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Do chimpanzees know what others can and cannot do? Reasoning about 'capability'

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Abstract Much recent comparative work has been devoted to exploring what nonhuman primates understand about physical causality. However, few laboratory experiments have attempted to test what nonhumans understand about what physical acts others are capable of performing. We tested seven chimpanzees' ability to predict which of two human experimenters could deliver a tray containing a food reward. In the 'floor' condition, legs were required to push the tray toward the subject. In the 'lap' condition, arms were required to hand the tray to the subject. In Exp. 1, chimpanzees begged (by gesturing) to either an experimenter whose legs were not visible (LNV) or whose arms were not visible (ANV). Rather than flexibly altering their preferences between conditions, the chimpanzees preferred the ANV experimenter regardless of the task. In subsequent experiments, we manipulated various factors that might have controlled the chimpanzees' preferences, such as (a) distance between experimenter and subject (Experiment 2), (b) amount of occlusion of experimenters' body (Experiments 2 and 3), (c) contact with the food tray (Experiments 3 and 4) and (d) positioning of barriers that either impeded the movement of the limbs or not (Experiment 5). The chimpanzees' performance was best explained by attention

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to cues such as perceived proximity, contact, and maximal occlusion of body that although highly predictive in certain tasks, were irrelevant in others. When the discriminative role of such cues was eliminated, performance fell to chance levels, indicating that chimpanzees do not spontaneously (or after considerable training) use limb visibility as a cue to predict the ability of a human to perform particular physical tasks. Thus, the current findings suggest a possible failure of causal reasoning in the context of reasoning about the use of the limbs to perform physical acts.

Keywords Chimpanzees · Capability · Causal reasoning · Unobservability hypothesis

Introduction

A large corpus of data has been amassed to suggest that chimpanzees are capable of cognitive abilities previously ascribed only to humans. For instance, researchers now widely accept that chimpanzees possess the ability to reason about unobservable (psychological) states such as what others can see (Hare 2007; Hare et al. 2006; Kaminski et al. 2004; Melis et al. 2006; Tomasello et al. 2003a, b), or hear (Melis et al. 2006), even though alternative explanations for the chimpanzees' behavior exist (see Povinelli and Vonk 2003, 2004). The attribution of such cognitive feats has been extended to other species of primate as well (Flombaum and Santos 2005; Santos et al. 2006). Similarly, the results of recent studies have supported the notion that chimpanzees possess an understanding of causality (Call 2004; Horner and Whiten 2005), as do rhesus macaques (Hauser and Spaulding 2006), but again alternative accounts have been proposed (Penn and Povinelli 2007). With the overwhelming enthusiasm for models of primate

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cognitive continuity and an apparent reluctance to entertain models that highlight equally fascinating and evolutionarily illuminating discontinuities, we believe it is important to examine the exact conditions under which fundamental cognitive traits, such as causal reasoning, may be employed by other primates, and how such rules may be acquired in particular experimental contexts.

The role of the limbs in the execution of specific actions is linked to physical causality and has not previously been studied in non-human primates. It may be an important capacity about which primates might reason about their conspecifics, as well as themselves, in their natural environments because successful mates, foragers and allies in hunting, patrolling, mate-guarding and co-alitions depend on the functional use of their limbs to perform their required tasks in all of the aforementioned roles. In addition, the functional use of limbs becomes relevant when assessing the strengths and weaknesses of both predators and prey, so it may be vital that primates reason about the capabilities of members of other species as well. While we have adapted the question to a somewhat unnatural laboratory setting we believe that we have created a paradigm that gets at a fundamental capacity with real world relevance for our subjects. To our knowledge, we have designed the first test of chimpanzees' abilities to use salient observable cues, such as the visibility of the arms and legs, to accurately predict 'capability'-an individual's physical ability to perform specific tasks.

Previous studies exploring primates' concept of capability have largely focused on the attribution of internal mental states such as goal directedness or intentionality to human actors. Both human infants (Behne et al. 2005; Carpenter et al. 1998) and chimpanzees (Call and Tomasello, 1998; Call et al. 1998; Povinelli et al. 1998) have been asked to discriminate between human experimenters who were either unwilling or unable to perform a particular task, or to distinguish between uncooperative actions that were either accidental or deliberate. Whereas both human infants of nine months and older (Behne et al. 2005; Carpenter et al. 1998), and adult chimpanzees (Call and Tomasello 1998; Call et al. 2004), discriminated between the actions of unwilling and unable human experimenters, chimpanzees did not preferentially gesture to experimenters who either accidentally or deliberately failed to offer a food reward (Povinelli et al. 1998). The results of previous research that focused on what apes understand about the role of the eyes in human visual attention, or what they inferred about actor's intended goals from observing actions, are difficult to interpret because physical cues, such as visibility of the eyes, or specific behavioral actions, are confounded with inferences about unobservable mental states such as visual attention or particular intentions (Povinelli and Vonk 2003, 2004). One of the strengths of the current approach is that all cues, those causally relevant to the task, and those causally irrelevant to the task, are available to the senses. Thus, chimpanzees do not need to reason about unobservables, such as mental states, to succeed at our task; however, causal relevance itself may be conceived as an unobservable concept, and one that may be beyond their capacity to reason about (Penn and Povinelli 2007). Their performance in our task should reveal whether they make inferences based on an underlying appreciation of causality, or rather, have difficulty discriminating between causally relevant and causally irrelevant observable regularities that may predict particular outcomes.

Andrews (2005) and Vonk (2005) have proposed a general causal-inference deficit whereby non-humans may be able to make predictions based upon observable cues but may fail to seek causal explanations for existing events (see also Premack and Premack 1994). Thus, the disparity between human and non-human cognition may reflect fundamental differences in the ability to make causal attributions for events and behavior. To date, only two experimental tests of this hypothesis exist. Consistent with the general causal deficit hypothesis, chimpanzees, unlike human children, did not appear to seek causal explanations for a failure to perform a physical task (Povinelli and Dunphy-Lelii 2001). They also failed to use current emotional states of conspecifics in order to make inferences about that individual's prior experience (Premack and Premack 1994). An inability to engage in backwards reasoning to explain events and behaviors may account for the observations that non-humans often behave according to statistical regularities regardless of whether these regularities are essential to completing the task (Povinelli 2003).

Rather than suggesting that chimpanzees will succeed at all tasks in which relevant cues are readily observable, we suggest that they may fail, even with very visible cues, if the use of such cues depends upon an appreciation of the causal role of such variables. For example, in Visalberghi's well-known trap-tube task (Visalberghi and Trinca 1989), chimpanzees learned to insert the tool in the opposite end of the tube from where it was initially inserted, even when this action no longer resulted in successful expulsion of the reward (Povinelli 2003). Thus they were unable to discriminate between the conditions that determined when this action was causally relevant and when it was not.

Here we probe chimpanzees' understanding of the capabilities of human experimenters who are physically (rather than motivationally) incapable of completing the task of delivering a food reward. To do this, we have adopted an experimental research program that removes chimpanzees from their natural environment in which selection likely sculpted their cognitive systems to respond to stimuli in specific ways. Only by exposing chimpanzees to less natural situations—that, nevertheless, tap into skills which

would be adaptive in their natural environments-can we tease apart learning that is narrow and constrained by context, from learning that is flexible and unconstrained by context and, thus, can be applied in novel and unusual situations. The latter type of learning epitomizes that which humans have expressed by their ability to adapt to a wide variety of environments, including those that are highly 'artificial' and bear little resemblance to the so-called, 'environment of evolutionary adaptedness' (Tooby and Cosmides 1992). Therefore, it is only in those albeit unnatural situations where one would not expect a species to be hardwired to respond in a particular way that they can express the ability to learn flexibly and to generalize in a manner that approaches what humans are capable of (cf., Hauser and Spaulding 2006). Granted, it remains possible that chimpanzees, failing at our task, would nonetheless show analogous causal reasoning skills in tasks involving more familiar objects and settings. What such results would imply, to our minds, is that their thinking is not as flexible as is human thinking. However, that result would not permit us to suggest global failures of causal reasoning abilities. In any case, we hope the current set of experiments will be a first step in generating multiple tests of such hypotheses.

In this series of experiments, we asked seven chimpanzees to predict which of two humans could deliver a tray containing a food reward in two conditions. In the 'floor' condition, legs were needed to push the tray toward the subject along the floor. In the 'lap' condition, arms were needed to hand the tray to the subject. In our tasks, the visual cues as to the human experimenters' capabilities, such as the visibility or invisibility of the legs and arms, were striking to human observers, but our experiments contained other observable cues that may not have been causally relevant, allowing us to disentangle the use of relevant and irrelevant observable cues in driving responses.

Experiment 1

In Experiment 1, chimpanzees begged by gesturing to either an experimenter whose legs were not visible (LNV) or whose arms were not visible (ANV). All other limbs were visible. If the chimpanzees are sensitive to observable cues indicative of the experimenter's capabilities, they should immediately gesture to the experimenter who is capable of providing them a food reward, either by extending the tray towards them with their arms in the 'lap' treatments, or pushing the tray towards them with their feet in the 'floor' treatments. In order to receive reinforcement, chimpanzees must develop the following rule(s): hands (in lap condition) or feet (in floor condition) making contact with the food tray equals reward. Thus, the subjects are required to form a concurrent conditional relational rule in order to succeed in both conditions. That is, if the tray is on the floor-choose experimenter with feet visible and making contact with the tray, but if the tray is in the lap-choose experiment with hands visible and making contact with the tray.

However, chimpanzees may develop more rigid and specific rules such as 'always choose experimenter with arms visible' or 'always avoid experimenter with legs not visible' which will result in above chance performance in one condition and below chance in the other condition. Using a combination of such rules randomly or a singular rule inconsistently would result in chance performance.

Chimpanzees might also develop more global rules pertaining to body occlusion such as 'choose experimenter with most limbs visible' or 'choose experimenter whose appearance is most 'typical.' Only the application of the flexible rule: 'choose the experimenter whose hands or feet make contact with food tray', will reliably lead to reinforcement. But note that such a rule is based entirely on observable cues and would yield results identical to the application of another rule but one that is premised on knowledge of an abstract, unobservable concept such as 'capability,' for example, 'choose experimenter who is capable of delivering food.' In this instance, 'capability' is entirely dependent on whether or not hands or feet are making contact with the food tray; the individual whose limbs are making contact with the tray is capable of delivering food and the one whose limbs are not visible is incapable of delivering food. Therefore we cannot interpret whether success in this experiment is indicative of reasoning abstractly about unobservable attributes such as capability or the use of a rule about observable features causally related to task performance. Here we wanted to evaluate whether chimpanzees spontaneously generated a conditional rule, or a more general but causally relevant rule, and responded accurately in both the lap and the floor conditions.

