



# Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others

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Chimpanzees, *Pan troglodytes*, interacted with a familiar human partner across a table that contained a piece of highly desirable food and an undesirable distracter object. We explored how the chimpanzees' deployed their gestures on trials in which the food and object were out of their reach, thus creating a context in which they needed to recruit their partner's assistance in order to obtain the food. The attentional focus of their partner was directed either at the food, at the distracter object, or at a neutral location on the ceiling. Although the location of the food exerted primary control over the location of the chimpanzees' gestures, the results also clearly show that when their partner's focus was on the distracter object, the subjects modified their pattern of gesturing to accommodate the discrepancy between the object they wanted and the object on which their partner was focused. We discuss the results in the context of the evolution of joint and shared attention in humans, chimpanzees and other primates.

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Over the past several decades, researchers have increasingly come to see social problems as a vital part of the natural lives of animals (e.g. Jolly 1966; Humphrey 1976; Gallup 1982; de Waal 1982; Krebs & Dawkins 1984; Cheney et al. 1986; Whiten & Byrne 1988; Dunbar 1993). Experimental studies exploring communication, social learning, understanding of social relationships, use of social cues, deception, and even an understanding of mental states, have been investigated in a wide range of taxa, including nonhuman primates, birds, cetaceans and dogs (recent examples include: Whiten 1996; Hare et al. 1998; Miklósi et al. 1998; Call & Tomasello 1999; Povinelli 1999; Emery & Clayton 2001; Tschudin et al. 2001). However, because of their high degree of sociality, and their evolutionary relationships to humans, non-human primates have become a focal point for research into the evolution of social cognition.

One particularly important area of research into the evolution of social cognition has focused on the ability of nonhuman primates to exploit and interpret information about the attentional systems of others. Undeniable similarities exist in how humans and other primates,

especially chimpanzees, *Pan troglodytes*, process information about these attentional systems. Humans share with a number of social primates the ability to use information about the posture and movement of the eyes, head and body of others in order to orient to important objects or events in the world. For example, chimpanzees spontaneously follow the gaze direction of others in response to their head and eye movements, or simply their eye movements alone, and also respond appropriately when another's line-of-sight strikes an opaque barrier (Itakura 1996; Povinelli & Eddy 1996a, b, 1997; Tomasello et al. 1998, 1999). Indeed, the results of current research suggest a nearly complete overlap in the gaze-following behaviour of chimpanzees and 18-month-old human infants (see Table 1 in Povinelli 2001, for an overview). Some, but not all, of these aspects of gaze following and processing of information about visual attention have been demonstrated in other nonhuman primates as well (e.g. Itakura 1996; Emery et al. 1997; Tomasello et al. 1998; Anderson & Mitchell 1999; Ferrari et al. 2000).

However, in contrast to the general acceptance of the existence of the phenomenon of gaze following in chimpanzees (and other nonhuman primates), there is considerably less agreement on whether these animals interpret the head and/or eye movements of others as observable manifestations of unobservable, internal mental states; in short, whether they attribute concepts such as 'seeing' or 'attending' to others. In their natural interactions, chimpanzees spontaneously produce visually based attention-getting behaviours in appropriate

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contexts (Tomasello et al. 1994), and in more experimental contexts, have been shown to immediately gesture to someone who is facing them, but not to someone whose back is towards them (Povinelli & Eddy 1996a). However, this same experimental research suggests that although they are quite sensitive to the orientation and postures of others, they may not construe these observable stimuli as evidence of unobservable, internal mental states (e.g. Povinelli & Eddy 1996a; Povinelli et al. 1999; Reaux et al. 1999; Theall & Povinelli 1999).

New evidence has suggested that chimpanzees may have a better understanding of such mental states in competitive interactions with other conspecifics across a variety of experimental situations (Hare et al. 2000, 2001). Hare and colleagues provided evidence that chimpanzees 'know what conspecifics can and cannot see' (Hare et al. 2001) and that chimpanzees can accurately track 'who has seen what', while at the same time raising doubts as to the chimpanzees' ability to track which of two rewards a single animal has seen (Experiment 3 in Hare et al. 2001). Using procedures as similar as possible to the original set of studies (e.g. Hare et al. 2000), extensive research from our own laboratory has failed to corroborate these initial findings (Karin-D'Arcy & Povinelli 2001). The sources of these differences are difficult to identify at this point, both because of inevitable methodological differences between the subjects and testing environments, and because (1) the original studies were not conducted under the guidance of a contemporaneous, written protocol that can now be examined, and (2) the studies were not recorded on videotape, and hence detailed retrospective comparisons between the studies are not possible. Future research will undoubtedly help to clarify the robustness of the Hare et al. (2000) findings, as well as the even stronger claims by Hare et al. (2001).

Other researchers have explored the ability of non-human primates, domestic dogs and dolphins to extract communicative information from the direction of the gaze of others (i.e. to choose a container at which an experimenter is gazing or glancing: e.g. Povinelli et al. 1992, 1997, 1999, 2002a; Call & Tomasello 1994; Anderson et al. 1995; Call et al. 1998; Miklósi et al. 1998; Hare & Tomasello 1999; Tschudin et al. 2001). Although some species (such as chimpanzees and domesticated dogs) appear to be able to use such social cues relatively easily, other species appear less able to do so. Whether or not these findings demonstrate an explicit understanding that other organisms have internally mediated visual experiences (such as 'seeing' or 'attention') remains controversial, and important (see Povinelli et al. 2002a).

