

Tracking the Displacement of Objects: A Series of Tasks With Great Apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and Young Children (*Homo sapiens*)

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The authors administered a series of object displacement tasks to 24 great apes and 24 30-month-old children (*Homo sapiens*). Objects were placed under 1 or 2 of 3 cups by visible or invisible displacements. The series included 6 tasks: delayed response, inhibition test, A not B, rotations, transpositions, and object permanence. Apes and children solved most tasks performing at comparable levels except in the transposition task, in which apes performed better than children. Ape species performed at comparable levels in all tasks except in single transpositions, in which chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) performed better than gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*). All species found nonadjacent trials and rotations especially difficult. The number of elements that changed locations, the type of displacement, and having to inhibit predominant reaching responses were factors that negatively affected the subjects' performance.

Keywords: object permanence, inhibition, transpositions, rotations, spatial memory

Keeping track of objects is an important skill for many species, especially in the context of foraging, in which animals have to remember where they have seen food and which location they have already visited and exploited (Call, 2000; Milton, 1988). Therefore, topics such as the representation of objects as operationalized in object permanence and transposition tasks modeled after the pioneering ideas of Piaget (1954) have received much attention not only in developmental research but also in comparative research (see Doré & Dumas, 1987, for a review).

In object displacement tasks, an object is usually hidden under an opaque cup and then moved inside this cup in the presence of

other cups. There are two main cognitive challenges in such tasks. First, subjects have to understand that objects continue to exist when they are hidden (object permanence), and, second, they have to remember the objects' locations until they are given a chance to recover them. Numerous paradigms have been used to investigate this ability. For instance, in a delayed response task, an object is hidden under one of two or three cups. After a brief delay, the subject is then allowed to search for the object. This task recalls a classic study by Hunter (1913), who tested the memory of animals and children. Later, Harlow and colleagues conducted a series of delayed response studies in which apes and monkeys searched for food that was hidden in one of two locations (e.g., Harlow, 1932). They found that great apes remembered the location of food slightly better than did Old and New World monkeys. In a series of object displacement tasks, the delayed response task can function as a baseline measure to determine whether subjects understand the basic principles of the task and will search for an object that has been hidden in full view under one cup in the presence of additional cups.

In a more advanced version of this problem, objects are placed under either adjacent or nonadjacent cups in an array of three horizontally aligned cups. In the nonadjacent condition, the center cup is left empty. In a study with orangutans, chimpanzees, and young children, Call (2001) found that when subjects started searching for the objects, they usually started with the left or right cup and then made a peculiar mistake. After successful retrieval of the first object, they proceeded by choosing the middle container, which they had just seen a few seconds ago to be empty. Evidently, subjects have problems skipping the middle container. Call (2001) suggested that this search error is most likely to be explained by an inhibition problem rather than a memory deficit.

The second challenge in object displacement tasks arises from moving the objects from their initial positions to new locations. In

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the classical Piagetian A-not-B error task, an object is placed under the same cup for a number of trials, and then in full view of the subject, the object is displaced under another cup. Children younger than 12 months have problems recovering the object from the new location even after the visible displacement. Piaget (1954) initially attributed the error to infants' lack of object permanence and a presumed relation between their own actions and the existence of objects. However, in a classic study, Baillargeon (1987) showed that infants as young as 4 months look longer at impossible events occurring with hidden objects, demonstrating at least an implicit understanding of object permanence. Some researchers (Diamond, 1985; Harris, 1973) have suggested that memory plays a role in this error, as it increases with a delay between hiding and searching. Memory is, however, not a sufficient factor to explain the search error in Location B, as infants still make this error even when they can see the object in the new location (Bremner & Knowles, 1984; Butterworth, 1977; Harris, 1974). Perseverative reaching and inhibition errors again seem to play a role in this task.

Displacements are further complicated when they occur invisibly, that is, when the reward changes location by being transported in an opaque container. To solve this task, subjects have to understand that after an object has disappeared under a cup, it moves with this cup when the cup is moved. Additionally, subjects have to visually track the movements of objects that are now represented by the cup(s) in the presence of distractions such as irrelevant cups or movements. This means that the spatial representations and positions have to be updated constantly. Three main types of invisible displacements have been investigated depending on what is being moved: the reward; the reward and the containers; or the reward, containers, and the substrate where the containers (and the reward) rest. Let us begin by discussing the latter.

Rotations consist of an invisible displacement in which an object is first visibly placed under a cup in an array of other cups that are resting on a platform. Then the platform is rotated whereby the object invisibly changes its location. For example, if the left cup of an array of three cups is baited and the platform is rotated by 180°, the object will now be at the opposite location, under the right cup. Beran and Minahan (2000) showed that bonobos and chimpanzees recovered the food after a 180° rotation well above chance levels in such a task. Beran, Beran, and Menzel (2005) extended those results to 360° rotations in a study with chimpanzees and also administered 180° rotations using a five-container array with two rewards. Subjects were able to select the correct container above chance in their first choice but not in their second one. Thus, subjects were capable of tracking one of the two items, seemingly the one that was hidden last before the rotation took place. Potì (2000) found that 2 capuchin monkeys were able to solve a rotations task when the target location was indicated by the presence of a landmark close to the reward but not when the landmark had to be used independently of the target location. In another study with orangutans and chimpanzees (Call, 2003), the subjects could solve 180° and 360° rotations only when they had seen the initial location of the food but not when the location of the reward was signaled by a marker placed on the baited container before the rotation.

Another invisible object displacement is the transposition task, which involves switching the locations of the containers (and the reward inside one of them) while the platform remains stationary. In this task, the object is hidden and then moved with the con-

tainer, whereby two adjacent or nonadjacent containers switch locations in single or double transpositions. For example, when in an array of three cups, the object is placed under the left container, and this container switches locations once with the nonadjacent container and then with the adjacent container, it will move with the left cup to the outer right position and then to the middle. In a study with bonobos and chimpanzees, Beran and Minahan (2000) found that their subjects had no problems solving spatial transpositions with three cups. Call (2003) reported that orangutans and chimpanzees solved spatial transpositions with two cups at ceiling levels. Similarly, Pepperberg, Willner, and Gravitz (1997) reported that 2 African grey parrots passed transposition trials, whereas cats and dogs failed them (Doré, Fiset, Goulet, Dumas, & Gagnon, 1996). In a study with 13-month-old and 21-month-old children, Sophian and Sage (1983) found that children had problems recovering a toy from the correct container after it had switched locations with another container. In two other studies, Sophian (1984, 1986) found evidence that it is not before 3–4 years of age that children solve spatial transpositions.

The Stage 6 object permanence task (e.g., Piaget, 1954; Sophian, 1985; Sophian & Sage, 1983) is another invisible displacement task that involves the displacement of the object while both the containers and the substrate remain stationary. In this task, a hand or cup is placed over an object in full view of the subject. The object is then moved and displaced under other containers. The experimenter thereby visits either only one container in single displacements or two containers in double displacements. The object is then secretly left under one of the visited containers, and the female experimenter shows the subject that she does not have the object anymore. This is the invisible displacement task that has received most research attention (see Doré & Dumas, 1987; Tomasello & Call, 1997, for a review). Although the lack of proper control procedures has cast some doubts on the conclusion coming from the initial comparative studies in this area, currently there is a consensus that children, great apes, and parrots, unlike other species tested, are capable of solving Stage 6 invisible displacements such as double adjacent displacements (Call, 2001; de Blois, Novak, & Bond, 1998; Pepperberg et al., 1997).

