaze direction could not help them hide themselves in Tests 2 and 3 when the experimenter always stared directly at the subject's starting position). Third, the 'avoid face' hypothesis predicts only that subjects will take a direct route to hide the competitor from their own view. Yet, the subjects often took an indirect, circuitous route to the food and only when their departure away from the food could be seen and their return would remain hidden. Finally, the 'avoid face' hypothesis cannot account for previous results in which chimpanzees show an understanding of the occluding properties of opaque barriers even when their competitor is out of sight (Hare et al., 2000, 2001). Thus, it seems plausible that in the current experiment subjects are using a similar understanding in deciding how best to hide themselves from their competitor's view. However, in the future experiments should be designed to test the prediction of the "avoid face" hypothesis further.

The current results, therefore, appear to replicate and extend other recent findings that chimpanzees' understand other's visual perception in the form of level 1 visual perspective-taking (Flavell, 1992). Studies of chimpanzee gaze following suggest that they may know when others can see things that they themselves cannot; for example, when chimpanzees gaze follow but do not see anything of interest, they look back to the gazer and follow her gaze a second time (Call et al., 2000) – this "checking back" being a common criteria in assessing human children's understanding of visual perception. If a chimpanzee is subsequently unable to detect anything of interest, they quickly habituate to the gaze of their social partner (Tomasello et al., 2001). If a visual barrier prevents a chimpanzee from matching their line of sight with that of another individual, they will move in order to see what the other individual can see (Povinelli & Eddy, 1996; Tomasello et al., 1999). In addition, chimpanzees ignore

interesting objects if their social partner is not gazing in the direction of the distraction (Tomasello et al., 1999). Moreover, the Hare et al. (2000, 2001) food competition studies suggest that chimpanzees know what others can and cannot see and even what others have seen or have not seen in the past. Meanwhile, the current results add a more active dimension to these findings, showing that chimpanzees can predict and manipulate what others do and do not see.

However, actively manipulating what another will be able to see does more than support the visual perspective hypothesis. Subjects hiding behavior also provides some of the strongest evidence that chimpanzees are capable of intentional deception. Although a number of authors (Goodall, 1986; Hirata & Matsuzawa, 2001; Menzel, 1974) have reported that chimpanzees often distance themselves from hidden food in the presence of dominants, prior findings could be explained if subjects simply learned over time to adjust their approach behavior in response to the behavior of their competitor (i.e., if the subordinate moves towards the hidden food so does the dominant). However, in the current study the hiding and indirect approaches cannot be characterized as adjustments to the competitor's behavior given that the competitive experimenter remained motionless while a subject made its choice. In addition, further support for interpreting the approach behavior of subjects as intentional deception is the frequency of indirect approaches. A number of authors have pointed out that there are constraints on the frequency for which deception can occur. To avoid detection and costly punishment it has been argued that rates of intentional deception will remain low in social species such as primates (Cheney & Seyfarth, 1990; Hauser, 1992). In this regard, it is interesting to note that subjects from the current experiment only attempted to approach indirectly, the most deceptive of approach behavior, in a minority of trials. Therefore, it is possible that the subjects' use of indirect approaches represents an experimental demonstration of intentional deception in chimpanzees – subjects were trying to hide their attempt to hide and did so infrequently to avoid detection of their deceptive strategy.

If it is the case that subjects' hiding and use of indirect approaches represents a case of intentional deception, it is even more difficult to know whether to characterize such behavior as a case of withholding or falsifying information (Cheney & Seyfarth, 1990). Subjects may have simply been trying to withhold visual information about their approach or, as might be suggested by their indirect approaches, they may even have been trying to provide false information about the ultimate goal of their movements. It is possible that the chimpazees' deceptive behavior is best characterized as some intermediate level of deception such as active concealment (i.e., subjects were trying to block their competitors' informational access). Unfortunately, the current results do not give us the resolution needed to determine more precisely on which deceptive level chimpanzees are capable of operating. Instead, the current results do more to suggest the need for future research on chimpanzee deception to clarify such issues. For example, it remains unclear exactly how flexible chimpanzees are in creating and deploying various deceptive strategies. Perhaps, chimpanzees are only deceptive in a very narrow set of context (i.e., hiding visually during food competition) suggesting they have little understanding of how to effectively manipulate their environment or behavior in order to affect other's psychological states. And of course there are still types of deception – for example, active falsification and deception involving language (i.e., lying) – that may prove to be the sole province of human beings (Call & Tomasello, 1999).