In the studies reported here, we sought to explore whether chimpanzees are able to coordinate their ability to follow the gaze of others with gestural expressions of their own first-order desires. In the context of their own species-typical food-begging gestures, we explicitly asked whether chimpanzees would spontaneously recognize and compensate for a mismatch between an object that they desired, and the attentional focus of a human partner. In the prototypical case, two objects are present within reach of the human partner but out of the

chimpanzee's reach; one is a highly desirable food item, the other is an undesirable distracter object. Thus, the chimpanzee needs their partner's assistance in retrieving the food item.

We evaluated two simple models for how chimpanzees might cope with this situation. First, if they are able to integrate their first-order desire (wanting the food) with their capacity for following the gaze direction of others, the location of their gestures should vary as a function of where their partner is attending. Hereafter, we shall refer to this as the integration model. On the other hand, if the systems modulating chimpanzees' gestures (which express their first-order desires) are sequestered from the psychological systems controlling the expression of their gaze-following response, they could be expected to process the attentional posture of their partner, and even follow his or her gaze direction, but their gestures would only vary as a function of the food's location. We shall refer to this as the sequestration model.

## EXPERIMENT 1

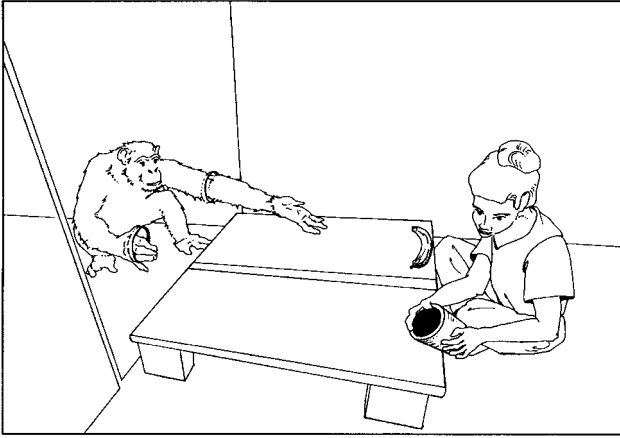
### Method

#### *Subjects and housing*

Six subadult female chimpanzees and one subadult male served as subjects. At the beginning of this study, the subjects ranged in age from 8.33 to 9.25 years. All subjects were born at the University of Louisiana at Lafayette New Iberia Research Center, were peer-raised in a nursery with extensive human contact, and have been continuously housed together in a large indoor-outdoor enclosure since infancy. When the animals were between 2 and 3 years of age, they became part of a long-term project designed to explore aspects of their reasoning about the social and physical world. Since their first year of life, they have had extensive daily contact with the same primary caretaker, as well as many other human caretakers and experimenters. A more detailed description of the subjects' rearing histories and living environment are provided in Povinelli (2001). All subjects had previously been tested on a variety of different experimental protocols as part of an ongoing project designed to examine their cognitive abilities. A list of all studies in which the subjects had participated prior to the studies reported here is available upon request.

#### *Apparatus and materials*

The experiment took place in an indoor test unit that was divided by a Plexiglas partition, physically separating the experimenters and the subjects (Fig. 1). Two large holes (separated by 50 cm) were located in the Plexiglas through which subjects could reach. A short table (117 × 91 × 15 cm) was placed directly in front of the Plexiglas partition and was accessible through both of the holes. The table was divided by a thick, easily visible line perpendicular to the Plexiglas partition to enable clear discrimination of gestures on either side of the table. A piece of PVC pipe (10 cm diameter, 10 cm length), was used as an undesirable (distracter) object.



**Figure 1.** Testing situation used in experiment 1. The at-distracter condition is shown here. See text for details.

Desirable objects consisted of fresh fruit, vanilla wafers and chocolate candies. The subjects were individually transferred out of their social group and into an outdoor waiting area that was connected, via a remotely operated shuttle door, to the indoor test unit. The subjects were intimately familiar with this procedure as they had participated in various kinds of testing (typically twice a day 5 days a week) for the previous 5 years.

#### *Procedure*

**Assessment phase.** To verify that the subjects preferred the food over the distracter object, we administered an initial assessment phase. During this phase, each session consisted of four trials, each lasting 60 s. One side of the table was baited with a desirable food reward (one-half of an apple or the candy equivalent) and the other was baited with the undesirable (distracter) object. Both of these items were within the subject's reach, and the left/right positions were counterbalanced across the four trials within each session. A partner familiar to the subject sat midline, directly behind the table, and tracked the subject by natural head and eye movements throughout each trial. The trial began when the trainer used a remote pulley system in the back of the test room to open the shuttle door, which allowed the subject to enter the test unit from the outside waiting area. The subject's task was to enter and retrieve the food reward from the table. The subject was then free to behave in any manner they desired, including retrieving and examining the distracter object, for the remainder of the 60-s trial. In order to advance to testing, each subject was required to demonstrate their preference for the food item by selecting it as their first choice on every trial across three consecutive sessions ( $N=12$  trials).

**Testing phase.** Testing consisted of 12 sessions, each containing four trials. Three trials in each session were baseline trials and one served as a probe trial in which the experimental conditions were administered. The general procedure for the baseline trials was similar to that used during the assessment phase with the following

exceptions. The duration for the baseline trials was 15, 20 or 25 s (randomly and exhaustively assigned to each of the three baseline trials within each session). In addition, the distracter object and the food reward were placed in one of two designated positions (near or far), both of which were within the subject's reach. The purpose of these two distances was to create some differential effort in retrieving the reward across the baseline trials so that on the probe trials, when the food was out of their reach, the subjects would still be likely to attend. Side and distance combinations were counterbalanced, then randomly and exhaustively assigned to the three baseline trials across sessions.

