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## **Do Chimpanzees Know What Each Other See? A Closer Look**

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Hare et al. (2000) reported that when placed into competitive feeding situations chimpanzees exhibit evidence of reasoning about what each other can see. Subjects were reported to select food items that were hidden behind barriers and therefore were not visible to a rival chimpanzee. We report eight experiments that attempted to replicate these findings and test alternative interpretations of them. Although we robustly replicated the finding that subjects obtained more hidden than visible food items, we consistently did *not* replicate the more relevant result of subjects' food choice. Further studies revealed that even those subjects who showed a tendency to approach the hidden food first did not differentiate between barriers which did and did not obscure the rival's view. Overall, the results support the idea that although chimpanzees may use a variety of competitive strategies in such tests, no predictive power is added by postulating that they are reasoning about what each other can or cannot see.

Explorations of whether nonhuman species possess the ability to reason about unobservable mental states has gathered momentum in recent years. Several research laboratories have explored other species' abilities to understand false belief, attention, the perceptual sources of knowledge, the communicative intention underlying the gestural acts of pointing and looking, visual perspective-taking, and even the distinction between accidental and intentional actions (for reviews, Call & Tomasello, in press; Hare, 2001; Heyes, 1998; Povinelli & Giambone, 2000; Suddendorf & Whiten, 2001). To date, however, the results of these investigations have not definitively established whether the ability to reason about mental states is present in species other than our own.

An especially fruitful area of research into the question of theory of mind in other species has been the investigation of what they understand about "seeing" —the ability to explicitly represent the visual perceptual states of others. A wide array of nonhuman primates have been shown to engage in at least simple gaze-following (e.g., Anderson & Mitchell, 1999; Emery et al., 1997; Ferrari et al., 2000; Itakura, 1996; Lorincz et al., 1999; Povinelli & Eddy, 1996a, 1996b, 1997; Povinelli et al., 1999; Tomasello et al., 1998, 1999). Chimpanzees, in particular, have been shown to (a) follow the gaze of others by responding to their head and

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eye movements, as well as their eye movements alone, (b) engage in gaze-following to a high degree of spatial specificity both inside and outside their immediate visual field, and (c) respond appropriately when another's gaze is directed at a clear vs. opaque barrier. In addition to gaze-following, a sensitivity to the eyes in communicative contexts has been observationally and experimentally explored, suggesting that chimpanzees and gorillas, at least, are attracted to communicative interactions in which direct eye contact is established (e.g., de Waal, 1989; Gomez, 1991; Povinelli & Eddy, 1996c). Other researchers have explored the ability of nonhuman primates, canines, and even cetaceans to extract communicative information from the direction of gaze and/or the presence or absence of the eyes (e.g., Anderson et al., 1995, 1996; Call & Tomasello, 1994; Call et al., 1998; Hare & Tomasello, 1999; Miklósi et al., 1998; Povinelli et al., 1992; Povinelli & Eddy, 1996a; Povinelli et al., 1997, 1999; Reaux et al., 1999; Theall & Povinelli, 1999; Tschudin et al., 2001). Although some of this research is suggestive of the presence of an understanding of seeing in other species, much of it casts serious doubts on this conclusion (e.g., Reaux et al., 1999).

Hare et al. (2000) reported a series of experiments addressing the question of visual perspective taking in chimpanzees (i.e., reasoning about what another chimpanzee can and cannot see). Following dominance tests (used to determine which of each pair of chimpanzees had priority of access to food), the subordinate chimpanzees were individually paired in food competition as the subject with a dominant rival. In these visual perspective taking tests, one piece of food was in the open and visible to both participants, while the other was hidden behind a barrier and only visible to the subject. Because the subjects preferentially took the food items associated with the barrier, Hare et al. concluded that they were capable of, and engaging in, visual perspective taking in this context.

Hare et al. (2000) recorded two dependent measures: (a) *approach* (the first food item toward which the subject headed before the rival was released; e.g., hidden or visible), and (b) *retain* (the total number of food items obtained by the subject at the end of each trial; either 0, 1 or 2). Of these two measures, only the *approach* is potentially relevant to the question of whether the subject is reasoning about what the rival can or cannot see. This is because once the rival takes the visible food item and departs, the subject may then retain the hidden food item simply because it is the only one remaining. Therefore, the conclusions drawn by Hare and his colleagues regarding visual perspective taking must stand on the data concerning of the chimpanzees' *approaches* to the food.

However, the measures used by Hare et al. (2000) are open to closer scrutiny. It is to this end that we conducted the series of experiments reported here. In the Hare et al. studies, both the *approach* and *retain* measures were based on a posttrial consensus reached between the two experimenters, with no reliability checks due to the absence of video recordings or independent observations. For *approach*, the experimenters present at the time of the trial simply discussed and came to a consensus on which way the subjects appeared to be headed when they were about half way to the food and while the rival's door was slowly opening. Even if scoring was straightforward, as the authors suggest, this procedure does not allow for measurement of interobserver reliability in making the judgement. Furthermore, in conducting our own experiments, we found that our subjects often

walked directly over a food item, disregarding it entirely for the moment, as they moved toward their rival's door. It would be misleading to score these walkovers as approaches to one food item or the other, as they would be scored under Hare et al.'s methodology. Due to the possible ambiguity of an approach to a food item, we chose to use the behaviors of reaching for and touching the food as indicators of food choice.

The research we report in this article was conducted as a detailed examination of the methodology, findings, and interpretation of Hare et al. (2000). We had three specific objectives. First, we examined the appropriateness of the measures taken as evidence for visual perspective taking. Second, we tested the replicability of the results (Experiment 1-5). Third, we tested an alternative hypothesis for the food choice behavior of the subjects in this competitive context (Experiment 6-8). Our critical results come from Experiments 3, 6, and 8, and are supported by additional controls implemented in Experiments 4, 5, and 7.

### **Dominance Tests**

Following the original procedure of Hare et al. (2000), all possible pairwise combinations of our chimpanzees were tested in one-on-one dominance tests. The logic of the dominance tests was to determine which of each pair of chimpanzees has priority of access to food in a paired food competition. Six dominance tests were conducted over the course of the study. The first dominance test was conducted prior to the pilot experiment (see below) and the final one prior to the last experiment.

In each pairwise competition, the chimpanzee failing to obtain the food was designated as the subject of the pair during the following experiments, while the winner of the food competition was designated as the rival. The competition losers would presumably be motivated to utilize more sophisticated social foraging strategies than would the winners who can rely on their social status or simple intimidation to obtain food.

### ***Method***

***Subjects.*** The subjects were seven adult chimpanzees (one male, six females) who ranged in age from 11 years, 0 months (11;0) to 11;11 at the beginning of these studies and 12;5 to 13;4 at the end of the entire series. The chimpanzees had been housed together since their infancy at the University of Louisiana at Lafayette, and had participated in numerous studies over an eleven-year period as a part of a longitudinal project exploring their cognitive abilities (see Povinelli, 2000, for details of rearing, housing, husbandry, and experimental history).

***Procedure.*** Dominance tests were conducted in the chimpanzees' living compound consisting of a series of adjoining interior and exterior enclosures. All seven subjects were first familiarized with the procedure of retrieving a food reward from a central exterior enclosure (the testing arena) after having been transferred from one of two adjoining enclosures.

To test each pair, the two chimpanzees were ushered into separate waiting areas on either side of the testing arena. With the animals behind their respective opaque shuttle doors, the experimenter entered the testing arena and placed one-half banana or apple on the floor at a point equidistant between the two doors. The experimenter then exited the testing arena. The doors were opened slightly (approximately 8-10 cm), allowing both animals to look into the testing arena and see the food and each other. Next, both of the doors were opened simultaneously, allowing the competitors to enter the testing arena. Each pair was tested four times. Placement of individual subjects into each waiting area followed a randomized and counterbalanced schedule. In these tests as

well as in each of the following experiments, subject-rival pairs were run in a random order. As a consequence, intertrial interval was not controlled. However, all pairs were run in each testing session. For the dominance tests, each ape was paired with each of the others (6 pairs) in random order during the course of each session. All trials were recorded on videotape.

Dominance testing was repeated through the course of these studies whenever there was indication that there might have been some changes in the group's relationships or if several weeks had passed since the last test, for a total of 6 dominance tests. All tests were conducted between experiments. The procedure was the same for each test except that the apes watched the actual baiting process through viewing slots in the doors or through transparent doors in tests 2-6, depending on the doors used for the experiments that followed (see Experiment 4-7). Thus, after Test 1, the doors were not partially opened before the chimpanzees were able to enter the testing arena, as they had visual access with the doors closed.

Following Hare et al., the dominance tests were scored by recording during live observation (a) which ape first touched the food and (b) which ape gained final possession of the food. A pair was determined to be eligible for the experiments if one member of the pair obtained the food reward on 75% or more of the trials.

### ***Results and Discussion***

Table 1 shows the results for all six dominance tests. Out of the 21 pairs, 14 showed a consistent relationship across all six tests. Following Hare et al., all pairs in which one chimpanzee obtained the food reward on at least 75% of the trials were used for each of the experiments that followed. This resulted in a variable number of pairs across the experiments, ranging from 18 to 20 pairs.

Hare et al. (2000) had access to 10 chimpanzees, nine of which qualified as subjects for the experiments following dominance testing, resulting in 27 pairs of chimpanzees when all pairs are used. Under their method, no subject was paired with the same set of rivals and the number of pairs (and hence also the number of trials) in which each subject was involved varied substantially (range = 1–6 pairs). This design poses both analytic and conceptual problems for collapsing the data for each subject. In planning our replications, we chose to conduct our studies using the Hare et al. method, despite problems with its statistical design. This would give our chimpanzees similar experience as theirs and would increase our chances of replicating the effects they reported.

For data analysis, we used a parametric approach (analysis of variance, ANOVA, and t-tests) to provide the greatest likelihood of findings effects and hence avoiding Type II errors (i.e., to avoid biasing us against replicating the Hare et al. findings). Although Hare et al. used nonparametric tests, which make fewer assumptions about the data, the typical objection to the use of parametric tests with such data sets concerns the normality assumption. ANOVAs, however, have repeatedly been shown to be robust with respect to such violations. In all the statistics reported in this paper, alpha was set at the 0.05 level.

### **Experiment 1: Pilot Test**

As noted by Hare et al. (2000), the first three experiments they reported did not provide strong tests of the visual perspective taking hypothesis. Nonetheless, Experiments 1 and 2 reported here were conducted to provide our apes with experiences as similar as possible to those of the chimpanzees used in the studies by Hare et al. As these experiments are not of central importance to this research program, they are described only in brief.

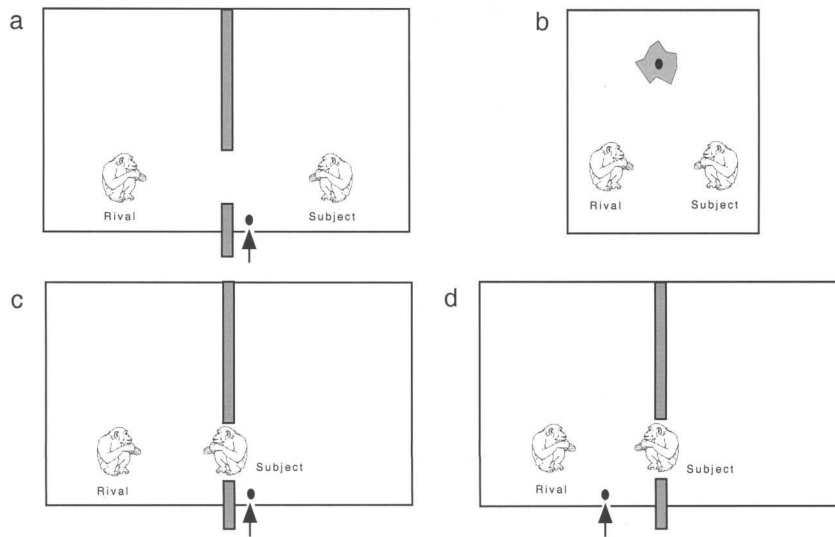
Table 1  
Results of Dominance Tests by Pairs of Subjects.