Despite the information available about the ability to solve object displacement tasks in various species, there is an important shortcoming that plagues the comparative literature. Ironically, comparisons are the exception rather than the rule in comparative psychology—a problem that occurs both at the species and the task level. At the species level, and just focusing on apes, there are very few studies with gorillas and bonobos. For example, there is only one study with a single infant gorilla on object permanence and rotations (Natale, Antinucci, Spinozzi, & Potì, 1986; Visalberghi, 1986) and no studies on transpositions. There is a single study on transpositions and rotations in bonobos (Beran & Minahan, 2000) but no studies on object permanence. Moreover, there are no studies that have compared the performance of various species using the same methods, and only three studies that have compared two ape species directly (chimpanzee and orangutan; Call, 2001, 2003; chimpanzee and bonobo; Beran & Minahan, 2000) in object displacement tasks. This shortcoming means that researchers still do not have a conclusive answer as to whether these species differ in their object displacement skills. This lack of comparative data can be extended to human–ape comparisons, which again seems

ironic given that the human developmental literature was the basis for most of the comparative research in this area.

From the lack of comparison between species and the emphasis on some species at the expense of others, there are very few studies that have tested the same subjects in more than one task. This has hindered researchers' ability to uncover the cognitive mechanisms that may be underlying the behavior of humans and apes in object displacement tasks. Moreover, there has been no systematic study to compare the difficulty level of object displacement tasks across species.

The purpose of this study was to alleviate these shortcomings by testing all great ape species and young children in a series of six object displacement tasks modeled after previous studies. These tasks included delayed response, inhibition test, A-not-B error, rotations, transpositions, and Stage 6 object permanence. The latter three tasks included several variations of object displacements including single and double invisible displacements. In this study, we were interested in the subjects' spontaneous responses to these tasks. We therefore reduced the number of trials and administered the tasks in short sessions.

Experiment 1: Apes

This experiment investigated the ability of great apes to retrieve hidden food rewards from an array of three cups after various spatial transformations representing various levels of complexity. We manipulated the number of containers, the location of the reward, and the time that had elapsed since the items were placed under the container as well as the type and number of displacements performed with the containers. On the basis of previous research, we predicted that introducing a time delay between hiding the reward and letting the subject choose would negatively affect the subjects' performance (e.g., Hunter, 1913); that those trials in which two rewards were placed in adjacent locations would be easier than those in which the rewards were in nonadjacent locations (Call, 2001); similarly, that adjacent displacements in the Stage 6 object permanence task would be easier than nonadjacent displacements (e.g., Call, 2001; de Blois et al., 1998; Mendes & Huber, 2004); that visible displacements in the A-not-B error would be easier than invisible displacements (Natale et al., 1986); and finally, that transpositions would be easier for the subjects than invisible displacements, which in turn would be easier than rotations (Call, 2003). We were especially interested in exploring possible species differences and variations among individuals' ability to solve object displacements.

Method

Subjects

Seven chimpanzees (*Pan troglodytes*), 4 bonobos (*Pan paniscus*), 7 gorillas (*Gorilla gorilla*), and 6 orangutans (*Pongo pygmaeus*) participated in this study. All 24 subjects were housed at the Wolfgang Köhler Primate Research Center located at the Zoo Leipzig, Germany. Our sample included 8 males and 16 females. There were 10 juveniles (4–8 years of age) and 14 adolescents and adults (>8 years of age). The mean age was 13.0 years (age range = 4–31). All apes were housed in social groups with their conspecifics in spacious indoor and outdoor areas. They were fed three times a day with their species-typical diets of vegetables and fruit. Water was available ad libitum. Subjects were not deprived of food or water at

any time. All subjects were used to being tested in observation rooms connected to their indoor areas. All subjects previously participated in experiments involving rewards hidden inside cups (e.g., Call, 2004). However, none of the subjects were previously tested on any of the present object displacement tasks. For a detailed overview of the subjects, see Table 1.

Apparatus and Materials

A wooden platform (82 cm × 60 cm) was attached to a metal frame of a Plexiglas observation window inside the testing unit. A panel (82 cm × 30 cm) rested on the platform and could be slid back and forward to present the task to the subjects. Two little handles were attached to the platform at the outer sides for allowing a controlled standardized movement with the platform. Three identical opaque square cups (11 cm wide, 8 cm high) were placed on the panel. Cups will occasionally be referred to according to their positions seen from the experimenter's perspective (left, middle, right). For one task (object permanence), an additional little cup (6 cm wide, 5.5 cm high) was used. Slices of banana and grapes were used as rewards.

Procedure

The tasks were administered in a similar fashion for Experiments 1 and 2. The locations of the rewards were randomly assigned to the left, middle, and right cup. Subjects received 30 trials in total. The order of the tasks was counterbalanced in blocks. Half of the subjects of each species received Tasks 1 and 2 on their first session, Tasks 3 and 4 on their second session, and Tasks 5 and 6 on their last session (A order). The other half of the subjects of each species received the tasks in the opposite order per session: 2 and 1, 4 and 3, and 6 and 5 (B order). We administered one session (8–13 trials, depending on the block) per day, with the next session typically following on the next day. Subjects were tested individually. We videotaped all trials.

Table 1

Species, Name, Sex, Age, and Rearing History of the Subjects That Participated in Experiment 1

Species	Name	Sex	Age	Rearing
Chimpanzee (<i>Pan troglodytes</i>)	Fraukje	F	26	Nursery
	Jahaga	F	9	Mother
	Gertruida	F	9	Mother
	Fifi	F	9	Mother
	Riet	F	24	Nursery
	Sandra	F	9	Mother
	Frodo	M	8	Mother
Bonobo (<i>Pan paniscus</i>)	Ulindi	F	8	Mother
	Joey	M	19	Nursery
	Limbuko	M	6	Nursery
	Kuno	M	5	Nursery
Gorilla (<i>Gorilla gorilla</i>)	Gorgo	M	21	Nursery
	N'Diki	F	24	Unknown
	N'Kwango	M	5	Mother
	Bebe	F	22	Unknown
	Ruby	F	4	Mother
	Viringika	F	7	Mother
Orangutan (<i>Pongo pygmaeus</i>)	Vizuri	F	7	Mother
	Bimbo	M	21	Mother
	Walter	M	13	Mother
	Dunja	F	31	Mother
	Toba	F	8	Mother
	Pini	F	14	Mother
	Padana	F	4	Mother

Note. F = female; M = male.