Probe trials occurred within a session as either trial 2 or 3, randomly determined and equated across sessions with each condition (see below) occurring equally often in each trial position. Probe trials lasted 60 s. The distracter object and food reward were placed in a designated far position out of the subject's reach. To ensure motivation, the food reward present during probe trials was increased to a whole banana or the candy equivalent. The trials began when the subject's partner initiated the choreographed condition assigned to that trial (see below). The shuttle door was then opened and the subject was allowed to enter the test room where he/she was able to reach towards either object on the table. The human partner remained engaged in this behaviour throughout the trial. On half of each of the three types of probe trials, after the 60 s had elapsed, the subjects' partner looked up and handed the subject the food that was on the table. This procedure was used to provide a variable reinforcement schedule to maintain the subjects' interest and motivation in gesturing to their partner. Counterbalancing ensured that the subjects were handed a food reward equally often from both sides of the table.

**Nature of the conditions.** We created three experimental conditions using multiple postural and behavioural indicators of the human partner's target of attention. In the at-distracter condition (Fig. 1), the partner was leaning and directing his/her gaze towards the distracter object while simultaneously manipulating the object with his/her hands. In the at-food condition, the partner adopted the exact same posture and behaviour, except it was towards the food item. Finally, in the at-ceiling condition, the partner was simply seated with hands on his or her knees, looking at a fixed location on the ceiling midway between the two objects. This condition was used as a control to assess the subjects' behaviour when their partner's gaze was not focused on either object.

#### *Predictions*

The integration model predicted that in the at-distracter condition the chimpanzees would gesture more towards the distracter object than to the food in order to gain the their partner's attention. This model also predicted that the chimpanzees would gesture more on the side of the food in the at-food condition, given that their partner was already focused on the object they wanted. For the at-ceiling condition, this model generated the prediction that the chimpanzees' gestures to the

food and distracter object would not differ since their partner's focus was midline between and above the two items. In contrast, the sequestration model predicted that the chimpanzees would gesture more on the side of the food than on the side of the distracter object in all three conditions, and thus not display an ability to coordinate their first-order desires with the discrepant focus of their partner in the at-distracter condition.

#### Videotape coding and reliability assessment

All test sessions were recorded by remote video cameras so that the subjects' behaviour could later be coded. We created a set of standardized, written instructions for coding the arm gestures of the subjects during the 60-s probe trials. A gesture was defined as a subject's wrist breaking the plane of the hole in the Plexiglas partition and extending an arm outward. Behaviours such as grabbing the table, rubbing the inside surface of the Plexiglas, and tactily examining the partition did not constitute a gesture and were not coded as such. Coding for the duration of a gesture began only after the subject's wrist had broken the plane of a hole and the subject extended an arm outward. The duration ended when the subject stopped gesturing for more than 1 s and/or his or her wrist exited the hole. A gesture was considered continuous unless it ended for at least 1 s. Before the raters began coding, they were shown videotaped examples of chimpanzee behaviours consistent and inconsistent with the criterion previously stated. The main rater was asked to score all 12 probe trials for each of the seven subjects ( $N=84$ ). A secondary rater scored 25% of these trials (3 of the 12 probe trials for each of the seven subjects,  $N=21$  trials). The two raters agreed on 95% (20/21) of the trials for the location of the first reach (Cohen's kappa:  $\kappa=0.92$ ). For frequency of gestures through each hole across trials, the secondary rater agreed with the main rater on 88% (35/40) of the trials ( $\kappa=0.80$ ). A correlational analysis of the two raters' data for duration of each gesture yielded a significant coefficient of determination ( $r_{40}^2=0.96$ ,  $P<0.0001$ , two tailed). The main rater's data was used for all analyses.