Therefore, given the need for more experimental work on chimpanzee deception, one promising direction for future investigations will be research aimed at testing whether chimpanzees can also assess and manipulate the perceptual states of others across modalities. Given observational evidence from the wild (Hauser, 1990; Watts & Mitani, 2001) and experimental evidence from captivity (Hauser et al., 1993) and the wild (Wilson, Hauser, & Wrangham, 2001) that chimpanzees withhold vocalizations (or avoid making loud noise in general) during contested matings, food competition, and territorial disputes, one future direction might be to use the current experimental paradigm to assess whether chimpanzees also know when others can and cannot hear them approaching contested food. In addition, another possibility would be to develop a new experimental paradigm to investigate whether chimpanzees also actively falsify vocalizations in order to intentionally deceive others.

Developing such non-verbal tests of social cognition in our closest primate relative will play a central role in not only testing a number of theories relevant to the evolution of human social cognition (e.g., Krebs & Dawkins, 1984; Povinelli, 2000; Tomasello & Call, 1997; Whiten, 1994), but will also directly test the predictions of a number of theories for human social cognitive development (e.g., Astington & Jenkins, 1999; Smith, 1996; Tomasello, 1999). Therefore, as experimental methods continue to be improved work with non-humans will continue to become increasingly relevant to a number of fields within the Cognitive Sciences (Hauser & Fitch, 2002).

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# References

Anderson, J. R., Kuroshima, H., Kuwahata, H., Fujita, K., & Vick, S.-J. (2001). Training squirrel monkeys (Saimiri sciureus) to deceive: Acquisition and analysis of behavior toward cooperative and competitive trainers. Journal of Comparative Psychology, 115(3), 282–293.

Astington, J. W., & Jenkins, J. M. (1999). A longitudinal study of the relation between language and theory-of-mind development. *Developmental Psychology*, 35, 1311–1320.

- Call, J., Agnetta, B., & Tomasello, M. (2000). Cues the chimpanzees do and do not use to find hidden objects. *Animal Cognition*, 3(1), 23–34.
- Call, J., & Tomasello, M. (1999). A nonverbal theory of mind test. The performance of children and apes. *Child Development*, 70, 381–395.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Illinois: University of Chicago Press, 377pp.
- Coussi-Korbel, S. (1994). Learning to outwit a competitor in Mangabeys. *Journal of Comparative Psychology*, 108(2), 164–171.
- de Waal, F. (1998). Chimpanzee politics: Power and sex among apes (Vol. xv, rev. ed., 235pp).
- Flavell, J. H. (1992). Perspectives on perspective taking. In H. Beilin & P. B. Pufall (Eds.), *Piaget's theory: Prospects and possibilities* (pp. 107–139). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Fujita, K., Kuroshima, H., & Masuda, T. (2002). Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive an opponent? A preliminary analysis of an experimental food-competition contest between monkeys. *Animal Cognition*, 5, 19–25.
- Goodall, J. (1986). The chimpanzees of gombe. Cambridge: Belknap Cambridge.
- Gygax, L. (2000). Hiding behaviour of long-tailed macaques (*Macaca fascicularis*): II. Use of hiding places during aggressive interactions. *Ethology*, 106(5), 441–451.
- Hare, B. (2001). Can competitive paradigms increase the validity of social cognitive experiments on primates? *Animal Cognition*, 4, 269–280.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59(4), 771–785.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61(1), 139–151.
- Hare, B., & Tomasello, M. (2004). Chimpanzees are more skillful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68, 571–581.
- Hauser, M. D. (1990). Do chimpanzee copulatory calls incite male–male competition? *Animal Behaviour*, 39(3), 596–597.
- Hauser, M. D. (1992). Costs of deception: Cheaters are punished in rhesus monkeys (Macaca mulatta). Proceedings of the National Academy of Sciences of the United States of America, 89, 12137–12139.
- Hauser, M. D. (1997). Minding the behaviour of deception. In A. Whiten & R. W. Byrne (Eds.), Machiavellian intelligence II: Extensions and evaluations (Vol. xii, pp. 112–143), 403pp.
- Hauser, M., & Fitch, T. (2002). What are the uniquely human components of the language faculty? In M. Christiansen & S. Kirby (Eds.), *Language evolution*. Oxford, England: Oxford University Press.
- Hauser, M. D., Teixidor, P., Field, L., & Flaherty, R. (1993). Food-elicited cells in chimpanzees: Effects of food quantity and divisibility. *Animal Behaviour*, 45(4), 817–819.
- Heyes, C. M. (1993). Anecdotes, training, trapping and triangulating: Do animals attribute mental states? *Animal Behaviour, 46*(1), 177–188.
- Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, 21(1), 101–134.
- Hirata, S., & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition*, 4(3-4), 285-295.
- Hostetter, A., Contera, M., & Hopkins, W. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, 115(4), 337–343.
- Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling ape's begging behavior from humans. *Animal Cognition*, 7(4), 216–233.
- Karin-Karin-D'Arcy, M. R., & Povinelli, D. J. (2002). Do chimpanzees know what each other see. A closer look. *International Journal of Comparative Psychology*, 15(1), 21–54.
- Krebs, J. R., & Dawkins, R. (1984). Animal signals: Mind reading and manipulation. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 380–401). Oxford, England: Blackwell.
- Kummer, H., Anzenberger, G., & Hemelrijk, C. (1996). Hiding and perspective taking in long-tailed macques (*Macaca fascicularis*). *Journal of Comparative Psychology*, 110, 97–102.