Pair	Test Number and Unanimous Winner (or % trials won)					
	1 n=4	2 n=4	3 n=8	4 n=4	5 n=4	6 n=4
Apo-Kar	Apo(75)	Apo	Apo	Apo(75)	Apo	Apo
Apo-Can	Apo	Apo	Apo	Apo	Apo	Apo
Apo-Jad	Apo	Apo	Apo	Apo	Apo	Apo
Apo-Bra	Apo	Apo	Apo	Apo	Apo	Apo
Apo-Meg	Apo	Apo	Apo	Apo	Apo	Apo
Apo-Min	Apo	Apo	Apo	Apo	Apo	Apo
Kar-Can	Kar	x	Can	Kar	Kar(75)	Kar
Kar-Jad	x	Kar	x	Kar	x	Jad
Kar-Bra	Kar	Kar(75)	Kar	Kar	Kar	Kar
Kar-Meg	Kar	Kar	Kar	Kar	Kar	Kar
Kar-Min	x	x	Min	x	Min	Min
Can-Jad	Jad	Can(75)	Jad	Jad	Jad	Jad
Can-Bra	Can	Can	Can	Can	Can	Can
Can-Meg	Can	Can	Can	Can	Can	Can
Can-Min	Min	Min(75)	Min(88)	Min	Min	Min
Jad-Bra	Jad	x	Jad	Jad	Jad	Jad
Jad-Meg	Jad	Jad(75)	Jad	Jad	Jad	Jad
Jad-Min	x	Min(75)	Jad(75)	Min	Min	Min
Bra-Meg	Bra(75)	Bra	Bra	Bra	Bra(75)	Bra
Bra-Min	Min(75)	Bra	x	Min(75)	Min	Min
Meg-Min	Min	Min	Min	Min	Min	Min

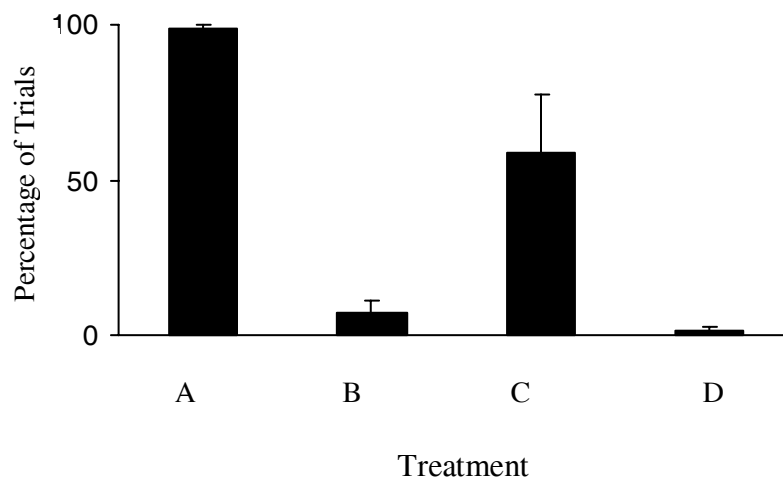
*Note.* All dominants won 100% of trials unless otherwise noted. x = no clear dominance (50% of trials won by each animal).

## Method

Experiment 1 involved competition between two chimpanzees for one large piece of food (a whole apple or banana) placed so that it is more accessible by one chimpanzee or the other. Subjects were paired with rivals based on the competitive dominance relationships established in Dominance Test 1 (Table 1), resulting in 18 pairs for testing. Each pair was tested in two adjacent exterior enclosures with the door between them open. Following Hare et al., the four conditions illustrated in Figure 1 were administered, with each pair receiving two trials per condition. Also after Hare et al., the following data were collected at the time of the trial: (a) which ape first touched the food, and (b) which ape gained final possession of the food.



**Figure 1.** Testing conditions (a-d) used in Experiment 1, showing enclosure layout, starting position of subject and rival, and placement of food. Food is represented by filled oval and arrows show where food was introduced into the enclosures. In condition b, food is on top of the cage.



**Figure 2.** Mean percentage of trials ( $\pm$  SEM) on which subjects obtained the food item as a function of conditions a-d in Experiment 1.

## ***Results and Discussion***

A percentage success score was calculated for the six subjects across each of their pairings, and these were then averaged to obtain the mean percentage of trials on which each subject obtained the food item as a function of the condition (Figure 2). The main data were analyzed using a one-way repeated measures ANOVA. The results indicated a significant effect of condition,  $F(3,15) = 24.46$ ,  $p < 0.0001$ . A Turkey-Kramer multiple comparisons test indicated that all pairwise comparisons among conditions were significantly different from one another ( $p < 0.05$  or smaller), except B vs. D. This corroborates the effects reported by Hare et al. (2000) in which the subjects obtained more food in conditions A and C (in which the food was closer to and visible only to the subject) than in conditions B and D (in which food was visible to and equidistant from both chimpanzees). Indeed, the effect appears to have been at least as strong as that reported by Hare et al. As Hare et al. (2000) acknowledged, whether this result is relevant to visual perspective taking is difficult to know given that the food was both visibly *and* physically more accessible to the subjects in Conditions A and C than it was in B and D.

### **Experiment 2: Wall Test**

Following Hare et al., Experiment 2 tested the subjects to determine if they would prefer an item that was hidden from the rival's view vs. an item that was not. This experiment, while maintaining an equal distance between the two chimpanzees and the food for which they were competing, is subject to the same ambiguities as Experiment 1 regarding visual perspective taking because of differences in physical accessibility as well as visibility of the food. Nonetheless, we maintained the research schedule used by Hare et al. in our attempt to replicate their pattern of results.

## ***Method***

***Subjects and Procedure.*** Each of the 18 subject-rival pairs established in Dominance Test 1 was tested in a series of four of the exterior enclosures (Figure 3a-c). Exterior enclosures 1 and 4 were waiting areas for the two participants. Enclosures 2 and 3 were designated as either the subject's enclosure or the rival's enclosure, depending on which ape was assigned to the adjacent waiting area on each trial (these designations were randomized and counterbalanced across the subjects). The shuttle door connecting enclosures 2 and 3 remained open at all times. Two banana or apple halves were used as the food items. Following Hare et al., the following three conditions were administered twice per subject-rival pair. The trials were administered randomly within the constraint that each pair received one trial of each type before being administered a second trial, and so on.

***Rival-Door:*** One piece of fruit was placed on the doorway ledge connecting enclosures 2 and 3 and was visible to both chimpanzees. The other piece of fruit was placed 50 cm from the first one, against the wall in the rival's enclosure such that the subject could not see it (Figure 3a).

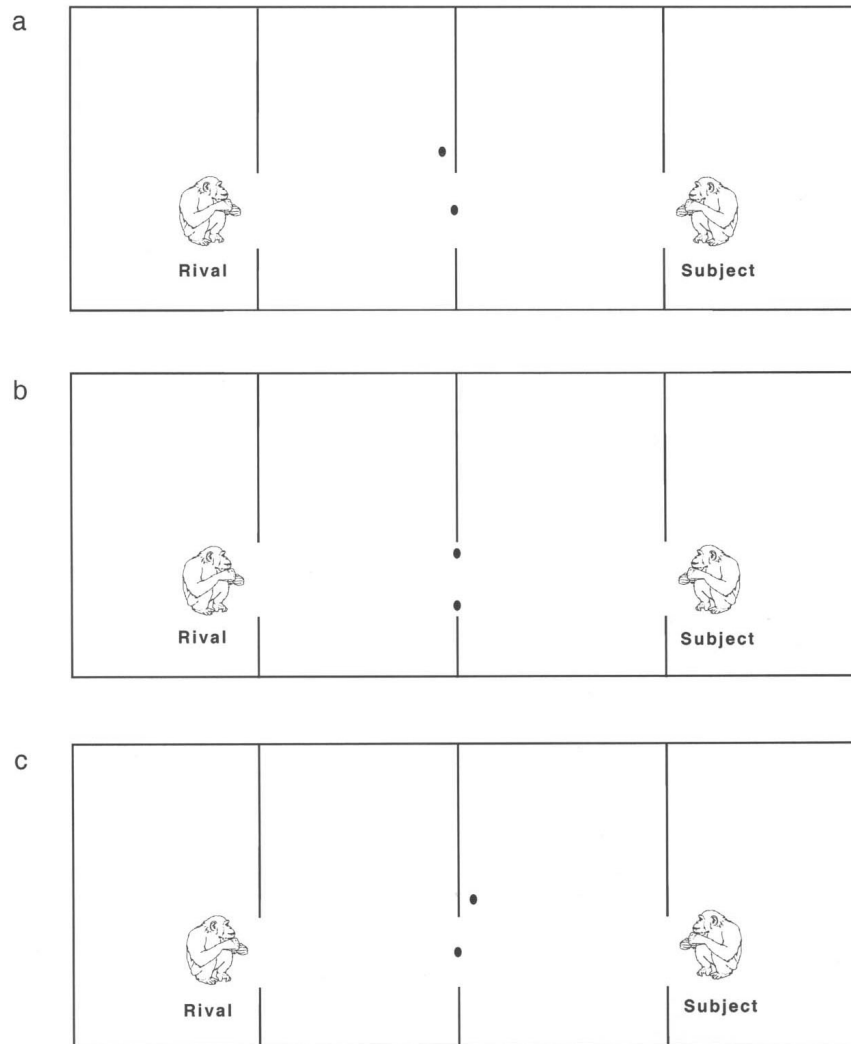
***Door-Door:*** Both pieces of fruit were placed 50 cm apart on the doorway ledge connecting enclosures 2 and 3 so that they were visible to both of the chimpanzees (Figure 3b).

***Subject-Door:*** One piece of fruit was placed on the doorway ledge connecting enclosures 2 and 3 so that both chimpanzees could see it, while the second one was placed 50 cm away in the subject's enclosure, close to the wall separating the enclosures so that the rival chimpanzee could not see it (Figure 3c).

After the experimenter baited both locations on each trial, the shuttle doors between the waiting areas and the test enclosures were raised 15 cm for approximately 5 s while both chimpanzees looked through into the test enclosures. Both doors were then simultaneously opened.



**Scoring and Reliability.** Scoring consisted of recording (at the time of the trial) the first piece of food that the subject touched and which food item (if any) the subject was able to retain at the end of the trial. All trials were also videotaped, focusing on the subject's behavior. For purposes of establishing observer reliability, a separate rater coded each trial from videotape, recording which ape touched each food item first. Given the size and geometry of the testing enclosure, the data on retention could not be coded from video. Two trials were inadvertently not fully recorded on video. The rater agreed with the first touch data for each of the two food items that was collected at the time of trial on 95% (202/212) of the data points (Cohen's Kappa,  $\kappa = 0.87$ ).

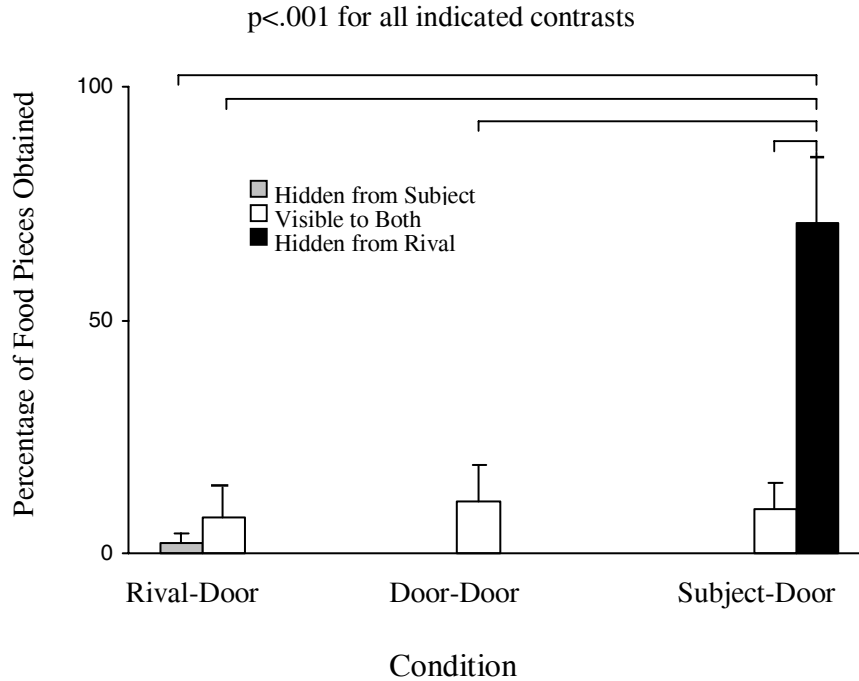


*Figure 3.* Testing conditions used in Experiment 2, showing enclosure layout, starting position of subject and rival, and placement of food.