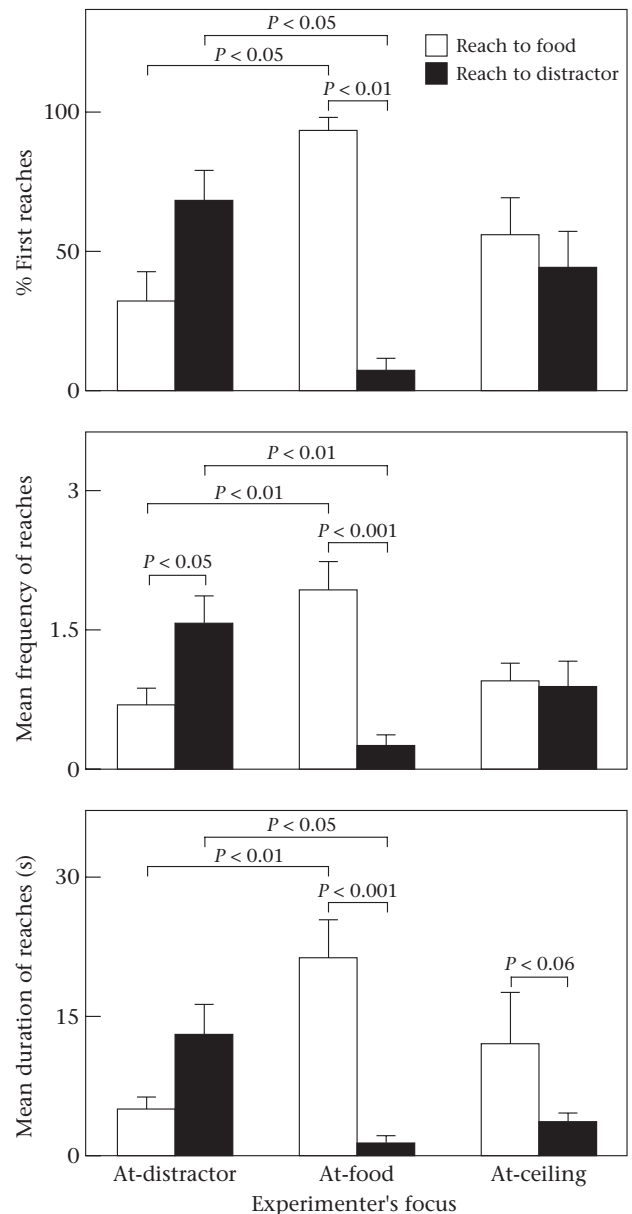
## Results

### Assessment phase

Six out of seven subjects met the criterion for advancing to testing (selecting the food before the distracter object on 12 consecutive trials) within the minimum number session possible. The remaining subject (Apollo) required 10 sessions to meet criterion. (This subject's interest in the distracter object caused him to occasionally reach for it first. However, this interest waned across sessions.)

### Testing phase

To evaluate the hypothesis that the chimpanzees would gesture differentially towards the food and the distracter object as a function of their partner's attentional focus, we examined the data to assess whether there was an interaction between the subjects' gestures and the



**Figure 2.** Results of experiment 1 for (a) first gestures, (b) frequency of gestures and (c) mean duration of gestures.

experimental conditions. Means for the individual subject's data, with  $N$  reduced to exclude trials where no gesture occurred, were obtained and used in all analyses. A one-way repeated measures analysis of variance (ANOVA) confirmed that the percentage of trials on which subjects did not produce any gesture was equally distributed across conditions ( $F_{2,12}=0.8478$ , NS).

We performed a two-way repeated measures ANOVA to analyse whether the target of the subjects' first gestures varied as a function of their partner's focus (see Fig. 2a). This analysis revealed an interaction of partner's focus  $\times$  object of subjects' gesture ( $F_{2,12}=8.71$ ,  $P<0.005$ ). An examination of the least squares means indicated that subjects deployed their first gesture significantly more on the side of the table where the food was located than the side where the distracter object was located in the

at-food condition ( $P < 0.002$ ). In addition, the subjects' first gestures were deployed significantly more on the side of the food in the at-food condition than in the at-distracter condition ( $P < 0.02$ ). Also, first gestures on the side of the distracter object in the at-distracter condition were significantly higher than in the at-food condition ( $P < 0.02$ ). There was no statistically significant difference in the mean number of first gestures on the side of the food or distracter object in the control (at-ceiling) condition.

We conducted a second repeated measures ANOVA with the same design as the one described above using the total frequency of gestures towards the food item and the distracter object across conditions (see Fig. 2b). The results were consistent with the pattern of results obtained for the analysis of first gestures. Again, there was an interaction between the target of partner's focus and the side (food or distracter object) of the subject's gesture ( $F_{2,12} = 12.36$ ,  $P < 0.002$ ). The least squares means revealed that subjects deployed significantly more gestures on the side of the food than on the side of the distracter object in the at-food condition ( $P = 0.0006$ ). Additionally, subjects gestured significantly more often on the side of the food in the at-food condition than in the at-distracter condition ( $P < 0.006$ ). Accordingly, subjects gestured on the side of the distracter object significantly more in the at-distracter condition than in the at-food condition ( $P < 0.004$ ). As was the case with the first gesture data, there was no statistically significant difference in the number of gestures deployed towards the different objects in the control condition.

A third repeated measures ANOVA of identical design was conducted to examine the mean duration of gestures across conditions (see Fig. 2c). This analysis also yielded a significant interaction of experimenter's focus  $\times$  side (food, distracter object) of subject's gesture ( $F_{2,12} = 12.54$ ,  $P = 0.005$ ). The least squares means revealed that subjects' gestures were significantly longer when they were gesturing on the side of the food than on the side of the distracter object in the at-food condition ( $P < 0.0003$ ). Also, the subjects' gestures towards the food were significantly longer in the at-food condition than in the at-distracter condition ( $P < 0.002$ ).

In contrast to the analyses of location of first gesture and frequency of gestures, a difference that approached significance was found in the mean duration of gestures to the different objects in the at-ceiling condition. The mean duration of the subjects' gestures tended to be longer towards the food than towards the distracter object in this control condition ( $P = 0.053$ ).

## Discussion

The results reveal that the chimpanzees noticed and altered their gesturing pattern when their partner's attention was not directed at the object that they themselves wanted. Of special interest was the robust interaction between the location of the chimpanzees' gestures and the location of their partner's attentional focus. This effect was robust and present in measures of the subjects'

first gesture, the frequency of their gestures, and the mean duration of the gestures. Also of interest was that in the control (at-ceiling) condition the subjects did not gesture differentially to the food or the distracter object, as reflected by at least two of the measures (first gesture, mean frequency of gesture), although there was a tendency in that direction for the mean duration of gestures towards food.

## EXPERIMENT 2

Six months after completing the first experiment, we conducted a second experiment in which we attempted to replicate and extend the findings described above. We used a procedure that was identical except that the attentional focus of the animal's partner was indicated only by the direction in which he or she was leaning and looking (the experimenter did not manipulate either object). Because the subjects were nondifferentially reinforced in the first experiment, we regarded this test as indicating their spontaneous reactions to the new conditions, tempered by habituation. The subjects participated in several unrelated studies in the interim.