The experimenter sat behind the table facing the subject, who sat behind the Plexiglas partition. Three holes of 6 cm in diameter cut into the partition allowed the subjects to make a choice by touching the cups on the table by using their fingers. All subjects were very familiar with this arrangement from their participation in previous studies. At the onset of each trial, the experimenter placed the cups on their side so that the open sides were facing the subject (this will be referred to as *open*) next to each other on the platform. The experimenter slid the platform back and forth by touching each of the attached handles with extended arms in a simultaneous and standardized movement. At the beginning of the trial, the platform was in a slid-back position out of the subjects' reach, to prevent the subjects from making any premature choices. Then a trial was started with the experimenter retrieving, depending on the task, one or two piece(s) of food from a bucket behind the experimenter's back. After showing the piece(s) to the subject, the experimenter placed them in front of one or two of the three cups and then placed the cups upside down concealing the reward(s). This will be referred to as *close*. The experimenter then administered the treatment(s) specific to the tasks and pushed the platform against the Plexiglas partition allowing the subject to choose any of the cups. The first cup the subject touched was turned over by the experimenter. If the subject chose the baited cup, the subject received the reward and verbal praise. If the subject chose an unbaited cup, the male experimenter first lifted the chosen cup to show the subject that it was empty. He then lifted the other cups in full view of the subject and put them back into their open position. He retrieved the piece of food from the platform and put it back into the food bucket behind his back. He then retrieved a new piece of food holding it up to the subject and a new trial was started. We administered the following six tasks (see Figure 1 for illustrations).

Delayed response (six trials). The experimenter placed one piece of food in front of one of the cups and then closed the cups. Two conditions were administered: (a) no delay and (b) 30-s delay. In the no-delay condition, the experimenter pushed the platform against the Plexiglas after he had closed all cups. In the 30-s delay condition, the experimenter waited for 30 s after closing the cups and then pushed the platform forward. During the delay, he remained in a neutral motionless posture. Subjects received six trials in total. The first three trials were always no-delay trials followed by three 30-s delay trials. The location of the food was randomly and exhaustively assigned to the left, middle, and right cup. The 30 s were timed by the experimenter with a stopwatch.

Inhibition test (four trials). The experimenter placed a piece of food in front of each of two cups and then closed all three cups. There were two different conditions: In (a) adjacent trials, the food was placed in front of the center cup and either the left or right cup. In (b) nonadjacent trials, the food was placed in front of the left and the right cup, thus leaving the center cup empty. We administered four trials in total, two adjacent and two nonadjacent trials. The sequence of the conditions was randomly assigned.

A not B (one trial). The experimenter placed a piece of food in front of the left cup; he then closed all cups and pushed the platform forward so the subject could choose a cup. The subject was required to find the reward under the left cup on three successive trials. Once the subject met this criterion, the reward was again hidden under the same cup. However, on the critical probe trial, the experimenter lifted the cup again and retrieved the reward. In full view of the subject, he then transferred and hid the reward under the right cup. Subjects received one probe trial.

Rotations (six trials). The experimenter placed a piece of food in front of one of the three open cups. After closing all cups, he performed a 180° rotation or a 360° rotation with the platform. The experimenter lifted the platform by the handles and made two 90° rotations for the 180° condition and four 90° rotations for the 360° condition. All rotations were made by using standardized movements in a clockwise direction. At the 12 o'clock position, the experimenter's left and right hand switched positions before completing the rotation. The platform was not attached to a swivel because this would have hindered the back and forth motion of the platform. Six

trials were given (3 cups × 2 conditions). All cups and conditions were randomly assigned. The conditions produced the following final locations of the reward: after a 180° rotation, the reward was located at the opposite side if the reward had been hidden under either one of the outer cups (left or right). After a 360° rotation, the reward always returned to its starting position. On trials in which the reward was placed under the middle cup, it remained in the middle position regardless of the rotation.

Transpositions (six trials). The experimenter placed a piece of food in front of one of the three open cups. After closing all cups, he performed one of the following transpositions: (a) single swap, the cup that contained the reward and another either adjacent or nonadjacent empty cup switched locations (two trials); (b) double swap, the cup that contained the reward switched locations with the next adjacent cups thereby moving to the outer location or it switched locations with the nonadjacent cup and then with the adjacent cup thereby returning to the middle location (two trials); (c) reverse swap, the left and the middle cup switched locations two times so that the reward returned to its initial location under the left cup (one trial); (d) unbaited swap, the two empty cups switched locations, and the baited cup was not moved (one trial).

Object permanence (seven trials). The experimenter closed all cups. Then he placed the reward on the platform to the left of the outer left cup. With his right hand, he then took a little cup and placed it over the reward. He slid the reward with the help of the closed little cup over the panel toward one of the closed cups. With his left hand, he carefully lifted a cup thereby only opening the side that was facing him so that the subject could not see the reward. He made a swapping movement with the white cup as if swapping the reward under the cup. The experimenter moved the reward either just under one cup (single, three trials), two adjacent cups (double adjacent, two trials), or two nonadjacent cups (double nonadjacent, two trials). In the single-swap condition, the reward remained under this cup; in the double-swap condition, the reward was left one time in the first location and one time in the last location that was visited. After the displacement(s), the experimenter showed the subject that the cup was now empty and put it aside on the floor and then slid the platform forward for the subject to choose.

Video Coding and Reliability Assessment

For each trial, the experimenter turned over the cup the subject touched. On almost all trials, the subjects' choice was very straightforward. After testing, the experimenter verified all data from the live coding by reviewing the video recordings. A second observer coded all trials of two randomly selected subjects of each species (32% of all total trials) from the video recordings. The agreement between the experimenter's data and the second observer's data was 99% (349/352) resulting in a Cohen's $\kappa > .99$. Therefore, only the data from the experimenter were used for analysis.

Data Analysis

First, we analyzed the overall task scores. Second, we analyzed the mean scores for each of the six tasks separately, with species and condition as independent variables. We also compared the observed scores with those expected by chance. All tests had an expected chance probability of $p = .33$, except the double displacements in the object permanence task whose value was $p = .50$. Third, we tested the predictions involving comparisons between tasks and conditions. Finally, we explored the individual scores for each task.

Because of the reduced number of trials in each condition, we used the following nonparametric statistics to analyze the effect of species and gender (Kruskal–Wallis and Mann–Whitney), task and condition (Friedman and Wilcoxon), and deviation from chance (Wilcoxon) on the percentage of correct trials. We used the Bonferroni–Holm (Holm, 1979) correction when conducting post hoc tests involving multiple comparisons.