Thus several hypotheses lead to the predictions that chimpanzees will correctly choose the ANV experimenter when the food trays are on the floor and will choose the LNV experimenter when the food trays are in the experimenters' laps. They are as follows: (1) chimpanzees reason causally about capability; (2) chimpanzees form conditional relational rules based on observable cues such as, (a) tray on lap-choose experimenter with hand on tray, tray on floor-choose experimenter with foot on tray, or (b) tray off ground-choose experimenter whose hands are visible, tray on ground-choose experimenter whose feet are visible. The latter two rules would have to be learned during the course of the experiment. Presumably use of the former rule might allow the chimpanzees to perform above chance from the beginning of the experiment.

Other hypotheses predict that the chimpanzees would not alter their choices flexibly depending upon the experimental condition and instead would show preferences for particular experimental configurations regardless of condition. For instance the Natural Experience Hypothesis predicts that chimpanzees will prefer human experimenters who are least occluded—that is humans with both legs and arms fully visible—as most humans commonly appeared in their natural lives. Thus they should prefer the ANV experimenters regardless of whether the experimental trial is of lap or floor condition. Chimpanzees might use even more concrete rules. The Proximity Hypothesis also predicts that they will choose the experimenter whose visible body part is closest to themselves. Thus they should also preferentially select the ANV experimenter, as in the Natural Experience Hypothesis.

Method

Subjects

Seven chimpanzees, one male and six females ranging in age from 15.6 to 16.5 at the beginning of this experiment, participated in this experiment. All of the chimpanzees were housed in a single social group at the New Iberia Primate Research Center for at least 13 years. They had participated regularly in cognitive and behavioral tests since they were 3–4 years of age, many of which involved directly interacting with human experimenters, including begging to humans for food and observing humans performing various physical tasks. For more details about the history of the study group see Povinelli (2003).

Materials

All experiments took place in an indoor "testing unit". The testing unit was divided by a Lexan barrier. Human experimenters were positioned on one side of the barrier, and chimpanzees entered the test unit individually from an outside waiting area on the other side of the barrier. Two holes in the Lexan barrier allowed the chimpanzees to make a response to one of the experimenters, each positioned in front of one response hole. A "response barrier" made of Lexan could be raised or lowered to cover and uncover the response holes.

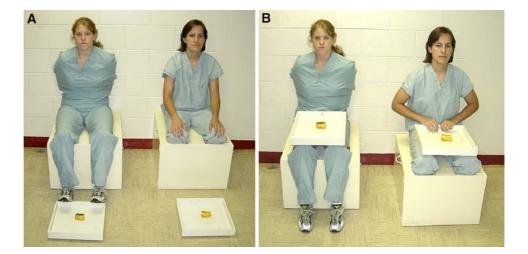
Two identical, wooden benches with solid fronts and sides, on which the experimenters were seated were used in this experiment. One bench had two holes cut into the front top section so that the experimenter in the legs not visible (LNV) treatment could place his legs inside the bench, hidden from the subjects. Several pairs of cotton pants ('scrubs') were cut on the backside of the lower leg to allow the experimenters in the "LNV" treatment to put their legs through this opening, while leaving the front of the scrub bottoms hanging loose in front of the bench. The scrub bottoms were shortened to make it obvious that there were no legs present. There was a locked latch on the side of the bench to ensure that the front of the bench could not be swung open to reveal the experimenter's legs hidden inside. Two identical wooden food trays with padded undersides were also used in this experiment. Figure 1 depicts the different conditions and treatments presented in Experiment 1.

Two cameras were used to present a picture in picture view that captured the entrance and exit of the subject into and out of the test unit, as well as a close-up view of the subject's wrist breaking the plane of the two holes through which they responded. The two seated experimenters were also visible on camera. All trials in all phases of all experiments were recorded on DVD. Subjects' choices recorded online by experimenters and live observers were later confirmed by raters observing video of the experiment.

Procedure

Criterion The subjects participated in four 4-trial sessions in which they were reminded that, on trials in which two

Fig. 1 Treatments and conditions used in Exp. 1. Floor conditions **a** Arms not visible $(ANV)^+$ versus legs not visible (LNV); Lap conditions **b** ANV versus LNV⁺



experimenters were seated in front of the two response holes, they could choose only one of the two experimenters to gesture to for a food reward. In addition, they had the opportunity to learn that, in the 'lap' condition, the experimenter's arms and hands are necessary (and therefore must be visible) to lift the tray from their lap and extend it forward to within reach of the subject, while, in the 'floor' condition, the experimenter needs legs and feet (and therefore they must be visible) to push the tray forward along the floor to within the subject's reach. In these criterion trials (as in subsequent testing trials) gesturing to an experimenter whose hands or feet were touching a tray containing food resulted in reinforcement. Consequently, these experiences exposed subjects to the behavioral regularities necessary to form the rule that limbs making contact with a tray containing food would lead to reinforcement.

Two trials within each session were lap trials and two were floor trials. Trials of each condition were presented in random order. Two familiar experimenters, different from the two individuals assigned to play E1 and E2 on probe trials in testing, participated in each session. Each experimenter participated as the correct experimenter an equal number of times within a session, once in the lap and once in the floor condition, in random order. Across two-session blocks, the side location of the correct experimenter was counterbalanced within each condition. No more than three trials within a session involved the correct experimenter, or the same experimenter seated on the same side.

The subjects entered the test unit to find one experimenter directly in front of the response hole on the left and another experimenter seated directly in front of the response hole on the right. Both experimenters faced forward, stared straight ahead to a designated point on the Lexan barrier, and did not make eye contact with the subjects. Both experimenters had all limbs visible in this phase of the experiment. The benches they were seated on were 110 cm away from the Lexan barrier on lap trials and 143 cm away on floor trials. The trays were 85 cm from the Lexan on floor trials, so as to be out of reach of the subject with the longest arm reach. On lap trials, one experimenter had the food reward in a tray placed on her lap, and the other experimenter did not have a tray or food. On floor trials, one experimenter had a food reward in a tray directly in front of her feet, while the other experimenter did not have a food reward or tray. A third experimenter (E3) was positioned at the back of the test unit, behind the partition, to control the response barrier and shuttle door. The response barrier was in raised position at the beginning of each trial, covering the response holes.

As soon as the subjects entered the test unit, they had one minute to indicate their readiness to respond by touching a symbol on the Lexan barrier, E3 then lowered the response barrier, exposing the response holes. The subjects then had one minute to gesture to one of the two experimenters. A gesture was defined as the subject's hand breaking the plane of the response hole. If the subject gestured to the correct experimenter on lap trials the experimenter extended the tray forward, using both arms, so that the tray was held level to the response hole and within the subject's reach. If the subject gestured to the correct experimenter on floor trials the experimenter slid the tray forward along the floor, using both feet, to within the subject's reach. The trial ended when the subject retrieved a food reward, or as soon as a gesture was made to the incorrect experimenter. The subject was not permitted to make more than one choice. Sessions continued until the subject performed correctly on 7/8 trials within each condition (lap and floor) across four consecutive sessions.

Testing This phase consisted of eight sessions of four trials, for a total of 16 probe and 16 standard trials. Two probe trial conditions (lap and floor) were administered eight times each. In both probe conditions, two experimenters were present. One experimenter had their legs not visible but their arms visible (LNV), and the other experimenter had their arms not visible but their legs visible (ANV). Of the 16 standard trials, which were identical to Criterion trials, eight were lap trials and eight were floor trials. Each four-session (16-trial) block included four of each of the probe trial conditions and four of each of the standard trial conditions, presented in random order with the following constraints. Two of the trials within each session were standard trials; one of these was a lap trial and one was a floor trial. Two probe trials were randomly assigned to each session.

The test unit and experimenters were configured as in Criterion, and the trials followed the same procedure as Criterion trials, using the same decision rules. Two experimenters were present on all trials, one seated on a bench in front of each response hole, one correct and one incorrect. Two individuals (the same two experimenters from Criterion) were assigned to the roles of E1 and E2 for standard trials, and two different individuals were assigned to the roles of E1 and E2 for probe trials. Side position of the correct experimenter was counterbalanced within each foursession block as follows. Within each probe trial condition, the correct experimenter was seated on the left twice, once as E1 and once as E2, and on the right twice, once as E1 and once as E2. In lap trials, the LNV experimenter was correct. In floor trials the ANV experimenter was correct. Within each of the standard trial conditions, the correct experimenter was seated on the left twice, once as E1 and once as E2 and on the right twice, once as E1 and once as E2. No more than three trials within a session involved the correct experimenter being seated on the same side, the same experimenter being seated on the same side, or the same experimenter being correct.

The experimenters assigned to the LNV treatment sat with their legs inserted (hidden) inside a covered wooden bench, with a pair of cut-off scrubs dangling below the knee. On ANV treatments, the experimenters' arms were hidden behind their backs inside their shirts, and not visible to the subjects, leaving the shirt sleeves dangling. On lap trials, the food reward was placed in a tray on the experimenters' laps. On floor trials, the food reward was placed in a food tray directly in front of the experimenters' feet (or equivalent distance if the experimenter's feet were not visible), and out of the subject's reach. The correct experimenters conferred food rewards as in Criterion, as soon as the subject gestured through the response hole that they were positioned in front of. Trials ended as soon as the subject retrieved the food reward or gestured through the hole in front of the incorrect experimenter. Subjects were not allowed to make second choices.

Results

Parametric tests were used to analyze the data (% correct) given that these tests have greater power for studies involving few subjects and a small number of trials.

Criterion

All subjects met criterion in the minimum number of trials (n = 16). Two subjects (MEG and JAD) made no errors. All

other subjects made one (CAN, BRA), or two (APO, KAR, MIN) incorrect choices. Three errors were made in the floor condition and five errors were made in the lap condition.