## Method

### Subjects

The same seven chimpanzees participated. At the beginning of this experiment, the subjects ranged in age from 8.83 to 9.75 years.

### Apparatus and materials

The apparatus and materials used in this experiment were the same as those used in experiment 1.

### Procedure

**Orientation.** Each subject received two sessions, each consisting of four trials, in order to reorient them to the apparatus and testing procedure. The procedure was the same as the one used in the assessment phase of experiment 1, with the following exception. Each trial lasted either 15, 20, 25 or 30 s, with each duration randomly and exhaustively assigned to one of the trials within each session (whereas all trials lasted 60 s in experiment 1). If the subjects chose the food item before the distracter object on at least seven of eight consecutive trials, they were advanced to the testing phase, which all of them did.

**Testing.** The general testing procedures were identical to those outlined in experiment 1, with the following exceptions: (1) only two of the conditions from experiment 1 were administered (at-food and at-distracter), (2) instead of physically manipulating the objects, each subject's partner simply leaned and intently stared at the object in a carefully choreographed position (the partner's hands rested on his or her knees throughout the duration of each probe trial), and (3) three trials of each condition were administered.

Testing consisted of six sessions, each composed of three trials. Two trials per session were standard trials and were identical to those in experiment 1 except that they lasted either 15 or 25 s, with one trial of each duration within each session (randomly assigned). The third trial served as a probe trial in which the experimental conditions were administered. Probe trials occurred on either trial 2 or 3, randomly determined and counterbalanced across all sessions within subjects. Each probe trial lasted 60 s. The same nondifferential reinforcement procedures used in experiment 1 were implemented so that the subjects received the food item on half of the probe trials in each condition. The same counterbalancing and randomization procedures for the interactions of the side and target of the partner's focus and the probe trials on which the subjects received the food item were used.

The predictions were the same as those outlined for experiment 1, with the idea that the effects reported in the first experiment could be replicated if the experimenter was simply looking at the objects, instead of looking at and physically manipulating them as in experiment 1.

#### Videotape coding and reliability assessment

Videotapes of the testing sessions were coded using the procedures described in experiment 1. The main rater scored all six probe trials for each of the seven subjects ( $N=42$ ). A secondary rater scored 33.3% of these trials (2/6 probe trials for each subject,  $N=14$  trials). The raters agreed on 100% (14/14) of the trials for the location of the first gesture ( $\kappa=1.0$ ). For frequency of gestures to each hole across trials, the secondary rater agreed with the main rater on 94.7% (18/19) of the trials ( $\kappa=0.92$ ). The inter-rater correlational analysis for the duration of each gesture yielded a significant coefficient of determination ( $r_{19}^2=0.93$ ,  $P<0.0001$ , two tailed).

## Results and Discussion

We examined the data to determine whether there was an overall effect of the experimenter's attentional focus. Again, individual subject's means, with reduced  $N$ s excluding trials with no gestures, were used for all data analyses. A paired  $t$  test indicated that the two conditions were equal with respect to the percentage of trials where subjects did not gesture to either object ( $t_6=1.922$ , NS).

We conducted a series of two-way repeated measures ANOVAs to assess any effect of the experimenter's focus on each subject's first gesture, frequency of gesture and duration of gesture (Fig. 3a–c). A significant interaction was found between the partner's focus and the side of the subjects' first gesture ( $F_{1,6}=10.68$ ,  $P<0.02$ ; Fig. 3a). The least squares means revealed that the chimpanzees were more likely to first gesture on the side of the distractor object than on the side of food in the at-distractor condition ( $P<0.05$ ). Also, the subjects' first gestures tended to occur more often on the side of the distractor object in the at-distractor condition than in the at-food condition, as well as more often on the side of the food in the at-food condition than in the at-distractor condition ( $P=0.06$  in both cases).

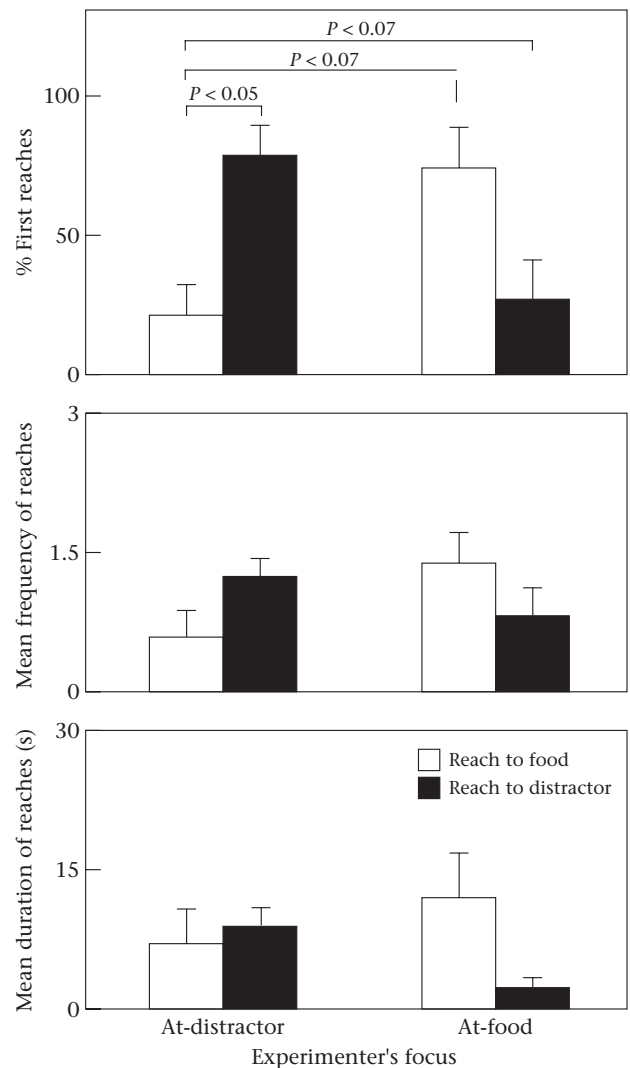


Figure 3. Results of experiment 2 for (a) first gestures, (b) frequency of gestures and (c) mean duration of gestures.