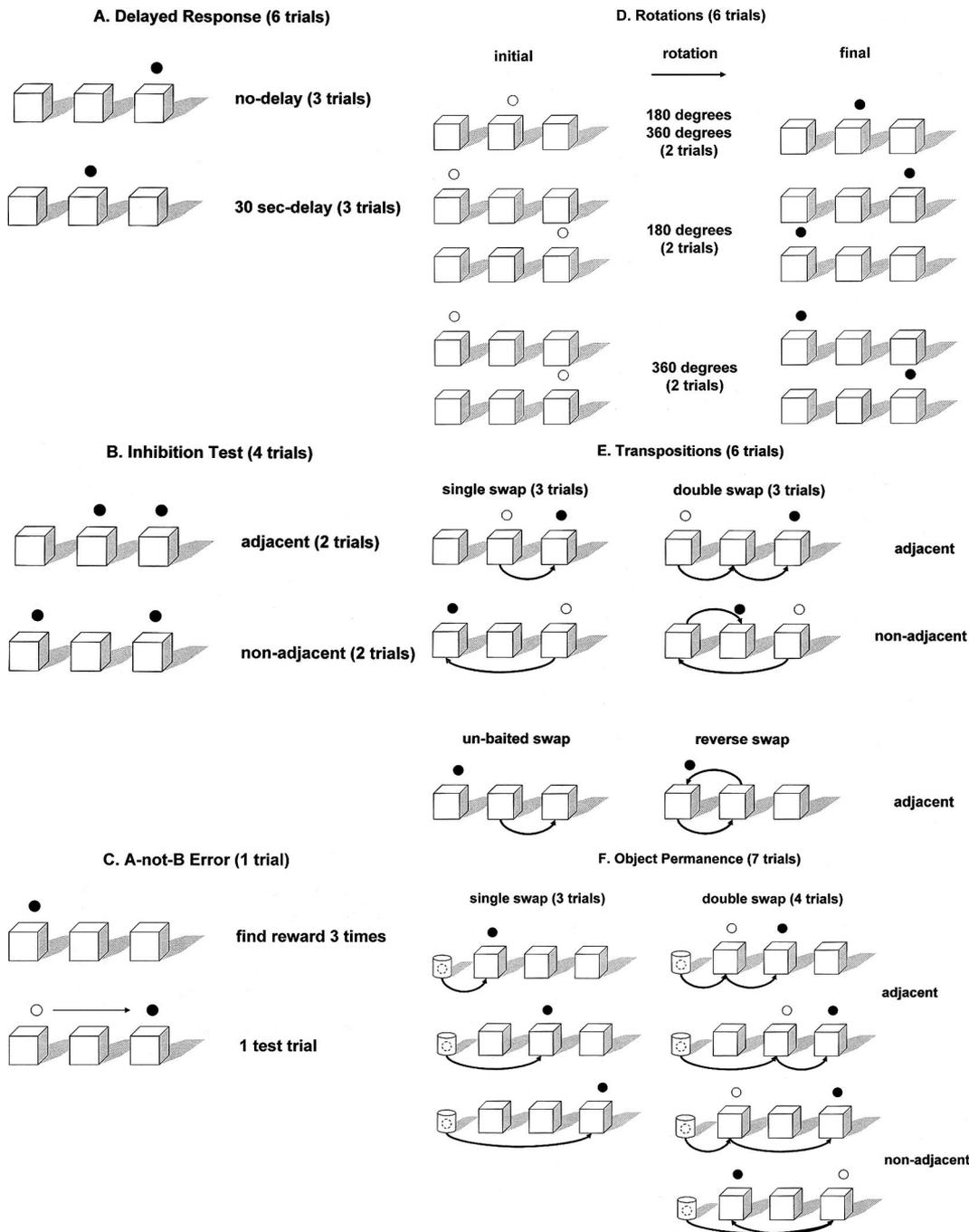


Figure 1. Illustrations of the six object displacement tasks used in Experiments 1 and 2. Black circles represent the final location of the reward(s). White circles represent the initial location of the reward(s). A: A reward was hidden under one of the three cups, and subjects were allowed to make a choice immediately or after a delay of 30 s (delayed response). B: Two rewards were hidden under two adjacent or two nonadjacent cups (inhibition test). C: After the subject found the reward three times in a row in Location A, the reward was moved in full sight from Location A to Location B (A-not-B error). D: The platform with the cups was rotated 180° or 360° (rotations). E: A reward changed positions by a single swap or a double swap (transpositions). The reward switched locations with an adjacent or a nonadjacent cup. Additionally, in one condition, the unbaited cups switched locations, and in another condition the reward switched locations twice with the adjacent cup in a reverse swap. F: A reward was moved under one of the cups with the help of an additional cup by either a single or a double swap (object permanence). In the double swap, the reward was moved under adjacent or nonadjacent locations.

Results

We did not detect any significant effect of sex on any of the tasks ($z = 0.96, p > .33$). Therefore, we collapsed this variable in subsequent analyses. Order of task presentation did not have any significant effect on any of the tasks ($z = 1.08, p > .28$), except for delayed response ($z = 2.44, p = .015$). Therefore, we collapsed this variable in subsequent analyses for all tasks except for delayed response. Table 2 presents the mean percentage of correct trials per species for each task and condition. Table 3 presents the number of subjects that selected the correct cup on all trials for each task and condition.

Overall Performance

A Friedman test showed significant differences between tasks, $\chi^2(5, N = 24) = 60.0, p < .001$. Post hoc Wilcoxon tests revealed that subjects performed significantly better in the A-not-B compared with inhibition ($p = .01$), object permanence ($p < .001$), and rotation ($p < .001$) tasks. Subjects also performed better in delayed response and transpositions compared with inhibition ($p = .001$) and rotation ($p < .001$) tasks. Finally, subjects performed better in object permanence compared with rotation ($p < .001$) tasks. To summarize, the A-not-B task (96% correct trials) was the easiest task, followed by the transpositions (86%) and delayed response (85%) tasks. The object permanence task (72%),

the inhibition test (64%), and especially the rotations task (49%) proved to be more difficult for the subjects.

Individual Tasks

Delayed response. Overall, subjects selected the correct cup an average of 85% of the trials, which is significantly above chance levels ($z = 4.35, p < .001$). Subjects performed better in the no-delay than in the delay condition ($z = 3.07, p = .002$). This difference was particularly clear in those subjects that received the delayed response task before the inhibition test (A order; $z = 2.46, p = .014$) but less so in those subjects that received the delayed response task after the inhibition test (B order; $z = 1.89, p = .059$). Species did not significantly differ in the delayed, $\chi^2(3, N = 24) = 3.21, p = .36$, or no-delayed, $\chi^2(3, N = 24) = 3.93, p = .27$, conditions. Order of presentation did not alter this result. Apes selected the correct cup significantly more often than would be expected by chance ($p = .33$) in both the delay condition ($z = 4.36, p < .001$) and in the no-delay condition ($z = 4.67, p < .001$). Inspection of the individual results showed that 22 of the 24 apes selected the correct cup on all three trials in the no-delay condition. Ten apes selected the correct cup on all three trials of the 30-s delay condition. The same 10 subjects selected the correct cup on all six trials of the task.