Testing

Five subjects performed perfectly on standard trials. KAR made one error in the floor condition. MIN made three errors; two in the floor and one in the lap condition. On probe trials, as a group, the subjects preferred the ANV experimenter regardless of the task, although their preference for ANV was stronger on floor trials, when that choice was correct, than on lap trials when that choice was incorrect (paired t test, $t_6 = 4.08$, P = 0.006). However, this overall preference for ANV lead to a significant difference in performance between conditions on probe trials (paired ttests, $t_6 = -2.87$, P = 0.03) and above chance performance on only the floor condition (one sample t-test, $t_6 = 4.22$, P = 0.01, see Table 1). Paired t tests comparing performance on the first block of trials to the last block of trials for probe trials revealed no effects of learning in either condition (both t_6 s < 1.0).

Binomial tests for individual subjects revealed that no subject was above chance on lap trials, but JAD was above chance on floor trials, (n = 8, P = 0.02, 1-tailed). KAR's and MEG's performance on floor trials were not significant (ns = 8, Ps = 0.07, 1-tailed). Only MIN preferred the correct LNV experimenter on lap trials, but this preference was

Table 1 Percent correct trials in given conditions and treatments in Experiments 1 and 2

Subject	Exp. 1 LNV vs. ANV		Exp. 2								
			ALLV vs. NOV (standard trials)				LNV vs. ANV (probe trials)				
	Lap	Floor	Body distance control		Bench distance control		Body distance control		Bench distance control		
			Lap	Floor	Lap	Floor	Lap	Floor	Lap	Floor	
APO	50.0	66.7	50.0	63.0	50.0	63.0	75.0	75.0	50.0	50.0	
KAR	50.0	75.0	75.0	88.0	63.0	75.0	38.0	75.0	13.0	63.0	
CAN	41.7	58.3	50.0	50.0	63.0	63.0	75.0	63.0	50.0	63.0	
JAD	41.7	83.3	38.0	75.0	63.0	100.0	13.0	100.0	57.0	100.0	
BRA	41.7	66.7	38.0	38.0	50.0	75.0	63.0	50.0	50.0	75.0	
MEG	33.3	75.0	38.0	100.0	75.0	44.0	63.0	88.0	50.0	50.0	
MIN	66.7	50.0	50.0	63.0	50.0	75.0	63.0	38.0	50.0	63.0	
Average	46.4	67.9	48.4	68.1	59.1	70.7	55.7	69.9	45.7	66.3	
SD	10.6	11.2	13.2	21.4	9.5	17.1	22.5	21.4	14.7	17.2	

In Experiment 1 the benches upon which the experimenters sat were aligned and positioned at the same distance from the subject. In Experiment 2, this positioning (bench distance control) was contrasted with another condition in which the distance from the subject to the experimenter's closest visible body part was equated (body distance control). In addition a novel treatment presented NOV and ALLV experimenters, an even more visually striking discrimination. Performance improved slightly from that of Experiment 1 in the bench distance control (which was familiar) but not in the new body distance control condition. In Experiment 2 there was no significant difference between bench and body controls, $F_{1, 48} = 0.04$, P = 0.84), or between (LNV vs. ANV) and (NOV vs. ALLV) trial types [$F_{1, 48} = 0.07$, P = 0.79]. There was still a significant difference between lap and floor conditions [$F_{1, 48} = 10.34$, P = 0.002], but no significant interactions

LNV, legs not visible; ANV, arms not visible; ALLV, all limbs visible; NOV, no limbs visible; for LAP conditions LNV is correct, for floor conditions, ANV is correct, ALLV is always correct, NOV is always incorrect not significantly above chance (n = 8, P = 0.09). The results are depicted in Fig. 2.

Discussion

Consistent with the Natural Experience and Proximity Hypotheses, and inconsistent with the Causal Understanding Hypothesis, the subjects displayed a general preference for the experimenter with arms not visible over the experimenter with legs not visible, regardless of condition. That is, whether the tray was on the floor or whether the tray was on the experimenters' laps, subjects, as a group, preferred to gesture to the experimenter whose legs were visible (and whose arms were not visible). Although this preference was greater in the floor trials, when it was the correct choice, chimpanzees did not flexibly alternate between choosing the experimenter with arms visible or the one with legs visible according to condition, indicative of a poor understanding of the task. This finding was particularly surprising because one might expect chimpanzees to be more biased to gesture to the experimenter whose arms and hands were visible, given that they had much more experience throughout their lifetimes with humans offering food by hand rather than by foot. Although having food trays passed to them by kicking was an unusual event for our subjects, they were, as a group, above chance in this condition. Three individuals were above chance at levels that were significant despite experiencing only eight probe trials of this condition. Although the general experimental condition was unnatural in some sense, chimpanzees were able to make accurate predictions about who could offer them a food reward in at least one of the two experimental conditions.

Granted this experiment may have been difficult for the chimpanzees given that they had no direct experience of what actions they might be able to perform with arms and legs rendered immobile. However, they have been able to

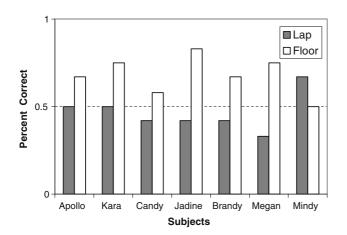


Fig. 2 Percent correct for individuals in Experiment 1 by condition (lap vs. floor)

make inferences in other experiments about actions they have not engaged in themselves (Call and Tomasello 1998; Call et al. 2004) in addition to purportedly reasoning about significantly more opaque notions of capability such as motivation or intention (Call et al. 2004).

A review of performance suggests that chimpanzees responded using one or a combination of the following: (1) a rigid rule, for example, a preference for the experimenter with legs visible or conversely, avoidance of the experimenter with legs not visible, or (2) cues that, although predictive in one condition, were irrelevant with regards to the experimenters' capability to perform each task, such as (a) the amount of the experimenter's body occluded/perceived completeness of the experimenter's body and (b) proximal distance from the subject to the experimenters. This last hypothesis was particularly worthy of further exploration because the experimenter with legs visible appeared perceptually closer to the subject than the experimenter with legs not visible who appeared to be further away.

Experiment 2

Experiment 2 was designed to test the possibility that, in Experiment 1, chimpanzees preferred to gesture to the experimenter whose legs were visible because both of the experimenters' benches were in a fixed position and equidistant from the Lexan; thus from the subject's perspective, the experimenter whose legs were visible was closer to the Lexan than the experimenter whose legs were not visible. According to the Proximity Hypothesis, if the chimpanzees were responding based upon the distance of the experimenter from the Lexan they should continue to prefer the person with legs visible (and arms not visible) on both lap and floor probe trials in the 'bench' treatment, where the two benches were equidistant from the Lexan, but should be at chance in the 'body' treatment, where the two experimenters' closest visible body parts were equidistant from the Lexan.

In addition, although the subjects generally appeared to respond differently in the two conditions, they did not seem to recognize the critical role of the arms in delivering food rewards in the lap condition. It is possible that chimpanzees avoided the LNV experimenter because more of her body was occluded. The lack of legs may have been more visually striking relative to the apparent lack of arms. Chimpanzees may thus have avoided the LNV experimenter because it was aversive to them, not because they understood the task. To test this Natural Experience hypothesis, standard trials of the present experiment presented the subjects with an experimenter whose entire body was visible in contrast with an experimenter whose legs *and* arms were not visible in order to determine whether the chimpanzees could discriminate between these two extreme conditions. Thus according to the Natural Experience Hypothesis, and if they find the lack of limbs aversive or if they are able to reason at all about the relevance of arms and legs with regards to the experimenter's ability to confer food rewards they should spontaneously and reliably prefer the experimenter with all limbs visible on standard trials.

Method

Subjects and materials were identical to those of Experiment 1

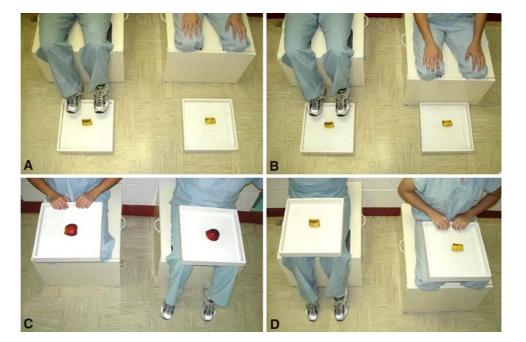
Procedure

Testing consisted of 16 sessions of four trials, for a total of 32 probe and 32 standard trials. The experiment followed the same general procedure, test unit configuration and decision rules as in Testing of Experiment One with the following exceptions. The same two experimenters who took part in standard trials also took part in probe trials. The identity of these experimenters remained the same throughout Testing to ensure proper counterbalancing.

On standard trials, one experimenter (the correct experimenter) had both legs and arms visible. The other experimenter (the incorrect experimenter) had neither legs nor arms visible, using the same means of hiding the limbs as in Experiment 1. Both experimenters had trays containing identical food rewards. Probe trials were identical to those in Experiment 1 with the following exception. Half of the lap standard and probe trials and half of the floor standard and probe trials utilized both benches being placed at equivalent distances (110 cm from the Lexan on lap trials and 143 cm from the Lexan on floor trials). These trials (equating the distance of the benches from the Lexan wall) were referred to as 'bench' trials. On the other half of all trials, the bench on which the experimenter with legs not visible was seated was moved forward such that the knees of that experimenter were at the same distance from the Lexan as the feet of the other experimenter, to equate the distance of their visible body parts from the Lexan. These trials (equating the distance of the body to the Lexan wall) were referred to as body trials. Thus, of the 32 standard trials, and of the 32 probe trials, 16 were lap trials and 16 were floor trials. Of each of these 16 trials of each condition, eight trials were bench distance control (bench) trials and eight trials were body distance control (body) trials, as described above. This design resulted in eight unique conditions. Each four-session (16-trial) block included two of each of the conditions presented in random order with the following constraints. Two of the trials within each session were standard trials; one of these was a lap trial and one was a floor trial. The remaining two trials within a session were probe trials; one of these was a lap trial and one was a floor trial. All four trials within a session could not be of only body trials or bench trials. Experimental conditions are depicted in Fig. 3.