Although no overall effects were found in the ANOVAs for the other dependent measures (frequency and duration of gestures), a visual inspection of these data indicates that they follow the same general patterns as those obtained in experiment 1 (see Fig. 3b,c). The mean frequency and durations of the gestures tended to be higher on the side of the food than on the side of the distractor object in the at-food condition. Although gestures on the side of the distractor object occurred at a higher frequency than those on the side of the food in the at-distractor condition, the durations of these gestures were very similar (Fig. 3b,c).

Overall, the data for first gesture robustly replicated the effects reported in experiment 1, confirming that even under conditions in which their partner's attentional focus was less overt (no physical manipulation of the target of attentional focus), the chimpanzees altered their gesturing patterns when their partner's attentional focus was not coordinated with the object of their first-order desire. Data for frequency of gestures and mean duration

of gestures, while not statistically reliable, also yielded patterns that fit these general trends.

## GENERAL DISCUSSION

The results of both experiments show that our chimpanzees were highly sensitive to the interaction of their own desires and the direction of the observable manifestations of their partner's attention. Although the subjects were inclined to gesture towards the side of the food in all conditions (except the control condition in experiment 1; see Fig. 2), the posture of their partner in the at-distracter condition served to reverse the location of the subjects' first gesture (experiments 1 and 2), the frequency of their gestures (experiment 1) and the mean duration of the gestures (experiment 1), with the subjects preferring to gesture to where their partner was attending. This sensitivity to the direction of the partner's attention is further illustrated by the multiple instances in which the chimpanzees were observed to follow their partner's gaze in the at-ceiling condition in experiment 1 (see also Povinelli & Eddy 1996b).

The difference in the results between experiments 1 and 2 may be due either to habituation to the general paradigm or to the stronger attentional cues employed in experiment 1. However, despite the differences, the same pattern of results was apparent in both experiments, and clearly demonstrate that chimpanzees are able to coordinate their gesturing behaviour by integrating their own first-order desires with the attentional focus of a partner. In this regard, it is important to stress that the chimpanzees' behaviour was not controlled exclusively by the location of the food item, or by the attentional posture of their partner who handed them the food item (as would have been evidenced by the subjects' consistent tendency to gesture to where their partner was attending). The patterns that were present in chimpanzees' begging gestures reveal a previously undemonstrated ability of chimpanzees to integrate information about the location of the object they desire with the direction of someone else's attentional focus. This is an indication that the chimpanzees are able to monitor the attentional state of another and recognize when it does and does not match their own goal.

Several methodological aspects of our study deserve further scrutiny. First, to what extent was our gloss of the subjects' arm extensions as 'gestures' appropriate? To assess this, two raters coded all 126 probe trials in the two experiments and recorded whether the subjects appeared to make a gesture of any kind (begging, attention-getting, or other), a direct reach, or made no response (Cohen's kappa:  $\kappa=0.72$ ). Ninety-two per cent (98/106) of the trials on which the subjects made a response were coded as gestures by the main rater, whereas only 8% were coded as reaches. This raises an additional concern, as to whether there were any detectable subtypes of gestures by the chimpanzees and whether these differed systematically by treatment. Because of the dynamic nature and subtlety of the gestures, it is possible that our two independent sets of coders were not able to reliably distinguish between what may have been different

gestural types. However, there were no cases of the chimpanzees using extreme attention-getting devices (such as pounding the surface of the apparatus or vocalizing during the probe trials). There were several noteworthy instances of the chimpanzees lightly tapping on the apparatus, but these did not occur with sufficient frequency to analyse.

One interesting question raised by our research remains unanswered. Did our chimpanzees modify the location of their gestures as part of their construal of their partner as a psychological agent, or strictly as part of their understanding of the observable dynamics of their partner's observable posture and behaviour? In short, were the chimpanzees attempting to modify their partner's behaviour and attentional state, or strictly their behaviour alone? The latter possibility should not be trivialized. Chimpanzees and other species may share with humans a rich set of psychological systems for reasoning about, keeping track of, and predicting the observable behaviour of others without necessarily interpreting that behaviour in terms of underlying psychological states.

In this context, it may be helpful to examine previous research looking at chimpanzees' use of gestures similar to those examined here in the context of attention-getting tasks: do chimpanzees use their gestures more when others are attending to them, with other cues like proximity, general bodily orientation, held constant? Gómez (1996a, b) has summarized unpublished experimental work in which juvenile chimpanzees used their natural begging gestures on about 50% of the trials in which an experimenter was near them, but inattentive (~50%, Gomez 1996b; 68%, Gomez 1996a). Although Gomez (1996a, b) did not report data that bears on the crucial question of differential gesture deployment with respect to the experimenter's visual attention, he provided supplemental information that 'the proportion of normal attentive trials in which chimps used attention-getting behaviors was 3%' (personal communication, 1998). Unfortunately, however, it is not possible to compare the frequency of gestures on Gomez's attentive and inattentive trials because the procedure used by Gomez for attentive trials left no need or opportunity for the chimpanzees to deploy attention-getting behaviours before being handed a food reward because 'the human was looking at the chimpanzee and would immediately answer any request' (Gomez 1996b, page 142). After controlling for this methodological problem, Theall & Povinelli (1999) reported that although their chimpanzees used attention-getting gestures (e.g. slapping or tugging at their partner) on 71% of all trials, they did so with the exact same frequency, duration and temporal structure whether their partner's eyes were open or closed, or whether their partner was intensively looking at them or away from them.