### ***Results and Discussion***

Replicating the effects of Hare et al. (2000), subjects retrieved food that was hidden from the rival significantly more than food visible to the rival in all three conditions. We used a repeated measures ANOVA to compare the mean percentage of trials on which the subject obtained the hidden vs. the visible food

items as reflected in the condition subtypes. The results are depicted in Figure 4. An overall effect is present,  $F(4,20) = 14.09$ ,  $p < 0.001$ . Tukey-Kramer posttests indicated that the subjects obtained significantly more pieces of food that were hidden from the rivals than ones that were visible (see the contrasts depicted in Figure 4). These results are nearly identical to those reported by Hare et al. (see their Figure 2).



**Figure 4.** Mean percentage of trials ( $\pm$  SEM) in Experiment 2 in which subjects obtained food items as a function of their visibility to the rival.

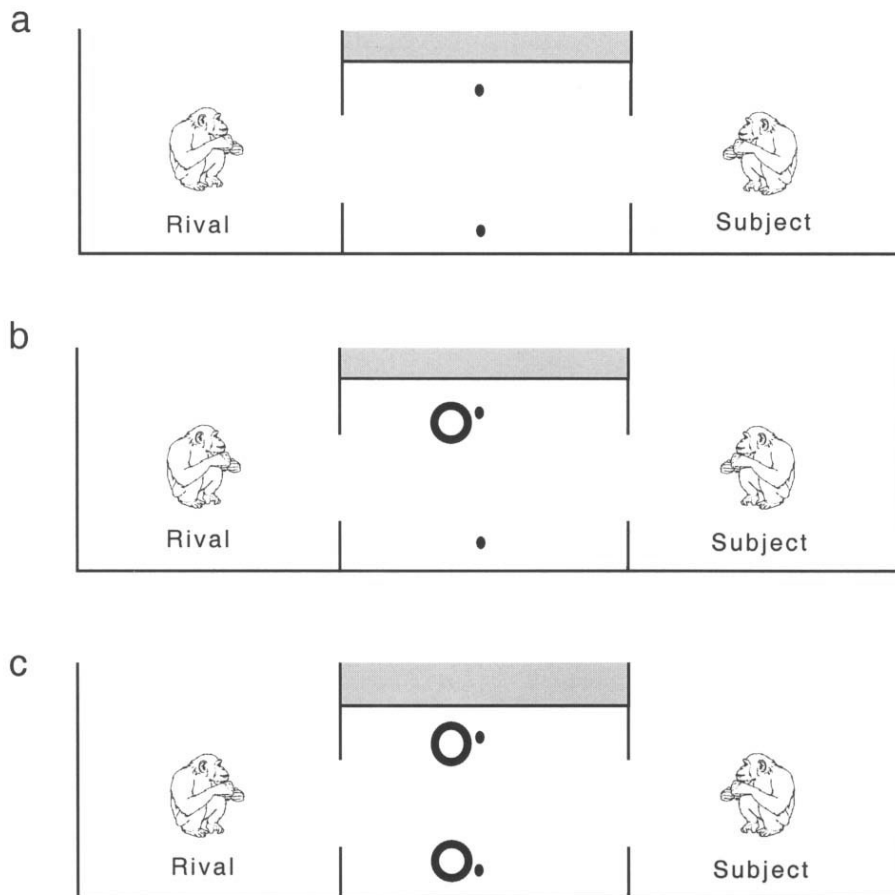
The results from the subject-door condition could be taken as evidence that the subjects understood what the rival could and could not see. There are, however, other possible interpretations (some of which are noted by Hare et al.): (a) the subject may understand that the wall temporarily blocks the rival ape's physical access to the food in her enclosure, (b) the subject may be drawn to the food along the wall in her enclosure to escape visual access to the rival (thereby reducing direct competition), (c) the subject may seek to avoid the rival during foraging, retrieving any food left behind by the rival after he or she moves away, or (d) some combination of each of these factors. Thus, although in this particular test the subjects did exhibit a greater likelihood of obtaining food that was not visible to the rivals, such results cannot distinguish among the alternative interpretations just described.

### ***Experiment 3: Barrier Test***

In order to provide a more direct test of the visual perspective taking hypothesis, Hare et al. (2000) conducted a test in which two food items were placed in an enclosure between the subject and rival. One piece of food was hidden

behind an opaque barrier so that only the subject could see it, while the other one was placed out in the open. Both pieces were equidistant from the two chimpanzees. The subject was given a slight head start into the testing arena. Hare et al. report that the subject was both more likely to first approach the food hidden from the rival and more likely to retain hidden food items by the end of the trial. Experiment 3 attempted to replicate both of these effects.

[Prior to conducting the barrier test, Hare et al. (2000) conducted an experiment involving a tire in which one piece of food was set on top of the tire (visible to both subject and rival) and another piece was hidden inside the tire (an act seen only by the subject). In attempting to replicate this experiment we encountered insurmountable procedural difficulties in following the published method. Testing was therefore halted after 3 trials. Correspondence with the senior author of the original study revealed that they encountered similar problems that were solved by an unmentioned procedural change involving hiding the banana under the tire (Brian Hare, personal communication, 7 May 2001). Given the fact that the later barrier tests were designed to reveal the same effects, the replication of the tire test was abandoned.]



**Figure 5.** Testing conditions used in Experiment 3: (a) visible-visible, (b) hidden-visible, and (c) hidden-hidden.

## **Method**

**Subjects.** The chimpanzees ranged in age from 11;6 to 12;5 at the time of this experiment. Two dominance tests were conducted between the end of Experiment 2 and the beginning of Experiment 3. Because the dominance results for two of the pairs were ambiguous (see Tests 2 and 3, Table 1), 19 of the 21 possible pairs were used in this experiment.

**Materials.** In preparation for this experiment, a wall was constructed 1.8 m from the front of the test enclosure. This created a testing arena in which the doors were centered and therefore the distance from each food item to the adjacent wall could be equalized (see Figure 5). This testing arena was 2.6 x 1.8 m (a testing environment similar to but slightly smaller than the 3 x 3 m testing arena used by Hare et al.). The smaller arena was necessitated by the fixed location of the shuttle doors. Prior to the construction of the wall, each subject-rival pair received 2 trials without the wall. However, the preexisting alignment of the doors meant that when the subjects entered the testing arena there was more space on one side than the other and the subjects virtually always headed in that direction because it allowed them to position themselves as far away as possible from where the rival would enter. The wall eliminated this problem. Although the apes had continuous access to similar objects, pieces of the specific PVC pipes that were used as barriers were placed in the animals' main compound for several days prior to testing.

**Procedure.** Enclosures 3 and 5 were waiting areas for the subject and rival. Enclosure 4 was the testing arena. Two pieces of PVC pipe of the same size as that reported by Hare et al. (20 x 25.4 cm) were used as visual barriers. The PVC pieces were positioned on their ends. Food items were half of an apple or banana. The following three conditions from Hare et al. were used.

**Visible-Visible:** No barriers were present. Both pieces of fruit were placed on the floor 1.25 m apart and 1.42 m from both shuttle doors so that they could be seen by both apes (Figure 5a).

**Hidden-Visible:** The pieces of food were placed as in the previous condition, with a barrier positioned so that the subject, but not the rival could see one food item while the other was visible to both (Figure 5b).

**Hidden-Hidden:** Two barriers were used so that both pieces of fruit were occluded from the rival's view while in their standard position on the floor (Figure 5c).

On each trial, the subject observed the experimenter's placement of the food items and barrier(s) through a viewing window cut into each shuttle door. The rival's viewing window was opened after the placement of the food was complete. These windows were used as an alternative to the procedure of partially opening the shuttle doors in order to reduce attempts by the rivals to intimidate the subjects through the partially opened door (a behavior that we witnessed repeatedly in Experiment 2). The windows provided both animals with a clear view of the entire testing arena and the other chimpanzee.

After setting up the food items and the barriers, and with both chimpanzees ready at their shuttle doors, an experimenter opened the subject's door. Once the subject reached for one of the food items, the other experimenter opened the rival's door. If the subject did not enter the arena or clearly reach for one of the food items after 5 s, she was vocally, but not gesturally, encouraged by one of the experimenters from where he stood at the door control mechanism. After 20 s, a "no-response" was scored and the rival's door was opened.

Following Hare et al., each subject-rival pair received two trials of the visible-visible and hidden-hidden condition and 4 trials of the critical hidden-visible condition. The order in which the pairs received trials was randomized within the constraint that all pairs were administered one trial before any pair was administered its second, and so on. The presentation order of the conditions was randomized within each pair. The waiting area assignments were balanced for each animal in both subject and rival roles across pairings, and then alternated each time a pair was given a trial. The left/right position of the barrier in the hidden-visible condition was also randomized and counterbalanced for each subject-rival pair. The behavior of the subject in the testing arena was videotaped on all trials.

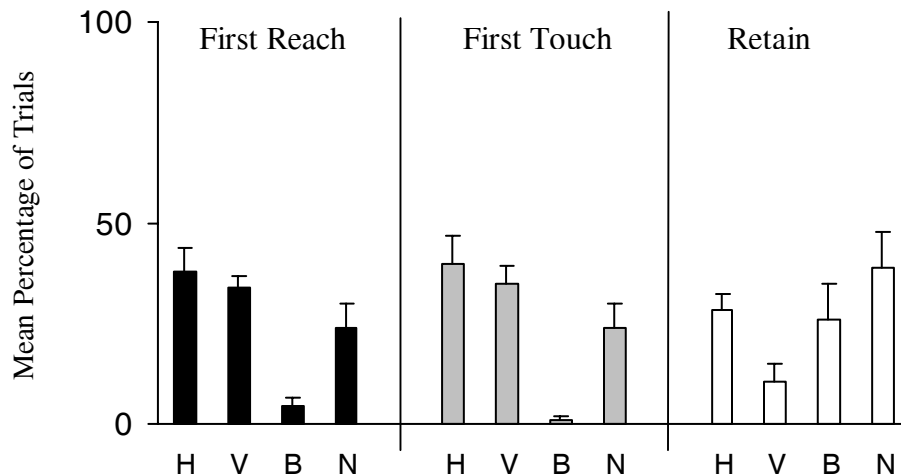
**Scoring and Reliability.** The following data were recorded from overhead by an observer during each trial: (a) the food item the subject reached for first, (b) the food item the subject touched

first, and (c) whether the subject retained and ate any food items, and if so, which one(s). An independent observer scored the subjects' first reaches from the video recordings in order to assess the reliability of the live observations. Interrater agreement was 93.4% for the 152 trials that were coded (Cohen's Kappa,  $\kappa = 0.90$ ). Disagreements between the original data and coding from video were resolved by reobserving and discussing the relevant trials. Consensus was reached easily in all cases.

We used *first reach* and *first touch* as measures of the subjects' choice of food items. We did not use the *approach* measure employed by Hare et al. (2000) due to the ambiguity of approaches. Further, the first food touched by a subject is a much better indication of which item she intended to retrieve. In addition to the first food item touched, we scored the first reach toward a food item because the touch was not consistently observable on the video recordings of the experiments due to the positioning of the camera and barriers. The data for first reaches and first touches were virtually the same throughout all the experiments. Although the food retained is unimportant in assessing food-choice strategies in feeding competitions, we nonetheless recorded it in order to compare our results to those reported by Hare et al. (2000).

### Results and Discussion

In order to test the original prediction of the visual perspective taking hypothesis that there should be a significant bias toward the hidden food item in the crucial hidden-visible condition, we separately analyzed the subjects' preferences for the hidden food as reflected by first reach, first touch, and food retained. Figure 6 presents the mean percentage of trials for each measure in the hidden-visible condition, and the percentage of trials in which the subjects showed no preference by responding toward both food items simultaneously or by not responding at all. Thus, these analyses were restricted to the trials in which the subjects exhibited a discrete first reach or first touch to one food item, and retained only one item.



**Figure 6.** Mean percentage of trials ( $\pm$  SEM) for Experiment 3 in which subjects exhibited the various response categories (hidden food, visible food, both, and neither) for (a) their first reaches, (b) their first touches, and (c) their retentions by the end of the trial. (hidden food, H; visible food, V; both, B; neither, N).