Side position of the correct experimenter was counterbalanced within each eight-session (32-trial) block as follows. Each of the eight unique conditions occurred four times across eight sessions. Within each of these conditions in each counterbalanced block, E1 was correct twice, and incorrect twice, once in front of one response hole and once in front of the other response hole. The same was true of

Fig. 3 Treatments and conditions used in Experiment 2. Floor conditions (*top*): **a** bench, arms not visible (ANV)⁺ versus legs not visible (LNV); **b** body, arms not visible (ANV)⁺ versus legs not visible (LNV); Lap conditions (*bottom*): **c** bench, legs not visible (LNV)⁺ versus arms not visible (ANV); **d** body, ANV versus LNV⁺



E2. No more than three trials within a session involved the correct experimenter being seated on the same side, the same experimenter being seated on the same side, or the same experimenter being correct.

Results

A univariate ANOVA of performance with trial type (standard or probe), condition (lap or floor) and treatment (bench, body) as factors revealed only a significant effect of condition $[F_{1,48} = 10.34, P = 0.02]$. Again, subjects performed better in floor than lap conditions. Performance did not significantly differ between bench and body treatments, suggesting that, here, subjects, taken together, were not exclusively using the distance of the experimenters' limbs from the Lexan partition to guide their choices. In addition, that performance did not significantly differ between probe and standard trials indicates that subjects, as a group, were not exclusively guided by the amount of body occlusion (see Table 1).

Single sample *t* tests were conducted to compare performance to chance, separately for standard and probe trials and for lap and floor trials collapsed across bench and body treatments. Performance on lap trials was not above chance on either standard or probe trials, both t'_{13} s < 1.2. In contrast, performance on floor trials was above chance on both standard ($t_{13} = 3.90$, P = 0.002) and probe trials ($t_{13} = 3.61$, P = 0.003).

In order to examine possible effects of learning, paired t tests were conducted comparing performance on the first half to performance on the last half of both standard and probe trials conducted separately according to condition (lap or floor). Bench and body trials were collapsed together as this control did not significantly affect performance and did not constitute a conceptually different discrimination. None of the four t tests exposed significant effects, suggesting that no learning took place in either condition or trial type during this experiment (all t'_{6} s < 1.6).

Examination of individual performance revealed differences in the pattern of results. For instance, on standard trials, all but one individual performed better or equivalently on floor versus lap trials in both bench and body treatments (ranging from 0 to 37% better on floor versus lap trials). MEG, however, performed substantially better on floor versus lap trials (62% better) on body control treatments but performed 31% worse on floor versus lap trials on bench control treatments. Thus, only MEG seemed affected by the bench/body control treatment. Binomial tests were conducted to determine when individual subjects performed above chance on standard trials. Only KAR, and JAD were above chance and only on floor trials collapsed across bench and body treatments (Ns = 16, Ps = 0.01 and 0.002, respectively). MEG was also above chance on floor trials but only in the body condition (N = 8, P = 0.04).

Binomial tests were also conducted to determine when individual subjects performed above chance on probe trials. On probe trials, there was more variation in performance. Only one subject, JAD, performed above chance, and only on floor probe trials, collapsed across bench and body treatments (N = 16, P < 0.001). APO performed exactly the same on lap and floor conditions in both bench and body treatments. However, he performed better on bench versus body trials, perhaps because he could use body distance from self as a discriminative cue. However, he would have had to use the cue differently on floor trials than on lap trials because, on floor trials, the experimenter whose body was closer to the subject was correct, while on lap trials, the experimenter whose body was farther from the subject was correct. APO performed just as well in both conditions suggesting he might have learned to use the body distance cue flexibly. In contrast, if most subjects were rigidly choosing the experimenter who was closer to them, leading to correct performance on floor trials but incorrect responses on lap trials, this rule might explain why they continued to perform better on floor than on lap trials in bench treatments (KAR, CAN, JAD, BRA and MIN). A few of these subjects performed better on floor conditions than lap conditions in the body treatment as well (KAR, JAD, MEG) where the incorrect experimenter's bench was closer to the subject on floor trials. Perhaps this result was due to subjects using a combination of body distance and bench distance cues to guide performance.

Discussion

Surprisingly, subjects did not perform significantly better on standard than on probe trials, despite the apparent salience of the differences between experimenters in the standard trials (where both arms and legs were visible or not visible). That the chimpanzees did not simply avoid the experimenter who had neither legs nor arms visible and did not spontaneously prefer the experimenter who had both legs and arms visible suggests that they did not immediately link the visibility of limbs with capability to perform tasks requiring the use of those limbs. Furthermore, they did not simply avoid the person who had a greater degree of her body occluded on standard trials, or performance would have been above chance on lap as well as floor conditions. Thus there did not appear to be a general aversion to a high degree of body occlusion as the Natural Experience Hypothesis predicts. Rather, these results support the hypothesis that chimpanzees applied a limb-specific rule such as "Choose experimenter with legs visible" or "Avoid experimenter with legs not visible."

It is possible that subjects generally performed better on floor relative to lap probe trials because, in lap trials, chimpanzees avoided the person who had a greater part of their body occluded (i.e., legs not visible). However, that explanation seems unlikely given that they did not successfully use this cue in standard trials. Another possibility is that subjects performed better on floor conditions because only the correct experimenter's tray made contact with a part of their body in that condition, thus making it possible for them to use body contact with tray as a discriminative cue. In the lap condition, LNV's tray made contact with the hands and thighs and ANV's food tray made contact with the thighs, so a simple body/tray contact rule could not be used as a cue to mediate performance in the lap condition. Use of a more specific rule "relevant body part (i.e., hands or feet) must make contact with tray" should have produced equivalent and above chance performance in both lap and floor conditions.

The results of Experiments 1 and 2 are consistent with the notion that chimpanzees are blind to the causally relevant statistical regularities associated with reinforcement. Specifically, chimpanzees appear blind to an association between the observable presence of a limb and obtaining a tray with food. The fact that chimpanzees did not make this association is particularly striking, given that in both experiments, and in 112 trials, the correct experimenter's visible limbs moved, came closer to the subject, and were in contact with the food tray at the beginning of the trial - all factors that should enhance the salience of the relevant cues (legs/arms or hands/feet and food tray) via stimulus and local enhancement (Spence 1937; Thorpe 1956), facilitating the application of the rule: hands/feet + contact with food tray = reinforcement. Thus, even though chimpanzees would not have experienced these particular tasks, or humans with missing limbs, in their life histories, they were given substantial experience with these contingencies in the present experimental context and could have demonstrated the ability to learn which cues were predictive, or causally relevant. Instead chimpanzees in some instances appeared to apply limb-specific rules and/or global contact rules that were limb independent; equating contact with thighs with contact with hands. This pattern of response is inconsistent with an understanding of the causal significance of the functionality of limbs belonging to familiar human experimenters.

Perhaps these experiments were initially difficult for chimpanzees because their limbs are not functionally equivalent to those of humans, and possibly because they had never been confronted with these specific discriminations. However, by the time they completed Experiment 2, they had been tested on a total of 112 trials. In all of these trials, the experimenter whose legs were occluded was never able to push the tray forward along the floor, and the experimenter whose arms were occluded was never able to hand the tray on her lap to the subjects.

If chimpanzees reasoned that the incorrect experimenters could lift their legs out of the box or take their arms out of the sleeves from behind their backs, this hypothesis should have been extinguished by subsequent trials as the experimenter without the relevant limbs visible never once in more than 100 trials reinforced the subject by exposing their hidden limbs and offering the tray with food. Instead, such experiences should have reinforced the rule that experimenters with the relevant limbs occluded or invisible would not reinforce them. If they were reasoning in a predictive fashion they should have reasoned that experimenters who had the relevant limbs visible were more likely to offer the food rewards. Certainly, at the very least, the incorrect experimenters would have been slower to perform the task even had they struggled to gain the use of their hidden limbs. Furthermore, although incorrect experimenters did not struggle in order to demonstrate that they were willing but unable to perform the task, these experimenters changed roles throughout the experiments so personal dispositions such as "unwilling" could not have been consistently applied to individual experimenters. In short, the chimpanzees' lack of success in this experiment suggests that they did not reason about which limbs were relevant to perform a specific task. However, it is clear that their performance was guided by some cues which, on some types of trials (namely floor trials), were predictive and allowed them to perform at above chance levels. Thus, the chimpanzees were not responding randomly but in a rule-governed fashion. Our interest was in determining which cues guided our subjects' immediate responses.

Experiment 3

Because the chimpanzees did not spontaneously demonstrate a preference for the experimenter with both arms and legs visible over the experimenter with no limbs visible in either lap or floor criterion and standard conditions, in Experiment Three, we wished to determine whether chimpanzees could eventually learn this discrimination before probing their understanding with what we perceived to be more subtle, yet more familiar, manipulations (i.e., either legs or arms not visible). In addition, we attempted to accentuate the differences between the capable and incapable experimenters, making the rule [hands/feet + contact with tray = reinforcement] more explicit. We sought to prime this rule by increasing the salience of the invisible limbs for the ANV experimenter conditions in both lap and floor treatments and consequently, maximizing the salience of the limbs making contact with the food tray (see Fig. 3). Furthermore, we modified the lap condition so that the tray of the incorrect experimenter would no longer make direct contact with the experimenter's thighs, thus allowing them to use the more general rule "body contact with tray" as a discriminative cue in this condition. Equating experimenter

proximity (body trials) generally resulted in better performance in probe trials, relative to when experimenter proximity was not equated (bench trials) in Experiment 2 (albeit not significantly so). Thus, only the body condition will be utilized in Experiment 3 as it equates the proximity of the two experimenters' closest limbs to the Lexan barrier, and thus to the subjects as well.

These modifications lead to a number of hypotheses: (1) subjects using body contact with the tray as a discriminative cue should respond correctly in the lap conditions, where contact predicts success; (2) the performance of subjects using amount of body occluded as a cue should decrease in floor conditions, where body occlusion is now better equated across LNV and ANV experimenters.

Method

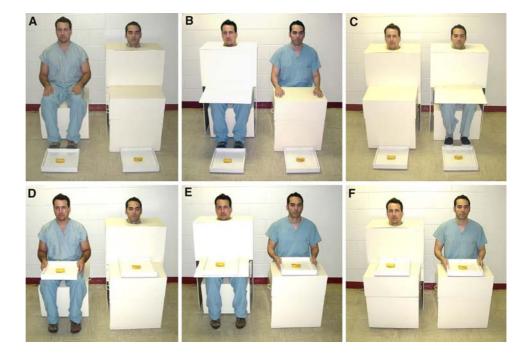
Subjects, Materials and Experimental set up were identical to the previous experiments except for changes noted below.