Other research has more directly targeted the question of whether chimpanzees actively reason about what others can and cannot see. Consistent with the findings just described, results of an extensive series of studies with the same chimpanzees used in the studies reported here have shown that when they use their food-begging gestures to request food from one of two familiar

experimenters, they appear to rely upon rule-based procedures related strictly to the observable postures of their partners (e.g. their bodily orientation, presence/absence of the face or eyes); they appear not to appeal to notions about who can or cannot see them (Povinelli & Eddy 1996a; Reaux et al. 1999). Other procedures involving food competition among pairs of chimpanzees have yielded conflicting results concerning what chimpanzees understand about such attentional and/or perceptual states in others (e.g. cf. Hare et al. 2000; Karin-D'Arcy & Povinelli 2001).

Perhaps one of the most striking differences in the gestures of chimpanzees and humans is the early and robust appearance of what have been labelled proto-declarative gestures in human infants. At some point during the first year and a half of life, in addition to pointing at things for strictly imperative purposes (e.g. 'give me that'), human infants also begin pointing at things for declarative purposes; that is, drawing the attention of others to the object or event (e.g. 'look at that'; Bates et al. 1975; Bakeman & Adamson 1984). Recent experimental evidence confirms that by about the end of the second year, pointing becomes understood as a behaviour that can direct the internal attentional states of communicative partners (see Moore & D'Entremont 2001). Although chimpanzees learn to produce gestures that look and function like instrumental (or imperative) pointing gestures (e.g. Leavens et al. 1996), there is virtually no evidence that they use such gestures in a declarative fashion, and little strong evidence that they comprehend such gestures as anything other than a simple cue to direct their behaviour (see Povinelli et al. 1997, 2002b). Interestingly, there is evidence that domestic dogs comprehend the underlying referential aspects of the pointing gesture better than apes do (Soproni et al. 2002), perhaps as a result of selection for the ability to exploit human communicative signals during their domestication (Miklósi et al. 1998; Agnetta et al. 2000; Soproni et al. 2001).

In any event, regardless of whether chimpanzees explicitly reason about the mental states of attention or seeing in others, the results reported here reveal a previously undemonstrated flexibility in chimpanzees' use of their gestures in reaction to situations in which the attentional focus of others (as indicated through their posture and behaviour) is concordant or discordant with objects that they desire. Findings such as these should help us to more accurately model the psychological mechanisms that assist these highly social animals in manoeuvring their way through complex social environments. Ultimately, such work can assist in efforts to understand how cognitive systems of various social species have evolved to cope with both specific and general social problems.

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#### References

- Agnetta, B., Hare, B. & Tomasello, M. 2000. Cues to food locations that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition*, **3**, 107–112.
- Anderson, J. R. & Mitchell, R. W. 1999. Macaques but not lemurs co-orient visually with humans. *Folia Primatologica*, **70**, 17–22.
- Anderson, J. R., Sallaberry, P. & Barbier, H. 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, **49**, 201–208.
- Bakeman, M. & Adamson, L. B. 1984. Co-ordinating attention to people and objects in mother–infant and peer–infant interaction. *Child Development*, **55**, 1278–1289.
- Bates, E., Camaioni, L. & Volterra, V. 1975. The acquisition of preformatives prior to speech. *Merrill–Palmer Quarterly*, **21**, 205–226.
- Call, J. & Tomasello, M. 1994. The production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, **108**, 307–317.
- Call, J. & Tomasello, M. 1999. A nonverbal theory of mind test. The performance of children and apes. *Child Development*, **70**, 381–395.
- Call, J., Hare, M. & Tomasello, M. 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition*, **1**, 89–99.
- Cheney, D., Seyfarth, R. & Smuts, B. 1986. Social relationships and social cognition in non-human primates. *Science*, **234**, 1361–1366.
- Dunbar, R. I. M. 1993. Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, **16**, 681–735.
- Emery, N. J. & Clayton, N. S. 2001. Effects of experience and social context on prospective caching strategies in scrub jays. *Nature*, **414**, 443–446.
- Emery, N. J., Lorincz, E. N., Perret, D. I., Oram, M. W. & Baker, C. I. 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, **111**, 286–293.
- Ferrari, P. F., Kohler, E., Fogassi, L. & Gallese, V. 2000. The ability to follow gaze and its emergence during development in macaque monkeys. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 13997–14002.
- Gallup, G. G. Jr 1982. Self-awareness and the emergence of mind in primates. *American Journal of Primatology*, **2**, 237–248.
- Gómez, J. C. 1996a. Non-human primate theories of (non-human primate) minds: some issues concerning the origins of mind-reading. In: *Theories of Theories of Mind* (Ed. by P. Carruthers & P. K. Smith), pp. 330–343. New York: Cambridge University Press.
- Gómez, J. C. 1996b. Ostensive behavior in great apes: the role of eye contact. In: *Reaching into Thought: the Minds of the Great Apes* (Ed. by A. E. Russon, K. A. Bard & S. T. Parker), pp. 131–151. New York: Cambridge University Press.
- Hare, B. & Tomasello, M. 1999. Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, **113**, 173–177.
- Hare, B., Call, J. & Tomasello, M. 1998. Communication of food location between human and dog (*Canis familiaris*). *Evolution of Communication*, **2**, 137–159.

- Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, **59**, 771–785.
- Hare, B., Call, J. & Tomasello, M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, **61**, 139–151.
- Humphrey, N. K. 1976. The social function of intellect. In: *Growing Points in Ethology* (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge: Cambridge University Press.
- Itakura, S. 1996. An exploratory study of gaze-monitoring in nonhuman primates. *Japanese Psychological Research*, **38**, 174–180.
- Jolly, A. 1966. Lemur social intelligence and primate intelligence. *Science*, **153**, 501–506.
- Karin-D'Arcy, M. R. & Povinelli, D. J. 2001. Do chimpanzees know what each other see? A closer look. *International Journal of Comparative Psychology*, **15**, 21–54.
- Krebs, J. R. & Dawkins, R. 1984. Animal signals: mindreading and manipulation. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Oxford: Blackwell Scientific.
- Leavens, D. A., Hopkins, W. D. & Bard, K. A. 1996. Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **110**, 346–353.
- Miklósi, A., Polgardi, R., Topal, J. & Csányi, V. 1998. Use of experimenter-given cues in dogs. *Animal Cognition*, **1**, 113–121.
- Moore, C. & D'Entremont, B. 2001. Developmental changes in pointing as a function of parent's attentional focus. *Journal of Cognition and Development*, **2**, 109–129.
- Povinelli, D. J. 1999. Social understanding in chimpanzees: new evidence from a longitudinal approach. In: *Developing Theories of Intention: Social Understanding and Self-control* (Ed. by P. Zelazo, J. Astington & D. Olson), pp. 195–225. Hillsdale, New Jersey: L. Erlbaum.
- Povinelli, D. J. 2001. The minds of humans and apes are different outcomes of an evolutionary experiment. In: *Carving Our Destiny: Scientific Research Faces a New Millennium* (Ed. by S. Fitzpatrick & J. Bruer), pp. 1–40. Washington, D.C.: National Academy of Sciences and Joseph Henry Press.
- Povinelli, D. J. & Eddy, T. J. 1996a. What chimpanzees know about seeing. Monographs of the Society for Research in Child Development. Vol. 61, No. 2, Serial No. 247.
- Povinelli, D. J. & Eddy, T. J. 1996b. Chimpanzees: joint visual attention. *Psychological Science*, **7**, 129–135.
- Povinelli, D. J. & Eddy, T. J. 1997. Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology*, **15**, 213–222.
- Povinelli, D. J., Parks, K. A. & Novak, M. A. 1992. Role reversal in rhesus monkeys, but no evidence of empathy. *Animal Behaviour*, **44**, 269–281.
- Povinelli, D. J., Reaux, J. E., Bierschwale, D. T., Allain, A. D. & Simon, B. B. 1997. Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cognitive Development*, **12**, 423–461.
- Povinelli, D. J., Bierschwale, D. T. & Čech, C. G. 1999. Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, **17**, 37–60.
- Povinelli, D. J., Dunphy-Lelii, S., Reaux, J. E. & Mazza, M. P. 2002a. Psychological diversity in chimpanzees and humans: new longitudinal assessments of chimpanzees' understanding of attention. *Brain, Behavior and Evolution*, **59**, 33–53.
- Povinelli, D. J., Bering, J. & Giambone, S. 2002b. Chimpanzee 'pointing': another error of the argument by analogy? In: *Pointing: Where Language, Culture and Cognition Meet* (Ed. by S. Kita), pp. 35–68. Hillsdale, New Jersey: L. Erlbaum.
- Reaux, J. E., Theall, L. A. & Povinelli, D. J. 1999. A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development*, **70**, 275–290.
- Soproni, K., Miklósi, Á., Topál, J. & Csányi, V. 2001. Comprehension of human communicative signs in pet dogs. *Journal of Comparative Psychology*, **115**, 122–126.
- Soproni, K., Miklósi, Á., Topál, J. & Csányi, V. 2002. Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, **116**, 27–34.
- Theall, L. A. & Povinelli, D. J. 1999. Do chimpanzees tailor their attention-getting behaviours to fit the attentional states of others? *Animal Cognition*, **2**, 207–214.
- Tomasello, M., Call, J., Nagell, K., Olguin, K. & Carpenter, M. 1994. The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates*, **35**, 137–154.
- Tomasello, M., Call, J. & Hare, B. 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, **55**, 1036–1069.
- Tomasello, M., Hare, B. & Agnetta, B. 1999. Chimpanzees (*Pan troglodytes*) follow gaze direction geometrically. *Animal Behaviour*, **58**, 769–777.
- Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G. & van der Elst, C. 2001. Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology*, **115**, 100–105.
- de Waal, F. 1982. *Chimpanzee Politics: Power and Sex Among Apes*. New York: Harper & Row.
- Whiten, A. 1996. When does smart behaviour-reading become mind-reading? In: *Theories of Theories of Mind* (Ed. by P. Carruthers & P. Smith), pp. 277–292. Cambridge: Cambridge University Press.
- Whiten, A. & Byrne, R. W. 1988. Tactical deception in primates. *Behavioral and Brain Sciences*, **11**, 233–244.