In the critical hidden-visible condition, if the subjects retained only one of the pieces of food by the end of a trial, it was more likely to be the hidden than the

visible one (see Figure 6, Retain). However, this pattern was not present in the first reach or first touch data sets. For the three data sets, separate one-sample *t*-tests (two-tailed, hypothetical mean = 50%) were used to determine if the subjects showed bias toward the hidden food item. The results reveal that the subjects were significantly biased in retaining the hidden food item,  $t(5) = 3.80, p < 0.02$ , but not in first reaching for or first touching it,  $t(5) < 1, p > 0.78$ , in both cases. Thus, although the subjects retained more hidden than visible food by the end of the trial, this was not due to an initial preference for the hidden food. Rather, it was because the rival typically took the one in the open first (whether the subject tried to reach for it or not), leaving only the hidden one. The discrepancy between our measures emphasizes the inappropriateness of using the retrieval measure as an index of subject preference.

Although the data from the 19 pairs are not necessarily independent of each other, we informally analyzed these data to determine if there were more pairs in which the subject seemed to prefer the hidden over the visible food in the hidden-visible condition. For this analysis, we simply classified each pair as being biased toward the hidden, visible, or neither food item (using the first reach data set from the hidden-visible condition). We found no evidence to support a preference for the hidden food. If anything, the opposite trend was observed. Of the 11 pairs in which the subject was biased toward one or the other food item, 8 were biased to the visible food and only 4 were biased toward the hidden food (Table 2). In addition, we also examined the data for the individual subjects in terms of how many exhibited a greater number of first reaches toward hidden food than visible food (pooled across all pairs in which each individual subject participated). Three subjects showed a bias for the hidden food and 3 showed a bias for the visible food (Table 2).

These results replicate part of what Hare et al. report. In particular, our subjects retained more hidden than visible food items in the hidden-visible condition. More importantly, our results do *not* replicate the finding central to the visual perspective taking hypothesis: our subjects showed no initial preference for the hidden food. However, a post hoc analysis of response rates in the three conditions did reveal some effect. Generally, the greater the number food items that were hidden, the more likely the subjects were to initiate a first reach before the rival entered (regardless of whether the item they reached for was hidden or not). The subjects' response rates (SD) were 65.8% (0.4), 73.7% (0.4), and 76.3% (0.4) in the visible-visible (38 trials), hidden-visible (76 trials), and hidden-hidden (38 trials) conditions, respectively. This is the same pattern reported by Hare et al. However, although Hare et al. interpreted this finding as consistent with the visual perspective taking hypothesis, it is equally consistent with other hypotheses (e.g., the peripheral feeding hypothesis, see Experiment 6-8).

Table 2  
*Number of Pairs in which Subject Exhibited First Reach Preference for Hidden, Visible or Neither Food Item and Number of Subjects with Such Preferences (Experiment 3–5).*

	No. of pairs			No. of subjects		
	Hidden	Visible	Neither	Hidden	Visible	Neither
Experiment 3	4	8	7	3	3	0
Experiment 4	6	3	10	3	1	2
Experiment 5	6	5	8	2	2	2

One possibly important difference between our procedure and that used by Hare et al. is that the distance between the food items differed due to incorrect information in a preprint version of the first study provided to us by the authors prior to its publication. The food items in this and the following experiments were closer together than in Hare et al.'s studies, and could not be corrected given the constraints of our testing arena. With the food items 1.25 m apart, our subjects occasionally (although only rarely) reached for both rewards at the same time (see first reach data, Figure 6), whereas in the Hare et al. study, the subjects always had to move toward one side of the enclosure or the other in order to reach a food item. It is unclear whether any of these differences account for the disparate findings for initial choice between our study and that of Hare et al. It should be noted, however, that any such differences did not affect the pattern of the retention data, as this effect was robustly replicated. Further, the exact distance between the food items did not seem to be a critical variable, as their apes repeatedly exhibited the same effects when the food was only 50 cm apart (see, for example, their Experiment 2).

An unanticipated aspect of the rivals' behavior became apparent as the experiment progressed. In both the hidden-visible and hidden-hidden conditions, when the rivals were released, they increasingly proceeded to immediately look behind the barriers, suggesting that they had learned that there was always food there. We found through communication with the first author of Hare et al. (October 2000 by telephone) that they encountered this difficulty as well.

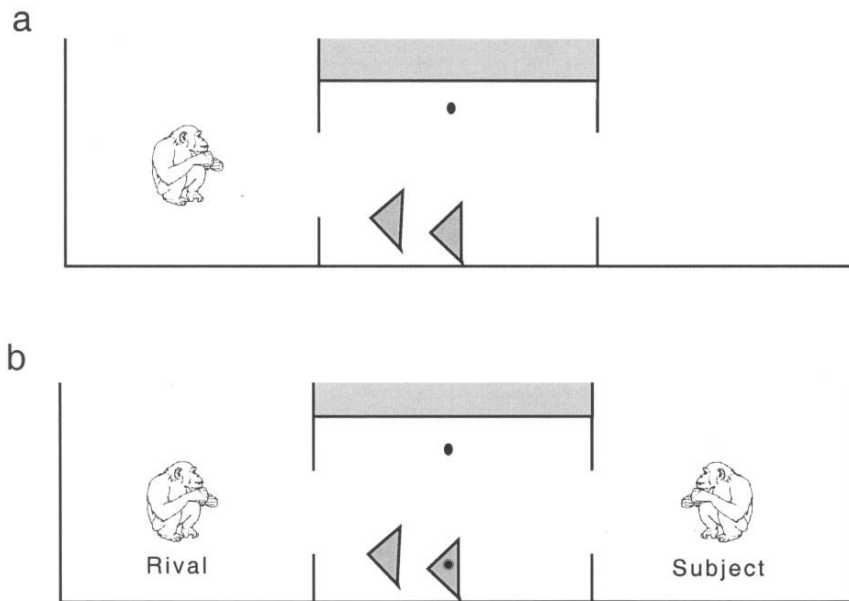
#### **Experiment 4: First Revised Barrier Test**

Experiments 4 and 5 were designed to control for potentially important variables in a further attempt to replicate the results of Hare et al. (2000) before moving on to testing alternatives to the visual perspective taking hypothesis.

#### ***Method***

Experiment 4 had two main purposes. First, we improved the design of the barrier to offer a better impression of the food item being hidden from the rivals' view, and also to minimize the likelihood that the rivals would accidentally notice the hidden piece of food if they retrieved the visible food item. The new barriers were of triangular shape with two sides and a top. Second, we sought to combat the problem that the rivals appeared to be learning that two food items were always present, even in trials with barriers. This was accomplished with an extinction phase during which there was never food behind the barriers, followed by a certain percentage of such trials during the testing phase of the experiment.

***Extinction Phase.*** The purpose of the extinction phase was to diminish the rivals' behavior of looking behind the barriers. All seven chimpanzees were tested individually (without a rival partner). A trial was prepared by placing a food item in one of two locations on the floor of the testing arena, as in Experiment 3. A barrier was placed to conceal the other location from the chimpanzee, although no food item was actually placed at that location. A second barrier was placed approximately 50 cm in front of and slightly offset from the first (see Figure 7a). The left/right positions of the food and barriers were counterbalanced for each chimpanzee. The window in the shuttle door was closed as the trial was prepared. The trial began by opening the chimpanzee's door, thereby giving the subject access to the testing arena (from the perspective of the rival in later competitive trials). In order for the chimpanzees to proceed to testing, we required them to meet a criterion of moving directly to the visible food item before checking for food behind either of the barriers on 10/12 trials across two consecutive 6-trial sessions, with a minimum of 4 sessions. All 7 chimpanzees met the extinction phase criterion in the minimum of 4 sessions.



**Figure 7.** Testing arena arrangements in Experiment 4: (a) Extinction Phase Trial and (b) Test Trial.

**Testing Phase.** In the testing phase, each of the 19 subject-rival pairs received 4 trials of each of two trial types, administered in random order with no more than one trial per day for each subject-rival pair. *Test trials* were identical to the hidden-visible trials in Experiment 3 in that one piece of food was in the open and one was hidden by a barrier; the only difference was that a distracter barrier was also present, as in the extinction phase of this experiment (see Figure 7b). *Maintenance trials* were identical to the test trials, except that only the piece of food in the open was present. The purpose of the maintenance trials was to continue to diminish the rivals' expectation that there was always food behind the barrier. Both trial types followed the same general procedures as Experiment 3. All trials were videotaped.

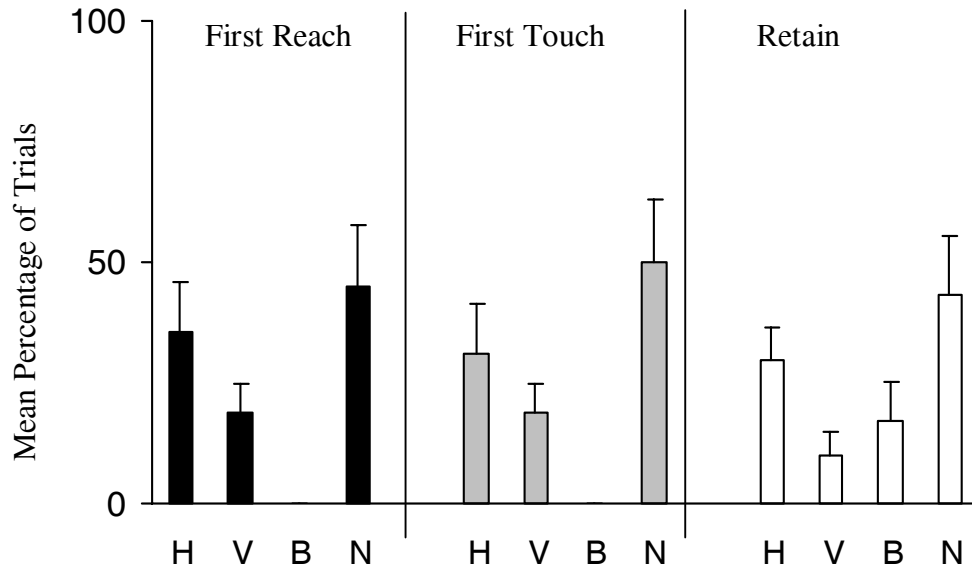
Data were collected during the testing phase just as in Experiment 3, and subjects' first reach was coded from video for reliability testing. The rater agreed with the data that had been recorded at the time of the trial on 96% (146/152) of the trials (Cohen's  $\kappa = 0.94$ ). The six cases of disagreement were reviewed, and consensus was easily reached in each case.

### **Results and Discussion**

Figure 8 displays the first reach, first touch, and retention data for the testing phase of Experiment 4, showing both the trials on which the subjects exhibited a discrete choice for the hidden or visible food item, and the trials on which they reached for both food items simultaneously, or for neither item. We structured and analyzed the data as in Experiment 3, focusing on just those trials in which the subjects exhibited a discrete response for the hidden or visible food items in each of the three data sets (first reach, first touch, retain). The data for one subject (Jadine) were not used because she failed to respond on all trials (notably because she was only paired with the dominant male, Apollo). One-sample *t*-tests indicated a marginally significant bias for retaining the hidden food item,  $t(4) = 2.70$ ,  $p = 0.054$ ,



but no such effects for the first reach or first touch data sets. However, the trends in the direction of a bias for reaching and touching the hidden food first were stronger in this experiment than in Experiment 3 (see Figure 8a-c), possibly indicating that our procedural change had an effect.



**Figure 8.** Mean percentage of trials ( $\pm$  SEM) for Experiment 4 in which subjects exhibited the various response categories (hidden food, visible food, both, and neither) for (a) their first reaches, (b) their first touches, and (c) their retentions by the end of the trial. (hidden food, H; visible food, V; both, B; neither, N).

As in the previous experiment, we also informally examined the total number of pairs in which the subjects exhibited a greater number of reaches toward either the hidden or visible food, as well as the number of individual subjects who exhibited these biases (see Table 2). An inspection of these data provide limited evidence that some of the subjects (or at least some of the subjects in some of their pairings) may have shown a bias for the hidden food in their first reaches.

The mean percentage of trials on which the subjects responded before the rival was released into the testing arena was 49% and 54.9% for the maintenance and test trials, respectively – considerably lower than in Experiment 3. The range of no-responses varied widely across individual subjects, from Mindy, who exhibited a no response on 18.8% of her trials, to Jadine, who never responded before Apollo entered the testing arena.