Procedure

In all conditions, experimenters with arms visible now extended their arms forward while placing their hands at the front of the sides of the trays to make the arms more visible. Experimenters with arms not visible now had their arms, upper torsos and the top part of their laps completely occluded by a box that was visually similar to the boxes used to occlude the experimenters' legs (see Fig. 4). Their trays thus now rested on the occluding apparatus instead of directly on their laps.

Fig. 4 Treatments and conditions used in Experiment 3 Floor conditions (*top*): **a** AllV⁺ versus NOV (criterion), **b** ANV⁺ versus LNV (difficult), **c** NOV versus ANV⁺ (easy). Lap conditions (*bottom*): **d** AllV⁺ versus NOV (criterion), **e** ANV versus LNV⁺ (difficult), **f** NOV versus LNV⁺ (easy) Because we wished to determine what the subjects could learn following modifications to the ANV experimenter treatment, we first implemented a Criterion phase involving only standard trials. The procedure for Criterion was identical to Testing except that sessions consisted of eight trials, four lap and four floor standard trials presented in random order. The incorrect experimenter had legs, arms and upper body occluded (NOV in Fig. 4). The correct experimenter had no parts of the body occluded (ALLV in Fig 4). Position and identity of the correct experimenter was counterbalanced within each condition within blocks of two sessions, or eight trials of each condition. When a subject completed 7/8 correct trials of each condition within a block of two counterbalanced sessions they moved on to testing.

Testing provided a measure of transfer once the subjects had learned the most extreme discrimination in Criterion, in which one experimenter had both legs and upper body occluded and the other experimenter had no body parts occluded. Across eight sessions, subjects were presented with two conditions (one lap and one floor) in which the incorrect experimenter had both legs and upper body occluded, and the correct experimenter had only upper body occluded (floor) or legs occluded (lap). These conditions were called 'easy' probe trials and used experimenter treatments depicted as ANV or LNV contrasted with NOV in Fig. 4. Subjects were also presented with two conditions (one lap and one floor) in which each experimenter had either legs or upper body occluded. These conditions were called 'difficult' probe trials and used experimenter conditions depicted in Fig. 4 as LNV versus ANV. Thus, Testing included four probe conditions: easy lap (EL), easy floor



(EF), difficult lap (DL) and difficult floor (DF), each presented 16 times to each subject. Experimenter identity and correctness were counterbalanced for position within each eight-trial session. Each session included two trials of each of the four conditions presented in random order.

Results

Criterion

BRA did not meet criterion within eight sessions (64 trials) and thus did not participate in Testing in Experiment Three. She was dropped from further participation in the study. All of the other subjects reached criterion within two to seven sessions (range 16–56 trials).

Testing

Condition and treatment means appear in Table 2. An ANOVA of performance with condition (lap, floor) and treatment (easy, difficult) as factors revealed only a significant effect of treatment, $F_{1, 10} = 5.93$, P = 0.04. In this experiment, there was no longer a significant difference between lap and floor conditions. However, as a group, subjects did perform better on easy relative to difficult trials, as expected. The only exception was MIN, who, in the lap condition, performed just as well on both easy and difficult trials (M = 0.75), and JAD, who performed better on the difficult than the easy trials in the floor condition (Difficult M = 0.88, Easy M = 0.75). One-sample t tests were con-

ducted separately for lap and floor trials, and separately for easy and difficult treatments in order to compare performance to chance. Now, subjects performed significantly above chance on lap trials for both treatments; on easy trials [$t_5 = 6.93$, P = 0.001] and on difficult trials [$t_5 = 3.41$, P = 0.02], and only on easy treatments for floor trials, [$t_5 = 3.11$, P = 0.03].

Binomial tests were conducted to examine when individual subjects were above chance. There was no condition/ treatment in which all subjects performed above chance. On easy lap trials, KAR, CAN, JAD, MEG, and MIN were above chance (Ns = 16, p's < 0.01). On difficult lap trials, KAR, CAN, MEG and MIN were above chance (Ns = 16, Ps < 0.04). On easy floor trials, APO, KAR, JAD, and MEG were above chance, (Ns = 16, Ps < 0.04). Finally, on difficult floor trials, only JAD and MEG were above chance, (Ns = 16, Ps = 0.002 and 0.01, respectively). Thus, only MEG was above chance on all four conditions, suggesting that she had learned separate rules that were predictive in all four conditions or one rule that could be flexibly used across conditions.

Paired *t* tests were conducted comparing performance on the first and last half of trials separately by condition (lap, floor) and treatment (easy, difficult). There were no effects of learning in any of these analyses (all t_5 s < 1.6).

Discussion

In the present study, subjects' responses are consistent with the use of the Natural Experience rule. This conclusion is

Table 2 Percent correct trials in given conditions and treatments in Experiments 3–5

Subject	Exp. 3		Exp. 4	Exp. 5					
	Criterion		Testing		Tray contact	Partial occlusion			
	ALLV vs. NOV		[LNV/UBNV] vs. NOV (E)		LNV vs. UBNV (D)		control		
	Lap	Floor	Lap	Floor	Lap	Floor	Floor	Lap	Floor
APO	81.3	68.8	63.0	81.0	44.0	63.0	56	63	69
KAR	78.6	89.3	88.0	75.0	81.0	25.0		50	56
CAN	87.5	70.8	94.0	50.0	81.0	25.0		44	56
JAD	100.0	87.5	81.0	75.0	63.0	88.0	69	44	50
BRA	66.0	75.0							
MEG	100.0	81.3	81.0	100.0	75.0	81.0	38	38	50
MIN	88.0	75.0	75.0	56.0	75.0	44.0		63	44
Average	85.9	78.2	80.0	73.0	70.0	54.0	54.3	50.3	54.2
SD	12.1	8.0	11.0	18.0	14.0	27.0	15.6	10.5	8.5

In Experiment 3 subjects were trained to criterion in the most extreme discrimination (ALLV vs. NOV). All but one subject (BRA) met criterion. In Experiment 3, discriminative cues such as tray contact were added to the lap condition and discriminative cues such as amount of body occluded were eliminated. Here performance improved in the lap condition and deteriorated in the floor conditions, as expected. In Experiment 4, tray contact was removed as a discriminative cue in the floor condition for subjects who had previously performed well in that condition, and performance was at chance. Experiment 5 controlled against the use of such cues and instead, presented constraints to restrict experimenter's use of the limbs. Again, performance was at chance

supported by the fact that, when given a choice between an experimenter with maximal occlusion of limbs (NOV) and an experimenter with no occlusion of limbs (ALLV) (criterion), performance rapidly reached ceiling levels for both floor and lap conditions, however, never 100% in both lap and floor conditions. Further, when given a choice between maximal occlusion (NOV) and partial occlusion of limbs they generally preferred the experimenter with less of his body occluded (e.g., LNV, ANV) (easy testing trials). However, the occlusion cue could not be used to cue successful responding on difficult trials as both experimenters had approximately the same amount of their bodies occluded (i.e., upper half versus lower half); consequently, accuracy was lower on these more difficult trials, as expected. This decrement was observed even though difficult trials were conceptually similar to probe trials from earlier experiments in the sense that experimenters had either legs or arms, but never had both limbs occluded, as in easy trials. However, the present experiment attempted to make the occlusion of limbs more apparent by enclosing them entirely in a box, eliminating any potential confusion that limbs are available but not in plain sight (e.g., behind the experimenters back). Thus, the difficult trials in the present experiment were not visually identical to prior probe trial treatments.

But, despite this improvement in performance, the chimpanzees' performance did not evidence a clear and robust understanding of physical capability. Rather, than using previously learned rules in a flexible fashion, chimpanzees' responses continued to rely on the same general rules of occlusion and contact. For instance, in the present study, the floor condition proved to be more difficult for the chimpanzees than the lap condition. We hypothesized that this was due to the fact that body contact with the tray was now available as a discriminative cue because only the correct experimenter's body (hands) made contact with the tray in the lap condition. Yet, the amount of body occluded was not confounded with correct choice because ANV now had as much body occluded as LNV. Consequently, performance in lap trials improved above chance but subjects' responses in difficult floor trials were at chance, as subjects could not use the amount of body occluded as a cue.

The results of Experiment 3, in some ways, were the mirror image of those of Experiment 2. As was hypothesized, subjects performed above chance on lap trials but not on floor trials. This reversal in performance supports the hypothesis that subjects were using occlusion rules and body and/or limb contact with the tray as a cue to guide performance on floor trials and applied this same rule, when available, to lap trials. In addition, chimpanzees' decline in performance on floor trials indicates that controlling for relative occlusion differences made the discrimination between LNV and ANV more difficult, suggesting that in Experiments 1 and 2 subjects were preferentially selecting the experimenter with more of their body visible.

Experiment 4

Performance improved in the lap conditions once body contact with the tray could be used as a cue to guide performance. Thus, an additional experiment was conducted immediately following the completion of Experiment 3 for all subjects who completed Experiment 3 with an overall performance in floor conditions of 70% or better. We wished to determine whether subjects who excelled in the floor treatment made use of a contact rule to do so; that is, whether chimpanzees chose the correct experimenter strictly because that experimenter's feet physically made contact with the food tray in the floor condition. In Experiment 4 we made a minor modification to the design of the experiment such that the correct experimenter's feet no longer rested on the tray at the beginning of the trial. We expected that the elimination of this discriminative cue would disrupt performance.

Method

Subjects

Only three of the six subjects (APO, JAD and MEG) reached the criterion in Experiment 3 and thus participated in Experiment 4.

Procedure

Testing consisted of two 8-trial sessions in which all eight trials involved the difficult floor (DF) condition of Experiment 3 with one modification. The correct experimenter's feet were no longer in contact with the tray at the beginning of the trial. The tray was extended approximately 15 cm in front of the experimenter and closer to the Lexan barrier. Thus, the boxes on which the experimenters sat were moved farther back. Experimenter position and valence (correct or incorrect) was counterbalanced within sessions. All other aspects of the procedure were identical to Testing in Experiment 3.

Results

Single sample *t* tests revealed that, taken together, subjects that responded above chance in the difficult floor condition in Experiment 3 did not perform above chance ($t_2 = 0.50$) when the correct experimenter's feet were no longer in contact with the food tray at the beginning of the tray. Binomial tests confirmed that no individual performed at above

chance levels (n = 16, all Ps > 0.24, 1-tailed). Furthermore, there was no evidence of learning as performance on the first eight trials was identical to performance on the last eight trials of testing (both Ms = 0.54, SDs = 1.5 and 1.2). The results appear in Table 2.