Inhibition test. Overall, subjects selected the correct cup an average of 64% of the trials, which is significantly above chance

Table 2
Mean Percentage of Correct Choices per Species for Each Task and Condition for Experiments 1 and 2

Task-condition	Species					
	Chimpanzee (<i>n</i> = 7)	Bonobo (<i>n</i> = 4)	Gorilla (<i>n</i> = 7)	Orangutan (<i>n</i> = 6)	Apes (<i>n</i> = 24)	Children (<i>n</i> = 24)
Delayed response (6)	93	88	79	83	85	76
0 (3)	100	92	86	100	94	92
30 (3)	86	83	71	61	75	60
Inhibition test (4)	75	88	54	46	64	51
Adjacent (2)	93	100	86	50	81	67
Nonadjacent (2)	57	75	21	42	46	33
A-not-B error (1)	100	100	100	83	96	96
Rotations (6)	67	29	52	36	49	47
180 (3)	71	31	43	42	49	50
360 (3)	61	31	68	25	49	60
180-LR (2)	57	12	43	50	44	21
360-LR (2)	79	38	50	33	52	46
180-M (1)	86	50	43	33	54	79
360-M (1)	43	25	86	17	46	75
Transpositions (6)	93	100	81	75	86	49
Single (2)	100	100	79	67	85	33
Double (2)	79	100	79	67	79	38
Reverse (1)	100	100	71	83	88	71
Unbaited (1)	100	100	100	100	100	75
Object permanence (7)	88	68	59	71	72	81
Single (3)	100	75	71	78	82	93
Double adjacent (2)	93	75	64	75	77	92
Double nonadjacent (2)	64	50	43	58	54	54
Total <i>M</i>	84	74	67	64	73	63

Note. The number of trials is indicated inside of parentheses. 0 = no delay, 30 = 30-s delay, 180 = the board was rotated 180°; 360 = the board was rotated 360°; LR = reward is located either under the left or the right cup; M = reward is located under the middle cup.

Table 3
Number of Subjects per Species Who Selected the Correct Cup on All Trials per Task and Condition in Experiments 1 and 2

Task-condition	Species					
	Chimpanzee (<i>n</i> = 7)	Bonobo (<i>n</i> = 4)	Gorilla (<i>n</i> = 7)	Orangutan (<i>n</i> = 6)	Apes (<i>n</i> = 24)	Children (<i>n</i> = 24)
Delayed response (6)	4	2	2	2	10	5
0 (3)	7	3	6	6	21	20
30 (3)	4	2	2	2	10	5
Inhibition test (4)	3	2	1	0	6	1
Adjacent (2)	6	4	5	2	17	9
Nonadjacent (2)	3	2	1	1	7	4
A-not-B error (1)	7	4	7	5	23	23
Rotation (6)	1	0	0	0	1	0
180 (3)	3	0	0	0	3	1
360 (3)	2	0	0	0	2	6
180-LR (2)	3	0	1	2	6	1
360-LR (2)	4	0	0	1	5	7
180-M (1)	6	2	3	2	13	19
360-M (1)	3	1	6	1	11	18
Transpositions (6)	4	4	2	1	11	0
Single (2)	7	4	4	2	17	4
Double (2)	4	4	4	3	15	3
Reverse (1)	7	4	5	5	21	17
Unbaited (1)	7	4	7	6	24	18
Object permanence (7)	2	0	0	0	2	5
Single (3)	7	2	3	3	15	20
Double adjacent (2)	6	2	3	4	15	20
Double nonadjacent (2)	2	1	0	1	4	6

Note. The number of trials is indicated inside of parentheses. 0 = no delay, 30 = 30-s delay, 180 = the board was rotated 180°; 360 = the board was rotated 360°; LR = reward is located either under the left or the right cup; M = reward is located under the middle cup.

levels ($z = 4.04, p < .001$). Subjects performed significantly better in the adjacent compared with the nonadjacent condition ($z = 2.67, p = .008$). Species did not significantly differ in either the adjacent, $\chi^2(3, N = 24) = 7.10, p = .069$, or nonadjacent, $\chi^2(3, N = 24) = 5.11, p = .16$, conditions. The apes selected the correct cup significantly more often than would be expected by chance in the adjacent condition ($z = 4.09, p < .001$) but not in the nonadjacent condition ($z = 0.96, p = .34$). On adjacent trials, subjects were correct on their first choice on 92% of the trials and on 89% of their second choices. On nonadjacent trials, subjects were correct on their first choice on 79% of the trials but only on 58% of their second choices. An inspection of the individual data showed that 17 of the 24 apes chose the correct cups on both adjacent trials, whereas only 7 chose the correct cups on both nonadjacent trials. Only 6 apes chose the correct cups on all four trials.

A not B. Overall, subjects selected the correct cup an average of 96% of the trials, which is significantly above chance levels ($z = 4.78, p < .001$). In fact, only 1 orangutan (Dunja) missed the correct cup on the transposition trial. Because of this ceiling effect, we conducted no further analyses.

Rotations. Overall, subjects selected the correct cup an average of 49% of the trials, which is significantly above chance levels ($z = 3.54, p < .001$). There were no differences between conditions, $\chi^2(3, N = 24) = 0.74, p = .86$. There were significant differences between species in the 360° condition, $\chi^2(3, N = 24) = 8.13, p = .043$, but post hoc Mann-Whitney *U* tests failed to confirm this effect. Apes selected the correct cup significantly

more often than would be expected by chance in the 180° condition when the reward was located in the middle cup ($z = 2.48, p = .013$) but not when it was under the left or right cup ($z = 0.70, p = .49$). Conversely, subjects selected the correct cup significantly more often than would be expected by chance in the 360° condition when the reward was located under the left or right cup ($z = 2.36, p = .018$) but not when it was located under the middle cup ($z = 1.74, p = .082$). Inspection of the individual data revealed that only 1 subject (Jahaga) selected the correct cup on all six trials. Additionally, 2 chimpanzees (Frodo and Sandra) selected the correct cup on all three trials of the 180° condition. One chimpanzee (Fifi) selected the correct cup on all three trials of the 360° condition. No other subject selected the correct cup on more than two trials per condition.

Transpositions. Overall, subjects selected the correct cup an average of 86% of the trials, which is significantly above chance levels ($z = 4.35, p < .001$). There were significant differences between conditions, $\chi^2(3, N = 24) = 11.59, p = .009$. Post hoc Wilcoxon tests indicated that subjects performed significantly better in the unbaited swap condition compared with the single ($p = .04$) and double ($p = .024$) displacements. Nevertheless, subjects were above chance in all conditions ($z > 4.1, p < .001$) in all cases.

Although there were significant differences among species in the single transposition condition, $\chi^2(3, N = 24) = 8.86, p = .031$, post hoc Mann-Whitney *U* tests failed to confirm such result. However, the two *Pan* species pooled together differed signifi-

cantly both from gorillas ($z = 2.31, p = .021$) and orangutans ($z = 3.0, p = .003$). There were no significant differences between gorillas and orangutans ($z = 0.83, p = .41$). On the unbaited swap trial, all 24 subjects chose the correct cup. Individual analyses indicated that 11 of the 24 apes chose the correct cup on all trials.

Object permanence. Overall, subjects selected the correct cup an average of 72% of the trials, which is significantly above chance levels ($z = 4.29, p < .001$). Even if we use the more conservative value of $p = .50$ associated with double displacements, subjects still performed above chance ($z = 3.80, p < .001$). Subjects performed significantly better in double adjacent compared with double nonadjacent trials ($z = 2.40, p = .016$). We made no direct comparison between single and double displacements because those conditions differed in their chance probabilities. Nevertheless, subjects selected the correct cup significantly more often than would be expected by chance ($p = .33$) in the single displacement condition ($z = 4.42, p < .001$). Subjects also selected the correct cup significantly more often than would be expected by chance ($p = .50$) in the double adjacent condition ($z = 3.15, p = .002$) but not in the double nonadjacent condition ($z = 0.82, p = .41$). Species did not significantly differ in the single, $\chi^2(3, N = 24) = 5.53, p = .14$, double adjacent, $\chi^2(3, N = 24) = 2.88, p = .41$, or double nonadjacent, $\chi^2(3, N = 24) = 2.78, p = .43$, conditions. Individual analyses indicated that only 2 of the 24 apes (Jahaga and Frodo) chose the correct cup on all seven trials. Fifteen apes chose the correct cup on both single-swap trials; also 15 apes chose the correct cup on both adjacent double-swap trials. In contrast, only 4 subjects chose the correct cup on both nonadjacent double-swap trials.