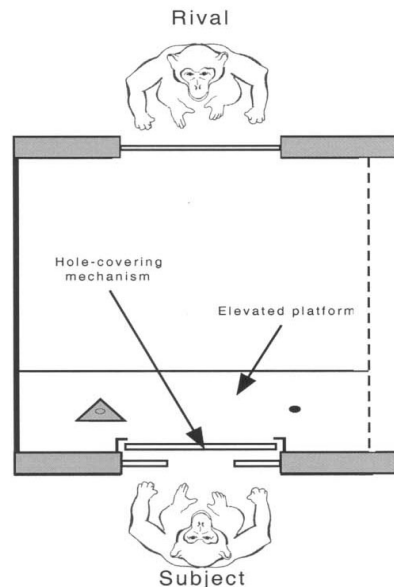
In summary, the results of Experiment 4 again replicated Hare et al.’s finding that by the end of the trial the subjects were more likely to retain the hidden than the visible food. Equally important, however, this experiment again failed to replicate the finding relevant to the visual perspective taking hypothesis that the subjects chose the hidden food first, although there were some trends in the data in this direction.

### Experiment 5: Second Revised Barrier Test

The percentages of trials in which the subjects did not make a response in Experiment 3 and 4 were fairly high and ranged widely, depending on the experiment and subject. Informal observations suggested that the subjects' unwillingness to respond reflected their relative fear of retaliation by the rival chimpanzee. In Experiment 5, we attempted to reduce the no-response rate by reducing the subjects' fear of retaliation, while at the same time maintaining the competitive pressure of the previous experiments. This was accomplished by placing a physical barrier between the subject and rival for the duration of each experimental trial.

#### *Method*

For Experiment 5, both of the opaque shuttle doors controlling the animals' access to the testing area were replaced by new doors made of transparent Plexiglas. A large, rectangular hole (41 x 12 cm) was cut into the bottom of the subjects' door through which they could reach. The hole was fitted with a transparent cover that was opened manually by an experimenter standing outside the enclosure. The placement of the food items and barrier were as in Experiment 3, except the food items were on a platform, closer together, and closer to the subject's door so that they could be reached through the hole in the door (see Figure 9). All of the chimpanzees were familiarized with the new testing apparatus before beginning this experiment. Once the testing arena was prepared for the trial and both chimpanzees were ready at their doors, the response-hole cover was raised and the subject was allowed to reach for a food item. As soon as the subject picked up one of the food items, the rival's door was opened. The subjects were allowed up to 5 min to respond. Four sessions were administered, with each of the 19 pairs (Table 1, Test 3) receiving one trial per session. Pair order was randomized for each session. The left/right position of the barrier was counterbalanced and randomized for each pair across the four sessions.

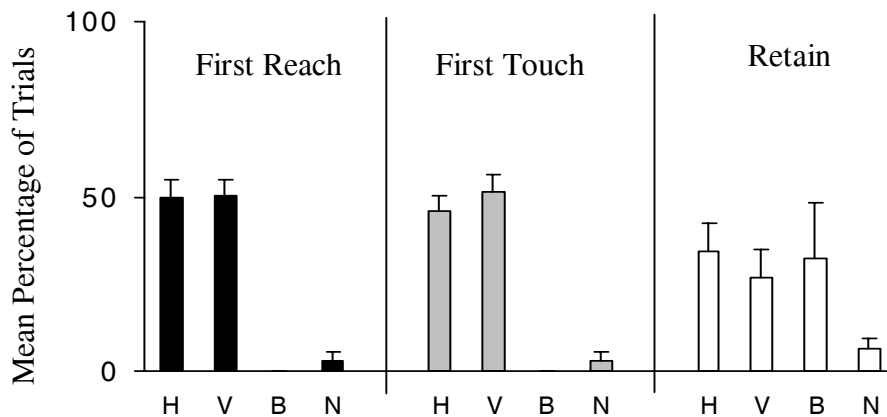


**Figure 9.** Experimental set up for Experiment 5, showing starting positions of the subject and rival and layout of testing arena. Note that doors were transparent plexiglass.

### Results and Discussion

The reach-through-door procedure coupled with more time to respond was effective in increasing to 97.2% the mean percentage of trials in which the subjects reached for at least one food item before the rival was released. There were also obvious signs that the subjects were still intimidated by the rivals, thus were under pressure to choose a food item. The subjects frequently hesitated, sometimes considerably, before reaching through the hole to grab one of the food items; they also appeared to carefully monitor whether the rival was at the door and oriented toward them, and often screamed and backed away after the rival was released.

Given that the procedure was effective in elevating the response rates of the subjects, we next examined the data from the test trials to determine if the subjects exhibited a preference for the hidden food item. The data depicted in Figure 10 show the discrete choices for the hidden or visible food items, as well as the percentage of trials on which the subjects reached for, touched, and obtained neither food item, or both. The data were structured and analyzed as in Experiment 3 and 4. The results of the separate analyses of the first reach, first touch and retention data sets indicated that the subjects did not display a bias for the hidden food item as reflected by any of these measures:  $t(5) = 0.21$  and  $0.65$ ,  $p = 0.84$  and  $0.54$ , for the first reach and first touch data sets, and  $t(4) = 1.70$ ,  $p = 0.16$ , for the retention data set. However, it should be noted that the retention data were in the same direction as obtained in Experiment 3 and 4. Thus, of the trials in which the subjects retained one or the other food item, the mean percentage of trials in which the subjects retained the hidden food was 57.6% ( $SD = 9.9$ ). In addition, the trends in the retention data for the number of pairs and the number of subjects who exhibited a bias for either hidden or visible food were also in the direction of a preference for the hidden food (6/10 of the pairs and 4/4 of the subjects). Notably, similar trends were *not* present for the critical data concerning first reach or first touch (see Table 2).



**Figure 10.** Mean percentage of trials ( $\pm$  SEM) for Experiment 5 in which subjects exhibited the various response categories (hidden food, visible food, both, and neither) for (a) their first reaches, (b) their first touches, and (c) their retentions by the end of the trial. (hidden food, H; visible food, V; both, B; neither, N).

The results of Experiment 3-5 revealed a fairly robust pattern in the outcome of the competitive situation: by the end of the trial, subjects were more likely to gain access to the food items hidden from the rival's perspective than the ones in the open. This pattern was revealed by analyses focusing on the mean percentage of trials on which the individual subjects retained a hidden vs. a visible food item (the data graphically depicted in Figures 6, 8 and 10). Equally robust, however, was our failure to replicate the Hare et al. results concerning the subjects' food preference in the competitive situation. We consistently found that the subjects' initial choices (measured by first reach and first touch) were not significantly biased toward the hidden food item, which would be necessary for supporting the visual perspective taking hypothesis.

Some subjects, and some subjects in particular pairs, did exhibit an apparent, but nonsignificant, first choice bias for the hidden food in some of the experiments (as indicated by a bias score greater than 50%). Thus, it is possible that some of the subjects, some of the time, were indeed taking into account the visual perspective of their rivals. However, any such data are equally consistent with the visual perspective taking (VPT) hypothesis and with the alternative peripheral feeding (PF) hypothesis, which we now describe.

The PF hypothesis posits that the subjects' initial choices are driven by several factors related to their extensive experience in coping with competition over food resources. These include (a) avoiding food that is out in the open, and (b) exploiting food resources that lie along the periphery of the foraging area (for a general discussion of such issues, see Fedigan, 1982; see also, Menzel, 1967; Kummer, 1971; Stynes et al., 1968; Wilson, 1972). In captive settings, such as those used for these tests, informal observations suggest that when chimpanzees are released into an enclosure with scattered food, dominants will tend to monopolize food resources that are most visible, whereas subordinates will feed along the walls or other structures, often turning their backs toward the dominants. Thus, in the context of these tests, the PF hypothesis predicts that subjects will tend to both avoid the food item that is perceived as most out in the open, and prefer the food item which is closest to a physical structure.

In Experiment 6-8, we sought to examine situations in which the VPT and PF hypotheses generate distinctly different predictions about the subjects' behavior when competing with a dominant rival for limited food resources in this experimental situation.

### **Experiment 6: Predictive Contrasts of the VPT and PF Hypotheses**

Experiment 6 was designed to test three alternative hypotheses concerning any apparent preferences of the subjects for hidden food. First, chimpanzees understand that a rival cannot see the hidden food item (VPT hypothesis). Second, chimpanzees understand that the barrier blocks the rival's physical access to the hidden food item but not the other (see also Hare et al.'s Experiment 5, using a transparent barrier). Third, in competitive situations, chimpanzees avoid food in the open, and are attracted to food located near physical structures, because of an extensive history of being peripheralized by dominant rivals during feeding competition (PF hypothesis).

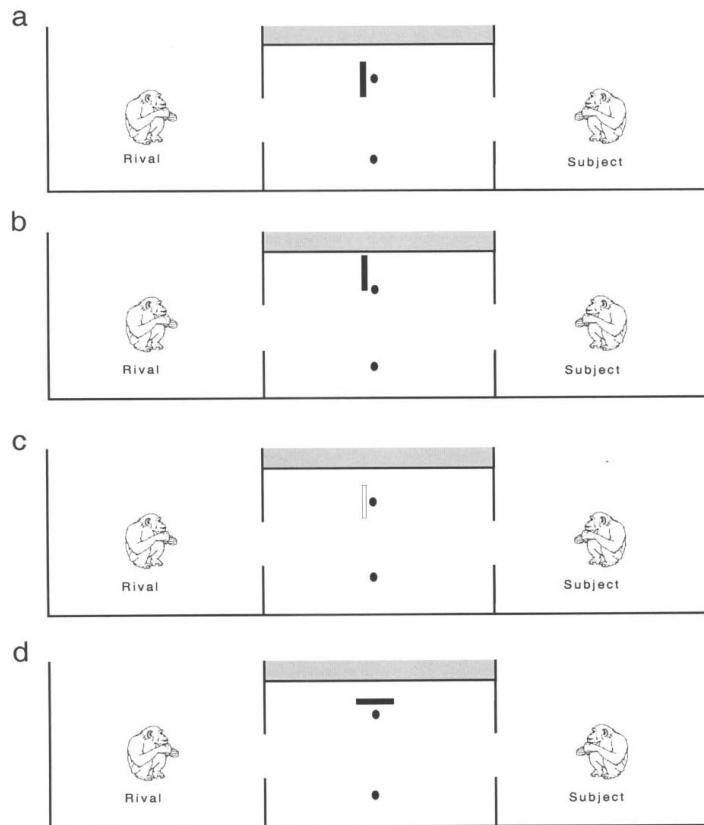
## Method

**Subjects and Materials.** The chimpanzees ranged in age from 11;9 to 12;8 at the beginning of this experiment. Before Experiment 6, a fourth series of dominance tests was conducted (see Table 1, Test 4). One of the 21 pairings from the dominance testing was ambiguous and therefore not used. In the two cases where winners and losers reversed between Dominance Test 3 and 4, the new relationships were used (see Table 1). (Hare et al. also reported two such changes during the course of their experiments.)

To maximize the subjects' attention, the opaque barriers used in this experiment were slightly novel. They were flat wood screens that measured 21 x 27 cm with a comparably sized base. A transparent barrier was also constructed from Plexiglas to exactly match the dimensions of the opaque barrier.

**Procedure.** Subject-rival pairs participated in four conditions in which two items were present on each trial, one in the open, and one associated with a structure in the manner described.

**Fully Occluding Barrier (Full):** The opaque barrier was positioned in front of one of the food items such that the rival chimpanzee's view was fully occluded while the subject had full visual and physical access to that food item (Figure 11a).



**Figure 11.** Experimental conditions used in Experiment 6: (a) Full (fully-occluded food), (b) Half (half-occluded food), (c) Clear (food behind a transparent barrier), (d) Side (barrier turned to side with food visible to both subject and rival).

**Half-Occluding Barrier (Half):** The opaque barrier was positioned in front of one of the food items such that the subject had full visual and physical access to the item while the rival had visual access only to half of it (Figure 11b).

**Transparent Barrier (Clear):** The transparent barrier was positioned in front of one of the food items to serve as a physical but not visual barrier to the rival chimpanzee's access while the subject had full visual and physical access to that food item (Figure 11c).

**Barrier to the Side (Side):** The opaque barrier was positioned to the side of one of the food items such that both the subject and the rival had full visual and physical access to both food items (Figure 11d).

Trials proceeded using the general steps described in Experiment 3. Each subject-rival pair participated in each condition four times, with the starting position of the subject (enclosure 2 or 4) and the left/right position of the barrier counterbalanced for each pair. The administration of the trials was completely randomized within the constraint that each pair received one trial before any pair received its next. Each pair received no more than one trial per day.