Discussion

These results suggest that these three subjects were using a very specific-limb contact rule in the floor condition. Removing the discriminative cue in which only the correct experimenter's feet made contact with the food tray at the beginning of the trial disrupted subjects' near ceiling performance. This outcome strongly suggests that performance in floor conditions in earlier experiments was likely mediated by this perceptual feature that was causally irrelevant to the task because the distance between the tray and the experimenter's feet (and lack of initial contact) did not prevent the experimenter from pushing the tray. The fact that a simple manipulation of a condition that was virtually identical to one in which chimpanzees had performed nearly at ceiling, could so dramatically disrupt performance suggests that chimpanzees generally reason concretely, not flexibly or abstractly, about environmental regularities. Thus, they appeared to reason about the consequences linked to contact but not about capability. Furthermore, had chimpanzees reasoned that experimenters whose legs and arms were contained within restrictive boxes or clothing could remove their legs or arms from such constraints to perform the task should have also reasoned in the present experiment that the experimenter whose feet were not touching the tray at the beginning of the trial could lift his feet to make contact with the tray. Thus the results of the present study are inconsistent with the view that difficulties in earlier experiments were due to a failure to understand the inability of humans to use occluded limbs.

Fig. 5 Treatments and conditions used in Experiment 5. Experimenters' bodies are equally occluded by a wooden bar and feet do not make contact with food tray. Floor treatment: a knees occluded⁺ versus ankles occluded; b Lap treatment: Wrist/forearm occluded versus shoulders occluded⁺ (+ = correct/capable choice)

Experiment 5

Subjects' overall pattern of performance in Experiments 1-4 suggests that they were using one of two rules on probe trials: contact rules, mediated by a body part touching the food tray, and/or occlusion rules, mediated by a global preference for a typical human agent with most limbs visible. In the present study, contact rules were neutralized as both experimenters either made contact (lap condition) or did not make contact (floor condition) with the food trays. Occlusion rules were neutralized as a barrier obscured equal amounts of each experimenter's body. In effect, Experiment 5 gave chimpanzees another opportunity to evidence an understanding of capability without relying exclusively on contact or occlusion rules. In this experiment, barriers were placed at different positions of the experimenters' bodies. For the correct experimenter the barrier was functionally irrelevant to the task, while for the incorrect experimenter, the barrier made it impossible to perform the task. Experimenter configurations appear in Fig. 5.

Method

Subjects

All six subjects (excluding BRA) participated in Experiment Five.

Procedure

Testing consisted of four 8-trial sessions. Each session included four lap and four floor trials presented in random order with the constraint that no more than three trials of the same condition occurred consecutively. Within each condition, experimenter position and valence (correct or incorrect) was completely counterbalanced within each session. The basic procedure was identical to that of



Experiment 3. However, here, both experimenters had most of their arms and legs visible in both conditions. Both experimenters in the floor condition now had a wooden Tbar apparatus placed directly in front of them. For the correct experimenter, the horizontal piece of wood covered the experimenter's knees, thus allowing him to kick the tray forward. For the incorrect experimenter, the horizontal piece of wood covered the ankles, preventing the experimenter from kicking the tray forward. Neither experimenter's feet were in contact with the tray and equal portions of both experimenters' legs were visible. In the lap condition, the horizontal piece of wood covered the incorrect experimenter's wrists and forearms, preventing him from moving his arms forward. An identical wooden bar was placed across the shoulders of the correct experimenter (just below the chin), allowing him to move the tray forward. Both experimenters were holding the tray. Thus subjects could not make choices based on visibility of the limbs or contact with the tray.

Results

Taken together, performance was not above chance in either the lap or floor condition (single sample *t* tests, both $ts_5 < 1.20$, Ps = 0.94 and 0.29). In addition, performance did not differ between conditions (paired *t* tests, $t_5 = 0.81$, P = 0.45), or between the first and last half of testing (both $ts_5 < 1.3$, P = 0.53). These results appear in Table 2. Binomial tests confirmed that no individual performed at above chance levels in either of the conditions (n = 8, all Ps > 0.24, 1-tailed).

Discussion

Subjects did not succeed in either condition in this experiment, nor did they show any evidence of learning during testing. We expected this task to be more difficult for the chimpanzees because neither contact nor occlusion rules were available to them. From our own perspective the discrimination could be perceived as even more subtle than those that preceded it. However, we felt that, given the extended training in the previous experiments, it was possible that the chimpanzees might be able to demonstrate transfer to this novel context and wished to provide them the opportunity to do so. Furthermore, if chimpanzees are capable of rapid learning based on the association of visual cues, such as the position of the wooden barriers, with reinforcement, one might have expected some learning to occur, even in the relatively short period of time we allowed for testing. Rather, these chimpanzees' poor performance constitutes further evidence against the notion that chimpanzees are particularly sensitive to causally relevant statistical regularities. In addition, the experiment satisfied the goal of controlling the use of cues that chimpanzees did appear to be using in at least some of the previous experiments-contact, proximity and occlusion, thus allowing us to potentially isolate successful performance in the absence of the use of such cues. The results of Experiment 5 show that when the use of specific rules is neutralized and other stable and equally predictive cues are provided, chimpanzees' performance can drop to chance levels and they can fail to evidence learning across sessions. Clearly this was a difficult discrimination for the chimpanzees to make, suggesting that they do not reason in the abstract about capability, in this task, even when provided with over 140 trials of experience with related problems (Experiments 1-4) where one experimenter was consistently capable of providing reinforcement and the other was not. It remains possible that providing more explicit observable cues of experimenters' inabilities to perform the task would have lead to higher levels of performance.

General discussion

In Experiment 1, we explored whether chimpanzees had a priori assumptions about human capability based on the visibility of limbs. To this end we presented chimpanzees with two tasks. One task required the use of the arms and hands. The other task required the use of the legs and feet. Chimpanzees did not differentiate between tasks, in terms of which limbs were necessary. Instead subjects preferred the individuals whose arms were not visible and avoided the individual whose legs were not visible regardless of condition. This preference for the ANV experimenter (or avoidance of LNV experimenter) was likely due to: (a) a greater part of the LNV experimenter's body being occluded, (b) the visible parts of the LNV experimenters' bodies were further away from subjects, or (c) the LNV experimenter's body was not in direct contact with the food tray. But this undifferentiated preference for the experimenter with legs visible (or arms not visible) meant that they performed above chance, from the beginning in the floor condition, where legs were necessary to push the food tray to within their reach, even though this task was more unnatural and completely unfamiliar to them, given that throughout their lives they had often been fed by hand by human caretakers.

In subsequent experiments we manipulated various factors that might have controlled the chimpanzees' spontaneous preferences for the ANV experimenter, such as (a) distance between experimenter and subject (Experiment 2), (b) amount of occlusion of experimenters' bodies (Experiments 2 and 3), and (c) contact with the food tray (Experiments 3 and 4). In Experiment 5, we controlled these variables and manipulated the positioning of barriers that either blocked movement of the limbs or did not. The chimpanzees' behavior was not random and often times rulegoverned, however, in all cases we found that the chimpanzees' performance could best be explained by their deference to rules based on observable but not causally relevant features of the discriminations, such as distance and contact. When these discriminative cues were eliminated, performance fell to chance levels (see Table 2). The chimpanzees' performance in many instances was affected by the amount of the experimenter's body that was occluded. However, their choices were most strongly influenced by whether or not there was contact between the food tray and the experimenter's body at the start of a trial.

Prior studies have demonstrated that physical contact is a very salient cue for chimpanzees in solving folk physics problems (Cacchione and Krist 2004; Povinelli 2003). So perhaps it was not surprising that contact between the tray holding the food reward and the experimenter's body appeared to be a cue the chimpanzees utilized in our experiments as well. However, it is not clear that they used this cue because it was causally relevant to the task at hand or simply because of its inherent salience in attracting their attention via stimulus and local enhancement (Thorpe 1956; Spence 1937). Moreover, recent investigations with rooks (Helme et al. 2006b) and bonobos (Helme et al. 2006a) failed to find evidence for a causal understanding of contact in these species. In addition, Hauser et al. (1999) found that tamarins learned to attend to functionally relevant rather than irrelevant task features when using tools to retrieve food, but appeared to attend to cues of connection more readily than to cues of contact. Furthermore, when contact between the food tray and the experimenters' bodies could not be used as a discriminative cue in our experiments, our chimpanzees were not readily able to make use of other causally relevant cues, despite their apparent salience-for instance, the complete occlusion of particular body parts that were essential to performing the given tasks.

These results demonstrate that in specific contexts chimpanzees can form specific rules based on certain observable features. There was no evidence that chimpanzees generated multiple nested rules of the form: (a) gesture to experimenter with hands or feet visible and (b) making contact with tray, let alone rules that required an abstraction of conditional limb-specific contact rules such as 'gesture to experimenter who is capable.' This finding is in keeping with previous research showing that chimpanzees attend to a hierarchy of salient cues when deciding who to gesture towards for food rewards in paradigms where one experimenter can see them and the other cannot. In an extensive series of experiments, Povinelli and Eddy (1996a) showed that chimpanzees first attended to the orientation of the experimenters, then to the visibility of the face, and finally to the visibility of the eyes. In their studies, such cues were causally related to the visual attention of the experimenters, making it difficult to determine whether chimpanzees reasoned about the relevance of such cues for assessing the internal mental states (attention) of the experimenters or simply made associations between these cues and positive outcomes (receiving food rewards). Others have replicated some of these results with different chimpanzees (Kaminski et al. 2005) and have come to similar conclusions regarding the ambiguity of paradigms involving the use of gaze cues with regards to supporting a theory of causal or mental state understanding (Call et al. 1998; Tomasello and Call 2006; Tomasello et al. 1999). Thus, this style of response does not seem unique to this particular group of chimpanzees. It remains possible that the unique experimental history of our chimpanzees caused them to focus on particular contingencies more than others. Only by testing other populations can these hypotheses be explored.