- Leavens, D., & Hopkins, W. (1998). Intentional communication by chimpanzees a cross-sectional study of the use of referential gestures. *Developmental Psychology*, 34(5), 813–822.
- Menzel, E. (1974). A group of young chimpanzees in a one-acre field: Leadership and communication. In A. M. Schrier & F. Stollnitze (Eds.), *Behavior of nonhuman primates* (pp. 83–153). New York: Academic Press.
- Mitchell, R. W., & Anderson, J. R. (1997). Pointing, withholding information, and deception in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111(4), 351–361.
- Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2003). Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*). *Cognition*, 89(2), B53–B64.
- Povinelli, D. J. (2000). Folk physics for apes: The chimpanzees theory of how the world works. Oxford: Oxford University Press.
- 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(Pt. 1), 37–60.
- Povinelli, D. J., & Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, 61(3), v-vi, 1–152.
- Povinelli, D. J., & Giambrone, S. (2001). Reasoning about beliefs: A human specialization? Commentary on "Meta-analysis of theory-of-mind development: The truth about false belief". *Child Development*, 72(3), 691–695.
- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human?. *Trends in Cognitive Sciences* 7(4), 157–160.
- Reaux, J. E., Theall, L. A., & Povinelli, D. J. (1999). A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development*, 70(2), 275–290.
- Ristau, C. A. (Ed.). (1991). Cognitive ethology: The minds of other animals: Essays in honor of Donald R. Griffin (Vol. xx, 332pp).
- Shettleworth, S. J. (1998). Cognition, evolution, and behavior. Oxford: Oxford University Press.
- Smith, P. (1996). Language and the evolution of mind-reading. In P. Carruthers & P. Smith (Eds.), *Theories of theories of mind* (pp. 344–354). Cambridge, England: Cambridge University Press.
- Theall, L. A., & Povinelli, D. J. (1999). Do chimpanzees tailor their gestural signals to fit the attentional states of others?. *Animal Cognition* 2(4), 207–214.
- Tomasello, M. (1999). The cultural origins of human cognition (Vol. vi, 248pp.).
- Tomasello, M., & Call, J. (1997). Primate cognition. New York, NY, USA: Oxford University Press, 517.
- 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(4), 153–156.
- Tomasello, M., Call, J., & Hare, B. (2003b). Chimpanzees versus humans: It's not that simple. *Trends in Cognitive Sciences*, 7(6), 239–240.
- Tomasello, M., Hare, B., & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour*, 58(4), 769–777.
- Tomasello, M., Hare, B., & Fogleman, T. (2001). The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, 61(2), 335–343.
- Watts, D., & Mitani, J. (2001). Boundry patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138, 299–327.
- Whiten, A. (1994). Grades of mindreading. In C. Lewis & P. Mitchell (Eds.), *Children's early understanding of mind: Origins and development*. Hove, UK: Erlbaum.
- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, 11(2), 233–273.
- Wilson, M., Hauser, M., & Wrangham, R. (2001). Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, 61, 1203–1216.
- Woodruff, G., & Premack, D. (1979). Intentional communication in the chimpanzee: The development of deception. *Cognition*, 7, 333–362.