**Scoring and Reliability.** Data collection and video coding followed the same procedures as in Experiment 3-5. Six of the 320 trials were inadvertently not recorded on video and hence could not be reviewed. The video coded data agreed with the live observations of first reach on 97% (304/314) of the trials (Cohen's  $\kappa = 0.95$ ). Disagreements were easily resolved by consensus, as described previously.

**Predictions. Overall Predictions:** The VPT hypothesis explains the preference behavior of the subjects as the result of what they know about what their rivals can or cannot see. As a result, the VPT hypothesis predicts a bias in responding toward the food near the structure only in the Full condition. In contrast, the PF hypothesis predicts an equal strength of responding to the Full and Side structures because in both cases the food item is fully projected against a structure, which peripheralizes the food. The PF hypothesis also predicts a bias toward the food item near the structure in the Half and Clear conditions (but less so than in the Full and Side conditions): in the Half condition the food item is at least partially projected against the structure, and in the Clear condition the food item is fully projected against an (optically) "partial" structure.

It is important to note that both the VPT and PF hypotheses may accurately capture different factors operating to govern the chimpanzees' behavior. Therefore, an additive hypothesis was also considered which predicts a bias greater than chance to the Side structure; unlike the PF or VPT hypothesis alone, this hypothesis also predicts an even stronger preference for the Full structure.

**Subject-Specific Predictions:** An additional purpose of this experiment was to separately examine the data for any individual subjects showing a bias for the hidden food in the Full condition. Even if there were no group-level effects, it might be the case that some individual subjects were behaving according to the predictions made by the VPT or additive hypotheses. This could be assessed by comparing their performance in the Full condition to their performance in the Side condition.

## **Results and Discussion**

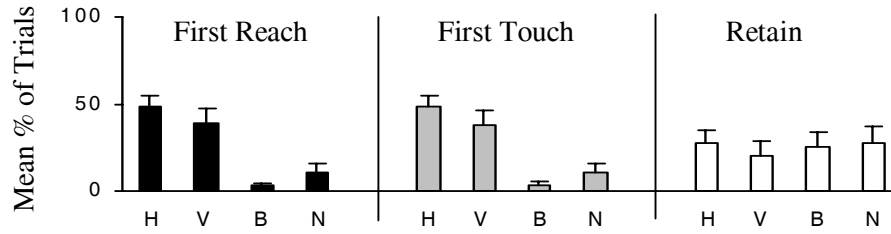
The subjects' rates of responding were fairly high and were not significantly different across the 4 conditions (89.6%, 76.3%, 73.2%, and 90.5% of trials for the Full, Half, Clear, and Side conditions, range of  $SD = 11.6$ —20.5).

**Group Data.** The main results are depicted in Figure 12 which displays the mean percentage of trials for each condition in which the subjects first reached for, first touched, and retained the food item associated with the structure, the food item in the open, both food items simultaneously, or neither item.

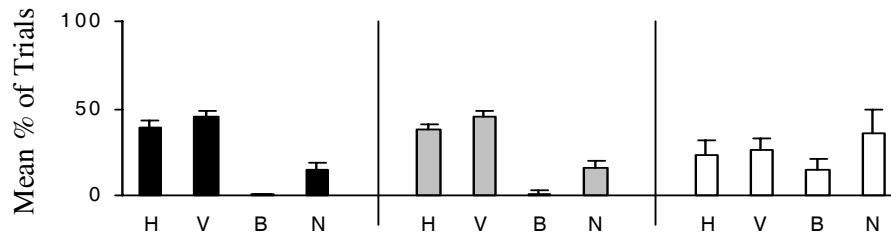
As in Experiment 3-5, the data sets for first reaches, first touches, and retains were analyzed separately. For each of these three data sets, we again restricted our analyses to just those trials in which a discrete response was exhibited for one or the other food item. These data were used to calculate the mean percentage of trials in which each subject first reached for, first touched, and retained the

food next to the structure in each condition for the three data sets, respectively.

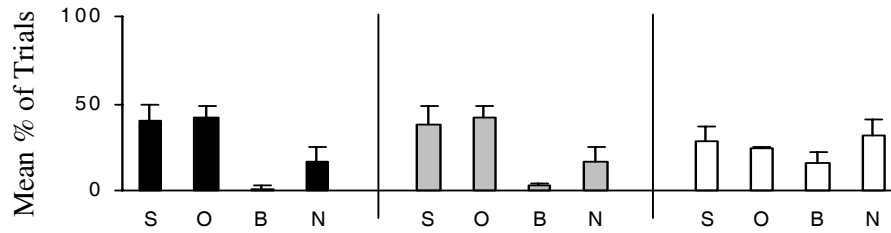
a Full



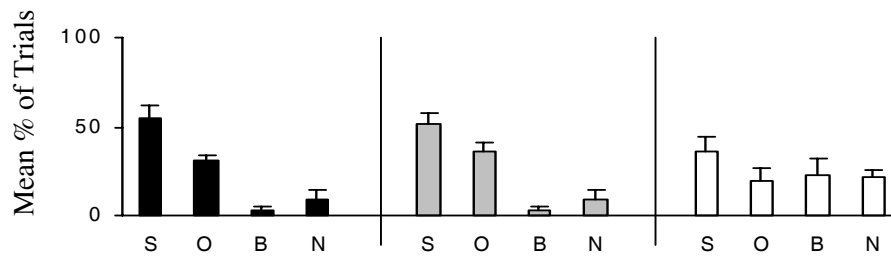
b Half



c Clear



d Side



**Figure 12.** Mean percentage of trials ( $\pm$  SEM) for Experiment 6 in which subjects exhibited the various response categories for their first reaches, first touches, and retentions by the end of the trial for (a) Full, (b) Clear, (c) Half, and (d) Side conditions. (food near structure, S; food in the open, O; both, B; and neither, N.)

We examined the data with respect to two main questions. First, we asked whether there was a stronger bias for reaching for, touching, or retaining the food item associated with the structure in some conditions as opposed to others. The results of two separate one-way, repeated-measure ANOVAs for the first reach and first touch data sets across the six subjects indicated nonsignificant overall effects,  $F(3,15) = 1.06$  and  $1.01$ ,  $ps < 0.42$ , for the two data sets respectively. The retention could not be analyzed in precisely the same manner because one of the subjects (Kara) never retained a food item in the Half condition, and hence a cell was missing in the data matrix, invalidating a repeated measures ANOVA. However, ANOVAs conducted on the data matrix without this subject or without the Half condition, indicated no significant effect of condition. At this level of analysis, then, the data do not fit the predictions of any of the three hypotheses tested.

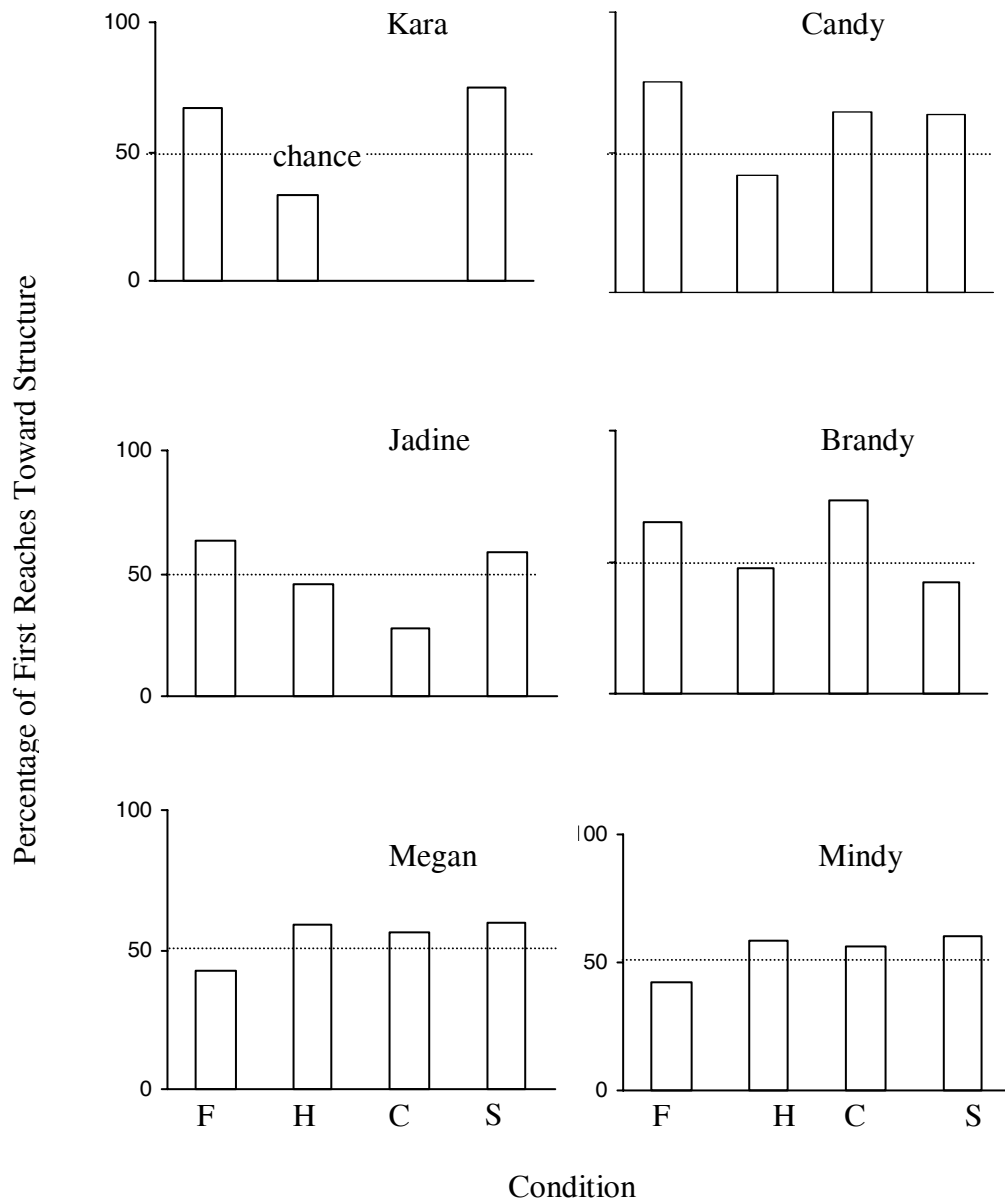
As in Experiment 3-5, we also examined the data to determine if the subjects exhibited biases significantly greater than chance (50%) for the food item associated with the structure in any of the conditions. To determine if this was so, the three data sets (first reach, first touch, retain) were analyzed using separate one-sample  $t$ -tests. The results for first reaches indicated that the subjects exhibited a marginally significant preference for the food near the structure in the Side condition,  $t(5) = 2.46$ ,  $p = 0.057$ , but exhibited no such preferences in any of the other three conditions ( $t = 0.81, 1.12, \text{ and } 0.43$ ,  $p = 0.45, 0.31, \text{ and } 0.69$ , for the Full, Half, and Clear conditions, respectively). The same pattern held with respect to the first touch and retention data sets, with nonsignificant, but suggestive biases for the food near the structure in the Side condition,  $ps < 0.09$ , but no such biases in the other conditions. The bias in the Side condition is consistent with the PF hypothesis (although the PF hypothesis incorrectly predicted an equal bias in the Full condition), but is difficult to reconcile with the VPT or the additive hypotheses.

Table 3  
*Number of Pairs in which Subject Exhibited First Reach Preference for Food Item Near Structure, Food Item in the Open, or Neither, and Number of Subjects with Such Preferences (Experiment 6 and 7).*

	No. of Pairs			No. of Subjects		
	Structure	Open	Neither	Structure	Open	Neither
Experiment 6						
Full	9	5	6	4	2	0
Half	5	7	8	1	4	1
Clear	7	3	10	3	2	1
Side	10	4	6	5	1	0
Experiment 7						
Full	3	3	14	2	2	2
Clear	6	6	8	3	3	0
Side	6	5	9	4	1	1



Finally, we again informally examined the data on the number of pairs and subjects in which subordinates exhibited a first reach preference for the food item near the structure, the one in the open, or neither. An examination of Table 3 reveals that in three of the four conditions (Full, Clear, and Side), the subjects of more pairs were biased toward the food item near the structure than to the food item in the open, and more individual subjects were biased in this way across their pairings. It is of interest that the strongest biases were in the Side condition (10/14 or 71% of the pairs, and 5/6 or 83% of the subjects), not in the Full condition (see Table 3).