However, the present study allows for a disentangling of the use of relevant and irrelevant perceptual cues. This series of experiments demonstrates that chimpanzees may not prioritize highly salient, relevant features over highly specific but irrelevant cues. Their performance therefore is less consistent with causal reasoning, and more consistent with the formation of particular associations between physical features of the experimenters and the likelihood of obtaining a reward from those experimenters. Unlike human children, who, by the age of three years, learn tasks better when actions are causally relevant (Want and Harris 2001), our results are at least consistent with the possibility that chimpanzees may fail to distinguish between relevant and irrelevant cues, even when both are available to the senses. This conclusion is in contrast to that of other researchers who found that primates may be particularly sensitive to cues that are causally relevant as opposed to arbitrary (Bräuer et al. 2006; Call 2004, 2006; Hauser et al. 1999; Hauser and Spaulding 2006; Horner and Whiten 2005). All of these tasks, in which primates apparently demonstrated evidence for attending exclusively to causally relevant features involved physical tasks. Perhaps the fact that our task, albeit one we envisioned to test an understanding of physical causality, involved human experimenters made it more difficult for the chimpanzees, if their causal reasoning deficit is specific to social reasoning (although see below).

What is particularly striking about our results is that chimpanzees failed to show evidence of learning the importance of the visibility of particular limbs for particular tasks, even though they could have used readily observable and causally relevant cues to govern their preference for an experimenter. While they were able to make use of some cues, they did not attend to those cues that were causally linked to the experimenter's ability to perform the task. It is important to emphasize that the chimpanzees were able to extract cues that were often predictive in terms of the likelihood of receiving reward, and sometimes performed above chance when such cues were available. However, they failed to reliably attend to the one cue that was causally and consistently linked to the ability to perform the tasks (limb visibility/availability). It is possible that, in previous studies suggesting that chimpanzees do reason causally, in particular about the predictive value of such cues as forward body orientation and visibility of the eyes, that chimpanzees happened to attend to the causally relevant cues by chance due to their salience or due to an innate predisposition to attend to eye-stimuli (Bräuer et al. 2005; Burkart and Heschl 2006; Hare et al. 2006; Hostetter et al. 2006; Kaminski et al. 2004; Povinelli and Eddy 1996a, b, c, 1997; Tomasello et al. 1998). Clearly, eye gaze is a very salient natural cue (Povinelli and Eddy 1996a).

It is possible that success in experimental tasks is differentiated by whether the relevant cues are salient rather than causally relevant for chimpanzees. This would make sense if chimpanzees are adept at forward reasoning (i.e., predictively) but not backward reasoning, evidencing the ability to explain events (see also Andrews 2005; Vonk 2005). In other words, chimpanzees might be able to form associations between cues that predict reinforcement after reasonable experience, whether specific or generalized, but they may not be able to reason about why these cues are predictive. This lack of understanding would make it difficult to infer, in the absence of direct experience, which observable cues might predict or explain unobserved consequences, thus making it impossible to distinguish between causally relevant and irrelevant cues. However, because chimpanzees do possess complex powers of observation and critical thinking skills, they may be extremely adept at quickly extracting abstract rules to predict patterns of behaviors and events in the world. In the absence of true causal reasoning one might expect that these abilities alone would allow chimpanzees to succeed at some tasks requiring abstract reasoning, and to fail at others. Thus their difficulties in the present experiments may not be so surprising even given their success in other challenging experimental contexts.

Certainly these experiments proved to be more difficult for chimpanzees than anticipated. There are a variety of reasons for this difficulty, including the ones we have outlined above. It is possible that our chimpanzees were simply overwhelmed by the number of unfamiliar and somewhat unnatural experimental configurations that we confronted them with, although we find this explanation unlikely given our chimpanzees' vast experimental history (see Povinelli 2003). These chimpanzees are accustomed to participating in many different experimental tasks with many artificial objects on a daily basis from the time that they were very young. They have often performed quite well with objects that they have never encountered before. The present experiments made use of a procedure that was highly familiar to them, and one that were quite successful at. Indeed, the rates of response in these experiments were quite high and we did not encounter any behavioral problems. It is unlikely that a lack of familiarity with novel experimental contexts was the culprit. Moreover, Call and colleagues (2004) have reported that chimpanzees can distinguish between 'unwilling' and 'unable' human experimenters in an unnaturalistic laboratory context (Call et al. 2004). Certainly, on the surface, the current problem would appear to be easier than the studies conducted by Call and colleagues, as the cues used here were transparent and highly salient and required neither a folk psychological inference such as 'unwilling' nor a complex and opaque distinction between 'unwilling' and 'unable' human experimenters. We make this claim because inferences about internal dispositions must be made on the basis of external, observable states, while inferences about external states can be made by observation alone. Therefore inferences about internal states require an extra level of inference.

Perhaps, still, one could argue that chimpanzees may not have realized that the experimenters could not break out of their constraints to use their invisible limbs—maintaining this belief despite persistent evidence to the contrary across hundreds of trials and multiple experiments—but then, again, why would chimpanzees not reason that 'competitive' experimenters looking away (e.g., Hare et al. 2006) could easily turn to face them and take their food? In addition, it seems unlikely that chimpanzees would reason about whether it made sense that the experimenters did not do so rather than base their predictions simply on the fact that they never did.

It is possible that we simply did not provide the chimpanzees with enough information about what experimenters lacking limbs could and could not do, in order for them to make informed inferences about the particular task at hand. So, if, for example, they were able to see the experimenters having difficulty walking without legs, having difficulty reaching and grasping objects without arms and hands, perhaps then they would have succeeded in the experiments. One can then imagine that, when confronted with limbless individuals in a natural setting, individuals whom they could observe in multiple contexts over a longer period of time, they might more fully be able to appreciate the limitations associated with such abnormalities. Obviously, because our experimenters were not really missing limbs, we could not provide the chimpanzees with the full range of such experiences. Had we had access to such human populations a more naturalistic study might be possible. We would encourage others to attempt such manipulations.

One other logistical detail may have contributed to the difficulty of chimpanzees in this paradigm. Chimpanzees may find it difficult to reason about human limbs because humans do not use arms and legs interchangeably as chimpanzees do. Although it is true that human limbs are not functionally equivalent to those of chimpanzees, our participants have lived since birth alongside humans and, as a result, had years of experience observing humans use their limbs in different ways in various tasks. Humans are presumably capable of making inferences about what chimpanzees can and cannot do despite functional inequivalences; if chimpanzees reason causally they might also be capable of making such inferences. Of course, it is possible that chimpanzees can reason only about chimpanzee capability and not the capability of any other animal, including familiar human caretakers. But certainly the ability to reason about the physical capability of potential competitors such as baboons as well as predators, whose physical composition may differ considerably from one's own, such as raptors and large cats, should carry at least as much adaptive value as the ability to reason about the capability of conspecifics. There are claims that other intelligent mammals, such as dolphins, are capable of copying familiar (and, perhaps, novel) motor actions executed by human models, despite the fact that the bodies of dolphins and those of humans are not only physically but also functionally very different (Herman 2002).

If the manner in which chimpanzees reason about capability is similar to how they purportedly reason about 'seeing'—in a highly context dependent fashion (i.e., only in 'competitive' but not in 'cooperative' contexts, c.f. Hare 2001), then it is very unlike the causal reasoning skills of even the youngest members of our species, *Homo sapiens*, who reason about various unobservables such as seeing in the most competitive playgrounds as well as in the most cooperative classrooms.

This is an important point to make because a common criticism often levied against paradigms requiring chimpanzees to request food from human competitors is that it is an unnatural context for this species (Hare 2001). However, it is not an unnatural context for captive chimpanzees, who are the participants of this research. However, a much larger point is as follows; the biggest challenge to such relative logic is that context dependent theories contradict the adaptive purposes of these abstract cognitive abilities, whose hypothetical purpose is to grant subjects greater behavioral flexibility across a variety of domains and to draw inferences about novel events and agents. At the very least, the inability of chimpanzees to reason in a flexible context-independent manner clearly indicates an important cognitive discontinuity between the minds of humans and our closest living relatives.

The issue we wished to examine was whether chimpanzees attended to cues that were predictive in a causally relevant versus irrelevant fashion when many cues were directly observable for their use. We were less interested in what they could learn through direct experience and a history of reinforcement—as we have no doubt that with sufficient experience chimpanzees would eventually develop appropriate response rules. Rather what we were interested in exploring was what chimpanzees would spontaneously infer in the absence of such experience. It is exactly these sorts of inferences that allow one to attribute the capacity for flexible reasoning and abstract generalization.

It is also true that our tasks were somewhat unnatural and confronted the chimpanzees with situations they had not encountered before but this is precisely when the ability to make inferences based on causal reasoning rather than previously learned behavioral associations might be revealed. It is also the best means of assessing whether cognitive skills are context dependent rather than context independent as is the case with much of human cognition. It is difficult to imagine natural selection favoring physical causal reasoning only in regard to members of one's own species. This is particularly unlikely, given that chimpanzees hunt and fall prey to animals with different capabilities than their own. As such, humans and chimpanzees by virtue of shared ancestry or shared evolutionary environments should have been subjected to the same evolutionary trends that favored a flexible understanding of physical capability. The fact that chimpanzees appear unable to flexibly reason about human capability suggests that this is a derived ability in Homo; one that does not appear to be shared with chimpanzees.

Other scientists have emphasized that chimpanzees are extremely adept at attending to and predicting outcomes from salient observable cues (Povinelli 2003). This statement should not be taken to imply that chimpanzees are equally adept at interpreting the relevance of all kinds of observable features in problem tasks. Instead, it appears that, rather than solely encountering difficulties in making inferences based on unobservable features, such as mental states and dispositions (Povinelli 2004; Vonk and Povinelli 2006), chimpanzees, and other non-human primates may suffer from a more global "deficit" in the ability to understand the causal role of physical features in certain tasks.