Testing the Predictions

The analysis of the delayed response task had already indicated that the delayed condition was significantly harder than the non-delayed condition ($p = .002$), thus confirming our first prediction. The ceiling effect observed in the A-not-B task also indicated this task was easier than invisible displacements, thus confirming our third prediction. For the remaining predictions, we first analyzed the effect of trajectory and displacement on the percentage of correct responses by directly comparing the two conditions of the inhibition tests and the two double displacements conditions in the object permanence test. Trajectory had an effect both on tasks with displacement (object permanence: $p = .016$) and without displacement (inhibition: $p = .008$). In contrast, displacement had no significant effect with either adjacent ($z = 0.46, p = .64$) or nonadjacent ($z = 1.0, p = .32$) trajectories. Thus, nonadjacent compared with adjacent trials significantly reduced the percentage of correct trials independently of the presence of a displacement of the containers.

Second, we analyzed the effect of type of displacement on the percentage of correct responses by directly comparing the double transposition, the Stage 6 double adjacent displacement, and the 180° rotation—all of those displacements involved a change in the position of the reward. A Friedman test revealed significant differences across conditions, $\chi^2(2, N = 24) = 10.55, p = .005$. Post hoc Wilcoxon tests revealed that the rotation was significantly harder than the transposition ($p = .021$) and the invisible displacement ($p = .018$). Contrary to our prediction, double displacement

transpositions were not easier than double invisible displacements ($p = .81$).

Discussion

In general, the results confirmed our predictions. After a 30-s delay, the subjects made fewer correct choices than when there was no delay. Adjacent trials were easier than nonadjacent trials independently of whether there was a displacement involved. The A-not-B visible displacement task presented no problem for subjects, and it was easier than invisible displacements. Finally, transpositions were easier than object permanence invisible displacements. Rotations proved to be the most difficult task.

Apes passed all of the conditions except those involving nonadjacent trials (with or without displacements) and various kinds of rotations. These results replicate previous findings (e.g., Call, 2001, 2003; de Blois et al., 1998) and extend the results to bonobos and gorillas. The results for nonadjacent trials replicate the findings of previous studies both with and without displacements (e.g., Call, 2001; de Blois et al., 1998; Natale et al., 1986). The current study also confirms that rotations were the hardest kind of displacement, a finding that the results of a previous study suggested but that was not tested directly (Call, 2003). Nevertheless, the current study shows much lower levels of success in rotations than previously reported. Call (2003) found that chimpanzees and orangutans responded correctly in 81% of the trials in the 180° rotation condition, whereas in the current study, subjects were correct in only 54% of the trials. A difference between that study and the present study is the number of cups used. Whereas Call (2003) used two cups, we used three cups in the present study. However, this difference can probably not explain the differences in results, because Beran and Minahan (2000) reported that chimpanzees and bonobos performed at high levels in their study using three cups.

We did not find any evidence that species differed in their performance with the various tasks, except that members of the genus *Pan* (chimpanzees and bonobos) performed better than gorillas and orangutans in single transpositions. However, such interspecies differences (or the lack of them) need to be viewed with caution because of the small sample size per species.

Experiment 2: Children

We tested 30-month-old children on the same series of tasks that we administered to the apes in the previous experiment. On the basis of previous studies, we had similar predictions as for the apes in Experiment 1, except that we predicted that young children would have problems solving transposition tasks (Sophian, 1984, 1986).

Method

Subjects

Twenty-four children (*Homo sapiens*; 12 girls, 12 boys) between 2 years 5 months and 2 years 7 months ($M = 2.6$ years) from Leipzig, a mid-sized town in Germany, participated in this study. The majority of the children come from a German-speaking middle-class background. They were recruited from a database that is maintained in collaboration with local kindergartens. The parents had approved their children's participation in

written form. All children were tested at the local kindergartens. The parents regularly received information materials about ongoing studies at the child lab.

Apparatus and Materials

Children were seated at a children's table, which was set up in the playroom of their kindergarten. A wooden platform (78 cm × 30 cm) was used to present the tasks to the children. Stamps with motifs of cartoon characters that children could stamp on a sheet of paper were used as rewards. Three identical square cups (11 cm wide, 8 cm high) were used to hide the stamp(s). The cups were identical in size and appearance to the cups used with the apes in Experiment 1. Again, we will occasionally refer to the cups according to their positions seen from the experimenter's perspective (left, middle, right). For one task (object permanence), an additional little cup (about 6 cm wide and 5 cm high) was used.

Procedure

The tasks were administered in a similar fashion as in Experiment 1. All subjects were tested individually with only the experimenter, an assistant, and the subject in the room. The experimenter sat on the floor behind the table facing the subject. The child was seated in the small chair in front of the table facing the experimenter. All trials were recorded on video.

Video Coding and Reliability Assessment

After presentation of the treatment, the experimenter slid the platform forward so that the subjects could reach out and turn over the cup of their choice by themselves. For each trial, the experimenter coded live which cup the subject touched first. On almost all trials, the subject's choice was very straightforward. After testing, the experimenter verified all data from the live coding by reviewing the video recordings. A second observer coded all trials of 8 randomly selected subjects, 4 boys and 4 girls (32% of total trials) from the video recordings. The agreement between the experimenter's data and the second observer's data was calculated using Cohen's Kappa. The observers agreed on 98% of the trials (367/375) resulting in $\kappa = .97$. Therefore, only the data from the experimenter were used for analysis.

Data Analysis

We applied the same analyses as in Experiment 1.

Results

We did not detect any significant effect for order of task presentation ($z < 1.82$, $p > .05$) and no effect of gender ($z < 1.20$, $p > .22$) on any of the tasks. Therefore, we collapsed these variables in subsequent analyses and analyzed the data of all 24 children together. Table 2 presents the mean percentage of correct trials for each task and condition. Table 3 presents the number of subjects who selected the correct cup on all trials for each task and condition.

Overall Performance

Children chose the correct cup on 63% of the experimental trials. There were significant differences between tasks, $\chi^2(5, N = 24) = 74.76$, $p < .001$. Post hoc Wilcoxon tests indicated that subjects performed significantly better in the A-not-B condition compared with all other conditions ($p < .01$). In addition, subjects performed significantly better in the object permanence and de-

layed response conditions compared with inhibition, transposition, and rotation ($p < .001$ in all cases). No other comparisons revealed a significant difference. This means that the A-not-B task (96% correct trials) was the easiest, followed by object permanence (81%) and delayed response (76%). The inhibition test (51%), transpositions (49%), and rotations (47%) proved to be more difficult for the subjects.