**Figure 13.** Subject-by-subject data for Experiment 6 results showing the percentage of trials in which subjects directed their first reaches at the food near the structure in each condition. (Full condition, F; Clear condition, C; Half condition, H; and Side condition, S.)

**Individual Data.** Figure 13 presents the mean percentage of first reaches for the food near the structure as a function of the four conditions for each of the six subjects separately. A visual inspection of these data indicate that 4/6 (67%) of the subjects (Kara, Candy, Jadine, Brandy) did exhibit a bias toward the food near the fully occluding structure. However, 3/4 (75%) of these same subjects (Kara, Candy, Jadine) also exhibited a bias of comparable magnitude in the Side condition. The fourth subject, Brandy, exhibited an even stronger bias toward the transparent structure, choosing it on 14/19 (74%) of her trials (binomial test,  $p < 0.04$ ). Conversely, when we examined the bias from the standpoint of the Side condition, more subjects (5/6, or 83%) were biased toward the food near the structure than in the Full condition. However one interprets these findings, they illustrate in a rather direct way that apparent biases for the structure in the Full (hidden-visible) condition cannot be used to support the VPT or the additive hypotheses. These findings are inconsistent with the Hare et al. (2000) interpretation of their results as visual perspective taking by chimpanzees.

### **Experiment 7: Replication of Experiment 6**

Given the fragile nature of the effects in Experiment 6, we replicated the procedure in Experiment 7. Twenty pairs were available for testing (see Table 1, Test 5). The same procedures were used as in Experiment 6 to readminister the Full, Clear, and Side conditions. The Half condition was not used given that there was no evidence from the previous experiment that the subjects preferred or avoided this structure.

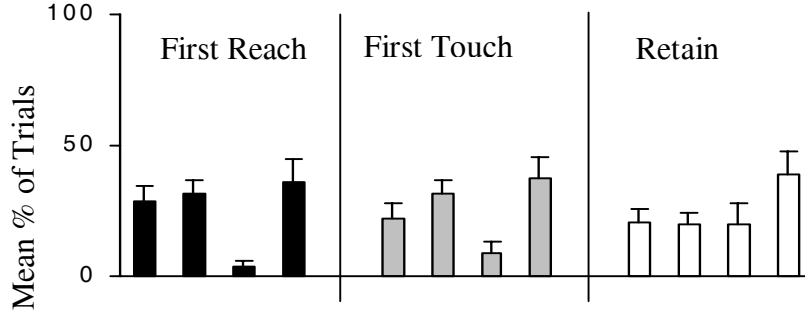
The subjects' rates of responding were slightly lower than in Experiment 6, and were not significantly different across the 3 conditions (63.8%, 69.2%, and 67.2% of the 80 trials for each of the Full, Clear, and Side conditions, range of  $SDs = 18.5-21.2$ ). The raw data for first reaches, first touches, and retention are plotted in Figure 14. We analyzed the data as in the previous experiment. The comparisons revealed no overall differences among the barrier in the subjects' preference for the food associated with the structure. Furthermore, there were no conditions in which the subjects exhibited a stronger initial tendency to reach toward, touch, or retain food items associated with the barrier. The marginal effects reported in the previous study for the Side structure were not replicated, although there were some weak indications in the informal analyses of initial reach biases (see Table 3). No such trends existed in the Full or Clear conditions (see Table 3).

### **Experiment 8: Response Latency Test**

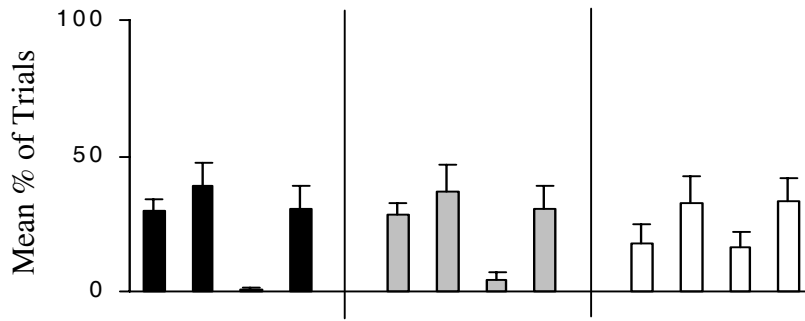
In Experiment 4-7, subjects showed an intermittent bias for retrieving food near a structure over food out in the open when given a choice between two pieces of food while in competition with a rival chimpanzee. Additionally, data from these experiments suggest that subjects may show differential response rates irrespective of the choice made across conditions. In Experiment 8, we used response latency as a measure of the subjects' willingness to respond, as opposed to the binomial measure of choice between two food items. Willingness to respond may be

more sensitive than food choice as an indication of cognitive strategies employed during these competitive foraging situations.

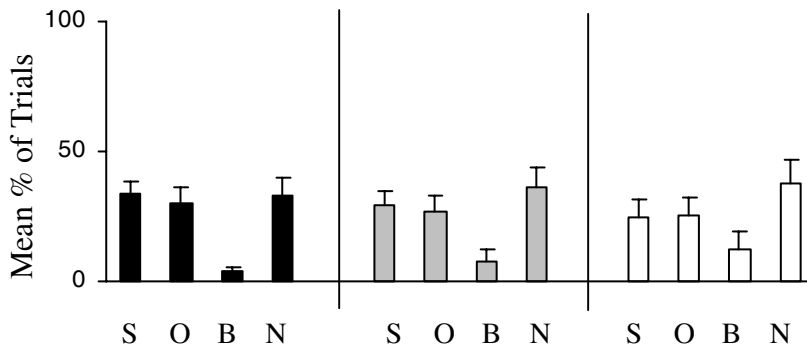
(a) Full



(b) Clear



(c) Side



**Figure 14.** Mean percentage of trials ( $\pm$  SEM) for Experiment 7 in which subjects exhibited the various response categories (food near structure, food in the open, both, and neither) for their first reaches, first touches, and retentions by the end of the trial for (a) Full, (b) Clear, and (c) Side conditions. (food near structure, S; food in the open, O; both, B; and neither, N.)

## **Method**

**Subjects.** The chimpanzees ranged in age from 12;3 to 13;2 at the beginning of this experiment. Subject-rival pairs are based on the results of dominance Test 6 (Table 1), resulting in 21 pairs for testing.

**Procedure.** One half-banana or half-apple was placed in the testing arena (with the previously added wall removed), centered within a clearly marked circle (20 cm diameter) on the floor. Novel wooden and clear barriers were used with the dimensions 70 x 20 cm. The subject observed the placement of the food and barrier through a clear Plexiglas door, while the process was shielded from the rival by an opaque door. The four treatments were (a) food placed behind an opaque barrier relative to the rival (Full), (b) food placed behind a clear barrier relative to the rival (Clear), (c) food associated with an opaque structure but with full visual and physical accessibility to both chimpanzees (Side), and (d) food placed in the open with no associated structure (Open).

Once the food and barrier were in place, the experimenter opened the rival's view slot until the subject and rival simultaneously looked into the testing arena, after which the view slot was closed. The subject's door was opened first and the subject was given 5 min to respond by displacing the reward out of the circle either by lifting it up or moving it along the floor. As soon as they did so, the rival's door was opened. Again, the administration of trials was completely randomized within the constraint that each pair received one trial before any pair received its next. Each pair participated four times in each of the four treatments, with a maximum of one trial per pair per day. All trials were recorded on video.

**Scoring and Reliability.** From the videotape, a coder timed the subjects' latency to enter the testing arena and to displace the food from the circle. A secondary coder reviewed 25% of the trials and obtained an interobserver correlation coefficient of  $r = 0.99$  on both latency measures.

## **Results**

The mean latencies in seconds (s) of the subjects to enter the testing arena for the Open, Clear, Side, and Full conditions were 15.64 ( $SD = 25.6$ ), 14.01 ( $SD = 10.2$ ), 22.39 ( $SD = 39.1$ ), and 25.37 ( $SD = 43.5$ ), respectively. A repeated measures ANOVA conducted on the grand mean latency for the six subjects to enter the testing arena revealed no significant differences between the treatments,  $F < 1$ . We also conducted three planned contrasts based on the predictions derived from the VPT, PF, and additive hypotheses. None resulted in significant  $F$ -scores.

The mean latencies (s) of the subjects to displace the food item for the Open, Clear, Side, and Full conditions were 79.86 ( $SD = 21.50$ ), 63.16 ( $SD = 23.9$ ), 82.25 ( $SD = 21.5$ ), and 73.56 ( $SD = 31.7$ ), respectively. Again, a repeated measure ANOVA revealed no significance in the omnibus test,  $F < 1$ , nor in any of the planned contrasts. A third ANOVA showed that the response rates among the conditions were not significantly different, either,  $F < 1$ .

## **Discussion**

These results corroborate the findings of the earlier studies. The subjects did not exhibit patterns of behavior which suggest that they were taking into account what their rivals could or could not see.

Our use of the latency measure mirrors the *approach* measure used by Hare et al. (2001) in a series of experiments following up those reviewed and replicated here. In those experiments, there was only one piece of food available to the subject, thus *approach* measured the subject's willingness to respond.

It can be argued that these later experiments by Hare, et al. (2001) dis-

credit the PF hypothesis, as the chimpanzees participating showed differential willingness to respond based on the visual access of the rival to the baiting procedure, and not to the proximity of the food to a structure. Our use of the latency measure did not discriminate among the experimental conditions used here, bringing further into question the results of all the Hare et al. (2000) experiments which do not measure willingness to respond. Because the subjects did not show a clear preference for one piece of food or the other in the choice tests, and they did not show differential willingness to respond in the latency test, neither the VPT hypothesis nor the PF hypothesis is supported by our results. Chimpanzee foraging decisions seem to be based on other factors. We discuss this further in the General Discussion.

### **Combined Analyses of Experiments 3-7: Competitive Asymmetry, Learning, and Estrous Cycle Analyses**

To determine whether certain factors may have minimized our ability to detect any initial preference effect that may have been present, we examined the data of the six subjects across Experiment 3-7 for the three most important conditions: Full, Clear, and Side. The purpose of each analysis is described below. Given their limitations and outcomes, we report these analyses only briefly, although a complete copy of the analyses is available from the authors. Experiment 8 was not included in this combined analysis because it used a different measure (response latency) than Experiments 3-7.

#### ***Competitive Asymmetry***

The logic of the Hare et al. (2000) tests was that competitive situations might help to elucidate evidence of perspective taking in chimpanzees (Hare, 2001). Thus, the lack of direct competitive asymmetry (where one member in the pair is at a distinct disadvantage in a direct competitive encounter) in some pairs might lessen the probability of finding evidence for the VPT hypothesis or PF hypothesis, assuming either was correct.

***Analyses of Stable Pairs.*** There were seven pairs of chimpanzees that did not exhibit completely stable dominance relationships in feeding competition across the year-long time frame of the experiments reported here. Thus, in order to focus only on those pairs that exhibited a stable competitive asymmetry in the dominance tests, we performed a restricted analysis of the 14 pairs that yielded a consistent outcome in all 6 tests. The patterns in these data were as follows: (a) for the first reach data, there was a trend toward a bias in the number of subjects who chose the food associated with the barrier in the Side condition (5/6 subjects), but not in the Full (3/6 subjects) or Clear (2/6 subjects) conditions; (b) for the retention data set, there was a bias in the Full condition (6/6 subjects, binomial  $p < 0.05$ ), a trend toward a bias in Side condition (5/6 subjects), and no trend in the Clear condition (1/6 subjects). Thus, these results show that even for the subject-rival pairings that remained stable across the duration of all of the studies reported here, there was no evidence that uniquely supported the VPT hypothesis, and some that was inconsistent with it.

***Strong Competitive Asymmetry.*** Another measure of the competitive asymmetry of a pair is how often the subject first reached for or retained both food items. If both items were frequently reached for simultaneously, or retained by the end of the trial, this might indicate that the subject was not at a competitive disadvantage when released slightly before her rival, or that only a weak asymmetry in the feeding dominance existed for that pair. The data sets for Experiment 3-7 show that the subjects exhibited a first reach for both food items simultaneously on only 2% (16/788) of the total number of trials (see Figures 6, 7, and 9). However, subjects did manage to obtain both food items by the end of the trial on 18% (142/788) of the trials.