A mosaic (domain-specific) pattern of performance has been demonstrated in children with autism who show a specific deficit in social reasoning, but not physical causality (Baron-Cohen 2003; Baron-Cohen et al. 1986; Leslie and Thaiss 1992). One possibility is that chimpanzees show the opposite domain-specific deficit. Following a series of studies of children and chimpanzees, Premack and Premack (1994) suggested that the concept of cause first emerged in the social or psychological domain and that physical causal reasoning may have emerged later in the human lineage. The chimpanzees' performance in the present study might suggest that chimpanzees have a specific impairment in physical causality, while other recent studies have suggested that they may not be so impaired with regards to social causality, where they may reason more flexibly about an actor's goals and intentions (Hare et al. 2006; Melis et al. 2006; Tomasello et al. 2003a, b). However, although the popular interpretation of this latter body of work is that chimpanzees may reason about some mental states, such as seeing (Tomasello et al. 2003a, b), the results have not unequivocally been accepted as supportive of such a conclusion (Povinelli and Vonk 2003, 2004; Subiaul et al. 2007; Vonk and Povinelli 2006). Moreover, Bräuer et al. (2006) have suggested that apes may reason causally while dogs reason socially-a conclusion that points to the opposite pattern of domain-specific deficits. Furthermore, a number of researchers have noted superior performance of dogs, relative to the performance of chimpanzees in tasks that require the use of eyes or gaze cues (Hare and Tomasello 2005; Povinelli et al. 1999; Soproni et al. 2001), or require cooperation (Hare 2007).

It is possible that our chimpanzees' performance may index a more global inability to reason about abstract, causal correlations across domains. In this view, the cognitive divide between humans and chimpanzees would be greater than even that proposed by the Unobservability Hypothesis (Povinelli 2003, 2004; Subiaul et al. 2007; Vonk and Povinelli 2006). Whereas this hypothesis proposes that nonhumans may not have the capacity to reason about theoretical entities that cannot be directly perceived through any of the senses, the real gap may lie in the ability to seek explanations rather than merely predicting events (see also Andrews 2005; Premack and Premack 1994; Vonk 2005). Previous work indicates that human children, but not chimpanzees seek causal explanations (Povinelli and Dunphy-Lelii 2001). Additional research that directly compares chimpanzees' physical-causal versus social-causal reasoning is necessary to distinguish whether the mosaic cognitive evolution hypothesis or the global causal deficit hypothesis is correct. Further, the pattern of deficits may be even more specific than that indexed by a physical/social distinction. Certainly, extending the current studies to human children will have further implications for determining the limits on shared representational and reasoning capacities between humans and other apes.

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References

- Andrews K (2005) Chimpanzee theory of mind: looking in all the wrong places? Mind Lang 20:521–536
- Baron-Cohen S (2003) The essential difference. Basic Books, New York
- Baron-Cohen S, Leslie AM, Frith U (1986) Mechanical, behavioral and intentional understanding of picture stories in autistic children. Br J Dev Psychol 4:113–125
- Behne T, Carpenter M, Call J, Tomasello M (2005) Unwilling versus unable: infants' understanding of intentional action. Dev Psychol 41:328–337
- Bräuer J, Call J, Tomasello M (2005) All great ape species follow gaze to distant locations and around barriers. J Comp Psychol 119:145–154
- Bräuer J, Kaminski J, Riedel J (2006) Making inferences about the location of hidden food: social dog, causal ape. J Comp Psychol 120:38–47
- Burkart J, Heschl A (2006) Geometrical gaze following in common marmosets (*Callithrix jacchus*). J Comp Psychol 120:120–130
- Cacchione T, Krist H (2004) Understanding object relations: What chimpanzees know about support. J Comp Psychol 118:140– 148
- Call J (2004) Inferences about the location of food in the Great Apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo pygmaeus*). J Comp Psychol 118:232–241
- Call J (2006) Descartes' two errors: reason and reflection in the great apes. In: Hurley S, Nudds M (eds) Rational animals. Oxford University press, New York, pp 219–234
- Call J, Hare B, Carpenter M, Tomasello M (2004) 'Unwilling' versus 'Unable': Chimpanzees' understanding of human intentional action. Dev Sci 7:488–498
- Call J, Hare BA, Tomasello M (1998) Chimpanzee gaze following in an object-choice task. Anim Cogn 1:89–99
- Call J, Tomasello M (1998) Distinguishing intentional from accidental actions in orangutans, chimpanzees, and human children. J Comp Psychol 112:192–206
- Carpenter M, Akhtar N, Tomasello M (1998) Fourteen- through 18month-old infants differentially imitate intentional and accidental actions. Infant Behav Dev 21:315–330
- Flombaum JI, Santos LR (2005) Rhesus monkeys attribute perceptions to others. Curr Biol 15:447–452
- Hare B (2007) From nonhuman to human mind. Curr Dir Psychol Sci 16:60–64
- Hare B (2001) Can competitive paradigms increase the validity of experiments on primate social cognition? Anim Cogn 4:269–280
- Hare B, Tomasello M (2005) Human-like social skills in dogs? Trends Cogn Sci 9:439–444
- Hare B, Call J, Tomasello M (2006) Chimpanzees deceive a human competitor by hiding. Cognition 101:495–514
- Hauser MD, Kralik J, Botto-Mahan C (1999) Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. Anim Behav 57:565–582
- Hauser MD, Spaulding B (2006) Wild rhesus monkeys generate causal inferences about possible and impossible physical transformations in the absence of experience. PNAS 103:7181–7185
- Helme AE, Call J, Clayton NS, Emery NJ (2006a) What do bonobos (*Pan paniscus*) understand about physical contact? J Comp Psychol 120:294–302
- Helme AE, Clayton NS, Emery NJ (2006b) What do rooks (*Corvus frugilegus*) understand about physical contact? J Comp Psychol 120:288–293
- Herman LH (2002) Vocal, social, and self-imitation by bottlenosed dolphins. In: Dautenhahn K, Nehaniv CL (eds) Imitation in animals and artifacts. MIT Press, Cambridge, pp 63–108

Horner V, Whiten A (2005) Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). Anim Cogn 8:164–181

Hostetter AB, Russell JL, Freeman H, Hopkins WD (2006) Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. Anim Cogn. Available online

- Kaminski J, Call J, Tomasello M (2004) Body orientation and face orientation: two factors controlling apes' begging behavior from humans. Anim Cogn 7:216–223
- 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. Anim Behav 69:11–18
- Leslie AM, Thaiss L (1992) Domain specificity in conceptual development: evidence from autism. Cognition 43:225–251
- Melis AP, Call J, Tomasello M (2006) Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. J Comp Psychol 120:154–162
- Penn DC, Povinelli DJ (2007) Causal cognition in human and nonhuman animals: a comparative, critical review. Annu Rev Psychol 58:97–118
- Povinelli DJ (2003) Folk physics for apes: the chimpanzee's theory of how the world works. Oxford University Press, Oxford
- Povinelli DJ (2004) Behind the ape's appearance: escaping anthropocentrism in the study of other minds. Daedalus J Am Acad Arts Sci Winter:29–41
- Povinelli DJ, Bierschwale DT, Cech CG (1999) Comprehension of seeing as a referential act in young children but not juvenile chimpanzees. Br J Dev Psychol 17:37–60
- Povinelli DJ, Dunphy-Lelii S (2001) Do chimpanzees seek explanations? Preliminary comparative investigations. Can J Exp Psychol 55:93–101
- Povinelli DJ, Eddy T (1996a) What young chimpanzees know about seeing. Monogr Soc Res Child Dev 61 247:1–152
- Povinelli DJ, Eddy TJ (1996b) Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. J Comp Psychol 110:336–345
- Povinelli DJ, Eddy TJ (1996c) Chimpanzees: joint visual attention. Psychol Sci 7:129–135
- Povinelli DJ, Eddy TJ (1997) Specificity of gaze-following in young chimpanzees. Br J Dev Psychol 15:213–222
- Povinelli D, Perilloux H, Reaux J, Bierschwale D (1998) Young chimpanzees' reactions to intentional versus accidental and inadvertent actions. Behav Process 42:205–218
- Povinelli DJ, Vonk J (2003) Chimpanzee minds: suspiciously human? Trends Cogn Sci 7:157–160
- Povinelli DJ, Vonk J (2004) We don't need a microscope to explore the Chimpanzee mind. Mind Lang 19:1–28

- Premack D, Premack AJ (1994) Levels of causal understanding in chimpanzees and children. Cognition 50:347–362
- Santos LR, Nissen AG, Ferrugia J (2006) Rhesus monkeys (*Macaca mulatta*) know what others can and cannot hear. Anim Behav 71:1175–1181
- Soproni K, Miklósi A, Topál J, Csanyi V (2001) Comprehension of human communicative signs in pet dogs (*Canis familiaris*). J Comp Psychol 115:122–126
- Spence KW (1937) Experimental studies of learning and the higher mental processes in infra-human primates. Psychol Bull 34:806– 850
- Subiaul F, Barth J, Okamoto-Barth S, Povinelli DJ (2007) Human cognitive specializations. In: Preuss TM, Kaas JH (eds) Evolution of nervous systems, vol V. The Evolution of primate nervous systems. Elsevier, New York

Thorpe WH (1956) Learning and instinct in animals. Methuen, London

Tomasello M, Call J (2006) Do chimpanzees know what others see or only what they are looking at? In: Nudds M, Hurley S (eds) Rational animals. Oxford University press, New York, pp 371–384

- Tomasello M, Call J, Hare B (1998) Five primate species follow the visual gaze of conspecifics. Anim Behav 58:769–777
- Tomasello M, Call J, Hare B (2003a) Chimpanzees understand psychological states—the question is which ones and to what extent. Trends Cogn Sci 7:153–156
- Tomasello M, Call J, Hare B (2003b) Chimpanzees versus humans: it's not that simple. Trends Cogn Sci 7:239–240
- Tomasello M, Hare B, Agnetta B (1999) Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. Anim Behav 58:769– 777
- Tooby J, Cosmides L (1992) The psychological foundations of culture.
 In: Barkow JH, Cosmides L, Tooby J (eds) The adapted mind: evolutionary psychology and the generation of culture. Oxford University Press, New York, pp 19–136
- Visalberghi E, Trinca L (1989) Tool use in Capachin monkeys: distinguishing between performing and understanding. Primates 30:511–521
- Vonk, J (2005). Causality in non-humans: empirical questions. Invited paper published online for Interdisciplines: Causality, May 23, 2005. http://www.interdisciplines.org/causality/papers/9
- Vonk J, Povinelli DJ (2006) Similarity and difference in the conceptual systems of primates: the unobservability hypothesis. In: Wasserman E, Zentall T (eds) Comparative cognition: experimental explorations of animal intelligence. Oxford University Press, England, pp 363–387
- Want SC, Harris PL (2001) Learning from other people's mistakes: causal understanding in learning to use a tool. Child Dev 72:431– 443