Individual Tasks

Delayed response. Overall, subjects selected the correct cup an average of 76% of the trials, which is significantly above chance levels ($z = 4.33$, $p < .001$). Subjects performed better in the no-delay compared with the delayed condition ($z = 3.70$, $p < .001$). Children selected the correct cup significantly more often than would be expected by chance in the no-delay condition ($z = 4.61$, $p < .001$) and in the delay condition ($z = 4.35$, $p < .001$). Inspection of the individual results showed that 20 of the 24 children selected the correct cup on all three trials in the no-delay condition. Five children selected the correct cup on all three trials of the 30-s delay condition. The same 5 subjects selected the correct cup on all six trials of the task.

Inhibition test. Overall, subjects selected the correct cup an average of 51% of the trials, which is significantly above chance levels ($z = 3.30$, $p = .001$). Subjects performed significantly better in the adjacent compared with the nonadjacent condition ($z = 2.75$, $p = .006$). Children selected the correct cup significantly more often than would be expected by chance in the adjacent condition ($z = 3.98$, $p < .001$) but not in the nonadjacent condition ($z = 0.70$, $p = .48$). We then compared the subjects' first and second choices depending on the conditions. On adjacent trials, subjects were correct on their first choice on 85% of the trials and on 76% of their second choices. On nonadjacent trials, subjects were correct on their first choice on 50% of the trials and on 67% of their second choices. An inspection of the individual data showed that 9 of the 24 children chose the correct cups on both adjacent trials, whereas only 4 chose the correct cups on both nonadjacent trials. Only 1 child chose the correct cups on all four trials.

A not B. Overall, subjects selected the correct cup an average of 96% of the trials, which is significantly above chance levels ($z = 4.78$, $p < .001$). Only 2 children missed the correct cup on the probe trial.

Rotations. Overall, subjects selected the correct cup an average of 47% of the trials, which is significantly above chance levels ($z = 3.84$, $p < .001$). There were significant differences across conditions, $\chi^2(3, N = 24) = 23.12$, $p < .001$. Post hoc Wilcoxon tests indicated that children performed significantly worse in the 180° rotation with change in the reward position compared with the 180° ($p < .001$) and 360° ($p = .005$) rotations without change in the reward position. Nevertheless, children selected the correct cup significantly more often than would be expected by chance when the reward remained in the same location throughout the trial (180°: $z = 4.11$, $p < .001$; 360°: $z = 3.89$, $p < .001$) but not when the reward changed positions. In fact, they performed below chance in the 180° condition ($z = 2.66$, $p = .008$) and at chance level in the 360° condition ($z = 0.96$, $p = .34$). Inspection of the individual data revealed that only 1 subject selected the correct cup on all three trials of the 180° condition. Six children selected the

correct cup on all three trials of the 360° condition. No subject selected the correct cup on all six trials.

Transpositions. Overall, subjects selected the correct cup an average of 49% of the trials, which is significantly above chance levels ($z = 3.54, p < .001$). A Friedman test revealed significant differences across conditions, $\chi^2(3, N = 24) = 17.11, p = .001$. Post hoc Wilcoxon tests indicated that children performed significantly better in the unbaited swap than in the single ($p = .024$) and double ($p = .036$) swap. Additionally, children performed significantly better in the reverse swap than the single ($p = .032$) and double ($p = .025$) swap. This means that subjects performed better in those conditions in which the reward did not change its original position. Children selected the correct cup significantly more often than would be expected by chance in the reverse swap ($z = 3.62, p < .001$) and in the unbaited swap ($z = 3.89, p < .001$) but not after the single swap ($z = 0.70, p = .48$) or the double swap ($z = 0.1, p = .93$). Individual analyses indicated that none of the 24 children chose the correct cup on all trials. Only 4 children chose the correct cup on more than 80% of the trials.

Object permanence. Overall, subjects selected the correct cup an average of 89% of the trials, which is significantly above chance (in this case, $p = .50; z = 4.29, p < .001$). Subjects performed significantly better in double adjacent than in double nonadjacent trials ($z = 3.45, p = .001$). We made no direct comparison between single and double displacements because those conditions differed in their chance probabilities. Nevertheless, subjects selected the correct cup significantly more often than would be expected by chance ($p = .33$) in the single displacement condition ($z = 4.61, p < .001$). Subjects also selected the correct cup significantly more often than would be expected by chance ($p = .50$) in the double adjacent condition ($z = 4.47, p < .001$) but not in the double nonadjacent condition ($z = 0.63, p = .53$). Individual analyses indicated that only 5 of the 24 children chose the correct cup on all seven trials. Twenty children chose the correct cup on both single-swap trials; also 20 children chose the correct cup on both adjacent double-swap trials. In contrast, only 6 subjects chose the correct cup on both nonadjacent double-swap trials.

Testing the Predictions

The analysis of the delayed response task indicated that the delayed condition was significantly harder than the nondelayed condition ($p < .001$), thus confirming our first prediction. Likewise, the ceiling effect observed in the A-not-B task also indicated that this task was easier than invisible displacements, thus confirming our third prediction. For the remaining predictions, we first analyzed the effect of trajectory and displacement on the percentage of correct responses by directly comparing the two conditions of the inhibition tests and the two double displacements conditions in the object permanence task. We analyzed the effect of trajectory and displacement on the percentage of correct responses by directly comparing the two conditions of the inhibition tests and the two double displacements conditions in the object permanence test. Trajectory had an effect both on tasks with displacement (object permanence: $p = .001$) and without displacement (inhibition: $p = .006$). Similarly, displacement had a significant effect with both adjacent ($z = 3.00, p = .003$) or nonadjacent ($z = 2.35, p = .019$) trajectories. Thus, the absence of displacements signif-

icantly reduced the percentage of correct trials independently of the reward locations.

Second, we analyzed the effect of type of displacement on the percentage of correct responses by directly comparing the double transposition, the Stage 6 double adjacent displacement, and the 180° rotation—all of those displacements involved a change in the position of the reward. There were significant differences across conditions, $\chi^2(2, N = 24) = 33.26, p < .001$. Post hoc Wilcoxon tests revealed that the rotation was significantly harder than the transposition ($p = .046$) and the invisible displacement ($p < .001$). Double adjacent displacements were easier than double transpositions ($p < .001$).

Comparison Between Apes and Children

Table 2 shows the mean percentage of correct trials for each task in apes and children. Apes performed better than children in the transpositions task ($z = 4.96, p < .001$). In contrast, Mann-Whitney U tests detected no significant differences between apes and children on the other tasks (delayed response: $z = 1.86, p = .063$; inhibition: $z = 1.60, p = .11$; A not B: $z = 0.0, p = 1.0$; rotations: $z = 0.03, p = .97$; object permanence: $z = 1.63, p = .10$).

Discussion

In general, the results confirmed our predictions. As expected, visible displacements in the A-not-B task presented no problems for the subjects, and it was the easiest task of all. As expected, no-delay trials were also easier than delay trials. A comparison between the trials in the inhibition and the object permanence tasks revealed that adjacent trials were easier than nonadjacent trials independently of whether there was a displacement involved, thus confirming previous results (Call, 2001). It is interesting to note that both adjacent and nonadjacent trials were easier when there was a displacement involved. Although this may seem counterintuitive, one has to recall that inhibition trials (which involve no displacement) have an expected probability of .33, whereas double invisible trials (which involve a displacement) have an expected probability of .50.