To examine whether the subjects' willingness and ability to retain both food items at the low level just described might have masked a first reach effect favoring the VPT hypothesis, we reanalyzed the data after excluding data from any pair (by experiment) in which the subject retained both food items on one or more trials. With this restricted data set, we then examined the first reach data again for the individual subjects. Four of the 6 subjects were represented in each of the three conditions and could thus be examined. The mean percentages (SD) of trials in which they chose the food near the structure were as follows: Full = 57.5 (3.1), Clear = 40.5 (15.4), Side = 57.6 (14.4). Clearly, even this highly restricted data set does not support the VPT hypothesis, and only weakly supports the PF hypothesis.

### ***Learning***

An interesting question concerns whether the performance of the 6 individual subjects changed over the multiple trials they received. In particular we examined the hidden-visible (or Full) condition, as this was the condition of which the subjects received the most trials. Across Experiment 3-7, the subjects received 40-120 trials of this type, depending upon the number of pairs in which each animal participated as the subject. For this analysis, we structured the data for all subjects in consecutive blocks of 8 trials using only those trials in which the subjects responded with a discrete choice by reaching for either the food in the open or the food near the structure. The results indicated that 5 of the 6 subjects exhibited no greater preference for the hidden food in their last block of 8 trials than they did in their first. In contrast, one subject, Jadine, did exhibit a strong change in her first reach preference for the hidden food item, increasing from 25% to 75% across her blocks of trials. Second, we measured changes in the average number of pieces of food the subjects retained with the data structured in blocks of 8 trials. None of the subjects except Jadine significantly increased their ability to obtain food across trials (and even her data do not fit the predictions of the VPT hypothesis). Thus, with the exception of Jadine, these data suggest a general stability in the chimpanzees' responses to the Full (or hidden-visible) condition across repeated administrations.

### ***Estrous Cycles***

We conducted several analyses to determine whether estrous status affected how the six female subjects directed their first reaches. For each trial, be-

ginning with Experiment 3, we rated the degree of sexual swelling for each female subject on a scale of 0 (no swelling), 1 (mild swelling), or 2 (full swelling). We also recorded whether they were pregnant. First, pregnancy status did not affect either the subjects' response rate or whether they selected food associated with a structure. Second, the estrous status of the subjects (as measured by their swellings) was not associated with differential levels of selecting food associated with a structure. Thus, there was no evidence that pregnancy or sexual receptivity was masking results that might have otherwise supported one of the hypotheses.

### **General Discussion**

Our experiments had two aims. First, we sought to assess the replicability of Hare et al.'s (2000) finding that chimpanzees prefer food hidden from a rival's visual perspective over food visible to the rival. Second, we sought to test Hare et al.'s idea that these findings can be accounted for by assuming that chimpanzees reason about a rival's visual perspective (VPT hypothesis), against an alternative hypothesis which accounted for the data on the basis of peripheralized feeding strategies used by chimpanzees (PF hypothesis).

With respect to the first aim, our initial studies (Experiment 1 and 2) robustly replicated various phenomena reported by Hare et al. that do not uniquely support the VPT hypothesis. In most of our later studies (Experiment 3-6, but not Experiment 7), we also consistently replicated the findings that, by the end of a trial, subjects were significantly more likely to have retained food items hidden behind opaque barriers than food in the open.

As we have seen, however, the retention effect may simply reflect the fact that after the rival enters the testing arena and takes the visible food item, the only item left for the subject is the hidden one. Because of this, genuine support for the VPT hypothesis is only present if the subjects' initial preference (that is, their behavior prior to the rival entering the testing arena) were for the hidden food item. Here, however, we consistently failed to find evidence that the chimpanzees preferentially directed their first reaches or touches to the hidden food (see Experiment 3-7), despite the use of several procedures designed to maximize the likelihood of finding such a bias if it were based on visual perspective taking.

The failure to replicate the initial preference effect, especially in the face of the robust replication of the end-of-the-trial retention effect, suggests careful scrutiny of certain aspects of the methods used by Hare et al. and the methods employed here. With respect to our methodology, it is possible that despite our ability to precisely record and code our tests, and our robust replication of the retention effect, there was something about our apes or our subtle changes in procedure that failed to produce an otherwise replicable initial preference effect. The likelihood of the former possibility should be tempered by noting that the subjects used in these studies have repeatedly been shown to respond to and exploit the gaze-direction of others in sophisticated ways (Povinelli & Eddy, 1996b, 1997; Povinelli et al., 1997, 1999).

With respect to the second aim of our research (testing the VPT and PF hypotheses), several findings are worth highlighting. First, there was again no evidence of an initial preference effect for the hidden food in the Full (hidden-visible) condition. Second, the subjects exhibited a statistically significant initial prefer-

ence for the food item near the barrier when the barrier was simply turned to the side so that the food near it was completely visible to both the subject and rival (see results for Side condition in Experiment 6), or exhibited trends in that direction (see Experiment 7). These two findings neatly falsify the predictions of the simple additive hypothesis that initial preferences for the structure ought to exist in the Side condition ("food near peripheral structure"), but even stronger preferences of this type ought to exist in the Full condition ("food near structure" plus "food blocked from rival's view").

Given that the VPT hypothesis was largely excluded by the results, and given that the PF hypothesis only produced a marginally better account of the pattern of the data, how might we account for the patterns obtained? Foraging in a competitive social context involves a suite of behaviors in which multiple strategies may interact in complex ways. For example, our chimpanzees engaged in a variety of social behaviors during the tests reported here, mirroring their behavior in other, nonexperimental foraging and feeding contexts. Apollo, the dominant male in the group, vocalized loudly before many of his trials, effectively reminding his partners of the social context in which they were situated. Even so, subjects occasionally risked reprisal by retrieving one or both of the food items. It appeared as if they were more likely to do so while sexually receptive (measured by the degree of genital swelling) than when not receptive, although there is no appropriate way of assessing this from the existing data set. Nonetheless, such behavior is consistent with experimental observations of chimpanzees suggesting that estrous swelling may allow females access to food in return for access to copulation (e.g., Nowlis, 1942). In such a context, whether the food item taken is hidden or visible to the rival, in any event, may be of little or no significance to the female chimpanzees.

The subjects often exhibited food barks and other soft vocalizations during the trials, and even frequently struck the rival's door, as if to call attention to the fact that there was food and that they were not taking it. This can be understood within the context of chimpanzee socio-ecology: subordinates will not typically initiate the act of taking highly prized food items when in competition with a dominant animal. The no-response rate among subjects witnessed in both our studies and in Hare et al.'s likely reflects their unwillingness to behave in ways that are at odds with what they have previously learned about such contexts. The experimental situation employed here did, however, allow room for the subjects to develop ways of coping with this inhibition. For example, in the later experiments, when Brandy was paired with an aggressive rival (Apollo or Candy), she would frequently enter the testing arena, and monitor the position and movements of the rival through the door. Her reaching responses appeared to typically coincide with the rival looking away (unfortunately, given the frame of the video image, this could not be coded). When subjects did take food, they would either run back into their pretrial waiting area or turn their backs as the rival chimpanzee approached. Occasionally, this diffused the rival's agonistic behavior.

Other social dynamics clearly play a role in these interactions, such as the nature and extent of the asymmetry of any given subject-rival pair. For example, although the dominance tests reveal which ape in any given pairing will obtain the food item, this fact does not indicate a uniform relationship among all pairs. Indeed, what may be most striking about the results of our tests was not whether the



subject initially took the hidden or visible food item, but the extraordinary variability in the nature of the subject-rival pairings. In some pairs, rivals seemed unconcerned as to whether the subject had obtained a food item as long as there was also one for them. In other pairs, rivals were extremely intolerant of this situation. Furthermore, some of the subjects in some of the pairs did not overtly compete for food after the rival had been released, whereas on other occasions they did so. Furthermore, some of the females challenged the dominant male's threats while others did not, and even these challenges did not appear consistent within pairs. Given the uniqueness of each relationship, it is questionable whether grouping pairs into independent composite data sets makes sense given that far more than just the orientation of the barriers and placement of the food items vary from trial to trial for each subject.

None of these social strategies or dynamics calls for visual perspective taking in order to successfully retrieve food. Indeed, keeping track of and reasoning about the observable contingencies inherent in such competitive situations may be sufficient. In this context, it is sensible that many different strategies may be employed even by a single chimpanzee in different competitive contexts. Even if chimpanzees were to use visual perspective taking in choosing a food item to retrieve, this strategy is only one of many which might be employed. If so, visual perspective taking was not strong enough to be clearly evidenced in this series of experiments, and furthermore, based on aspects of our results it is clear that the Hare et al. (2000) data cannot be taken as evidence in support of the existence or use of such an ability. Although the Hare et al. procedures provide an interesting avenue for exploring the means by which chimpanzees cope with the problem of feeding competition, we conclude that these procedures have not provided evidence that chimpanzees know what each other do and do not "see." Indeed, aspects of our findings are inconsistent with such a view.

## References

- Anderson, J.R. & Mitchell, R.W. (1999). Macaques but not lemurs co-orient visually with humans. *Folia Primatologica*, **70**, 17-22.
- Anderson, J.R., Montant, M., & Scmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*, **37**, 47-55.
- 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.
- Call, J., Hare, M., & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal Cognition*, **1**, 89-99.
- 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. (in press). Social cognition. In D. Maestripieri (Ed.), *Primate psychology: The mind and behavior of human and nonhuman primates*. Cambridge, MA: Harvard University Press.
- 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.
- Fedigan, L. (1982). *Primate paradigms*. Eden Press: Montreal.
- Ferrari, P.F., Kohler, E., Fogassi, L., & Gallese, V. (2000). The ability to follow gaze and its emergence during development in macaque monkeys. *Proceeding of the National Academy of Science USA*, **97**, 13997-14002.
- Gómez, J. C. (1991). Visual behavior as a window for reading the minds of others in primates. In A. Whiten (Ed.), *Natural theories of mind: Evolution, development and simulation of the everyday mindreading* (pp. 330-343). Oxford, UK: Blackwell.

- Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, **4**, 269-280.
- 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., 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.
- Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, **21**, 101-134.
- Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. *Japanese Psychological Research*, **38**, 174-180.
- Kummer, H. (1970). Spacing mechanisms in social behavior. *Social Science Information*, **9**, 109-122.
- Lempers, J. D., Flavell, E. R., & Flavell, J. H. (1977). The development in very young children of tacit knowledge concerning visual perception. *Genetic Psychology Monographs*, **95**, 3-53.
- Lorincz, E. N., Baker, C. I. & Perrett, D. I. (1999). Visual cues for attention following in rhesus monkeys. *Current Psychology of Cognition*, **18**, 973-1003.
- Menzel, E. (1967). Naturalistic and experimental research on primates. *Human Development*, **10**, 170-186.
- Miklósi, A., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, **1**, 113-121.
- Nowlis, V. (1942). Sexual status and degree of hunger in chimpanzee competitive interaction. *Journal of Comparative Psychology*, **34**, 185-194.
- Povinelli, D.J., Bierschwale, D.T., & Cech, C.G (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, **17**, 37-60.
- Povinelli, D.J. & Eddy, T.J. (1996a). Chimpanzees: Joint visual attention. *Psychological Science*, **7**, 129-135.
- Povinelli, D.J. & Eddy, T.J. (1996b). Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. *International Journal of Primatology*, **110**, 336-345.
- Povinelli, D.J. & Eddy, T.J. (1996c). 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. (1997). Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology*, **15**, 213-222.
- Povinelli, D. J. & Giambrone, S. (2000). Escaping the argument from analogy. In D. J. Povinelli (Ed.), *Folk physics for apes: The chimpanzee's theory of how the world works* (pp. 9-72). New York: Oxford University Press.
- Povinelli, D. J., Parks, K. A, Novak, M. A. (1992). Role reversal by 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.
- Reaux, J. E., Theall, L. A., & Povinelli, D. J. (1999). A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development*, **70**, 275-290.
- Stynes, A. J., Rosenblum, L. A., & Kaufman, I. C. (1968). The dominant male and behavior within heterospecific monkey groups. *Folia Primatologica*, **9**, 123-134.
- Suddenforf, T., & Whiten, A. (2001). Mental evolution and development: Evidence for secondary representation in children, great apes, and other animals. *Psychological Bulletin*, **127**, 629-650.
- Theall, L. A., & Povinelli, D. J. (1999). Do chimpanzees tailor their attention-getting behaviors to fit the attentional states of others? *Animal Cognition*, **2**, 207-214.
- 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.
- deWaal, F. B. M. (1989). *Peacemaking among primates*. Cambridge, MA: Harvard University Press.

sity Press.

Wilson, C. (1972). Spatial factors and the behavior of non-human primates. *Folia Primatologica*, **18**, 256-275.

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