As was the case with the apes, children found rotations particularly difficult. Additionally, unlike the apes, children found transpositions harder than object permanence displacements. Children experienced the greatest difficulties when the reward changed its initial position because of the rotation or transposition of cups. These results confirm previous studies with children that had suggested that rotations were the hardest type of displacement and object permanence displacements were the easiest (Lasky, Romano, & Wenters, 1980; Sophian, 1984, 1985). In fact, Lasky et al. (1980) found that children younger than 7 years of age find rotations particularly difficult.

General Discussion

Apes and young children showed proficiency in solving most kinds of object displacements. Overall, both groups performed at similar levels in all tasks except the transposition task, in which apes performed significantly better than children. Focusing on apes, chimpanzees and bonobos performed better in single trans-

positions than gorillas and orangutans. It is important to note that because the subjects showed a differential performance across conditions and tasks, the results cannot be explained by inadvertently given cues.

Several implications can be drawn from our results regarding the factors that control the successful search of objects in displacement tasks. First, there was a marked tendency to respond in certain ways that subjects had to inhibit to achieve a successful search. Thus, all species had serious difficulties with nonadjacent trials. Thus, on choosing one of the containers forming a straight line, subjects experienced great difficulty if they had to skip the next empty container. This error was observed independently of whether there was a displacement of the reward involved, because it appeared both in the inhibition task (no displacement) and in the object permanence task. Call (2001) suggested that this resulted from an inhibition problem. Subjects could not inhibit the tendency of choosing the container closest to their hand. In contrast, de Blois et al. (1998; de Blois, Novak, & Bond, 1999) argued that errors in the nonadjacent trials resulted from a memory problem. Subjects experienced difficulties recalling the exact location in which the second item may have been. However, Call (2001) argued that memory alone was unlikely to explain the results because subjects faced the same number of containers and rewards both in adjacent and nonadjacent trials. The only thing that changed was the location of the objects. Interestingly, children, who experienced this difficulty as much as the apes, showed a strong tendency to select the middle cup on their first choice on nonadjacent trials. It is quite striking that 30-month-olds chose an empty cup even though they had seen that it was empty just a few seconds earlier. Call (2001) postulated that a possible explanation for this result was the equally strong influence of the two containers and not the fact that children had forgotten about the location of the food. In fact, it may be precisely because they remembered the location of the rewards in this setup that they experienced difficulties.

Recently, Beran et al. (2005) contrasted the inhibition and the memory hypothesis by investigating chimpanzees' accuracy in retrieving two rewards each placed under one of five- or seven-container arrays (depending on the experiment) forming a straight line. Subjects were highly accurate in their first choice regardless of its position in the array, but performance deteriorated in their second choice as a function of the location of the second reward in relation to the reward that subjects had just recovered. Performance was worst when there was a single empty container between the two baited ones but steadily recovered proportionally to the distance between the two baited cups. Thus, subjects performed better on those trials in which there were five compared with two empty containers between the two baited containers. Subjects also performed at high levels when the two baited containers were adjacent (i.e., there was no container between them). Beran et al. (2005) convincingly argued that a memory failure rather than a lack of inhibitory control was a more likely explanation for the errors observed. Otherwise, one would have expected to see a distribution of errors independent of the distance between the baited containers (and this was not the case).

However, if a memory failure was solely responsible for these data, one would expect that search errors would be equally distributed around the vicinity of the remaining baited container, especially for those trials in which Containers A and C were baited, whereas Container B, located in between Containers A and

C, was empty. Of particular interest are those trials in which the containers occupied a central position (e.g., Positions 2, 3, and 4 out of five positions arranged in a straight line) so that there were selection possibilities on each side of each container. The inhibition hypothesis predicts that errors would be concentrated on Container B, whereas the memory hypothesis predicts that errors would be equally distributed to the left and to the right of Container C. There were 50 such trials in Experiment 3 (Beran, Beran, & Menzel, 2004; Beran et al., 2005). Subjects correctly selected both baited containers (A and C), thus skipping Container B, in 30 out of 50 trials. In the remaining 20 trials, subjects committed an error in their second choice, which was distributed in the following manner: 14 choices were directed to Container B, the adjacent container, whereas 5 choices were directed to the nonadjacent container. One additional choice was directed to the container adjacent to the first choice but in the opposite direction of Container B. Subjects directed significantly more responses to the adjacent ($14/19 = 74\%$) than the nonadjacent container, $\chi^2(1, N = 19) = 4.26, p = .039$, thus supporting the inhibition hypothesis. However, if one focuses on all trials regardless of success, subjects refrained from choosing Container B on 72% of the trials (Binomial test: $p < .001$). This means that although inhibition appeared to contribute to the errors observed, it was not strong enough to prevent subjects from making correct choices above chance levels.

Second, as noted above, there are also clear indications that memory load and certain object-container configurations determine successful object searches. Clearly, the most obvious indication of the role of memory is the substantially inferior performance in delayed trials compared with nondelayed trials in the delayed response task. In addition, a comparison of the three types of displacement tasks also suggests that the ability to keep track of multiple elements in the task plays an important role. Recall that apes and children performed best in the object permanence task and worst in the rotation task. This pattern of results could be a consequence of the number of elements that changed position during a displacement. In rotations, all three elements (platform, containers, and reward) experienced location changes, whereas in object permanence displacements, only the reward location changed.

Transpositions are a test case for the hypothesis that success is directly dependent on the number of elements that change locations. In the transpositions task, only the cups and the reward change locations. Because the platform is not moved in this task, one would predict that the difficulty level of this task would fall between that of the object permanence and the rotation displacements. Results indicated that apes found transpositions comparable with object permanence displacements and both tasks easier than rotations. In contrast, children found transpositions comparable with rotations and both tasks harder than object permanence displacements. Indeed, the difference between apes and children in transpositions is striking. Only 4 of 24 children solved this problem compared with 17 of the 24 apes. This result is quite puzzling, although not unexpected, as previous reports suggested that transposition problems are harder for children to solve than object permanence tasks (Sophian & Sage, 1983). Additional studies showed that children younger than 5 years of age have trouble with spatial transpositions (Sophian, 1984, 1986).

So why might transpositions be so difficult for children? According to Piaget (1954), it is not until after the sensorimotor stage

of development that children understand the movements of hidden objects, because they do not understand the representation of the cup as containing the object. One possibility is that children did not track the displacement of objects when the container also changed locations. This would explain why they succeeded in those transpositions and rotations that did not involve a change of the reward's initial location (i.e., reverse swap, unbaited swap, 180° in center, and 360°) but failed in those in which the reward changed locations (single and double transpositions and 180° side rotation). Some evidence suggests, however, that infants before the representational stage of development understand that objects hidden under a cup move with the cup (Sophian, 1985). The children in our study were old enough to understand that the object moved with the cups. We suggest that the challenges of the transposition task are the sequences of movements in which relevant containers are easily confused with irrelevant containers. That is, the children do not only have to represent the container as containing the object but have to update information constantly, especially in double transpositions. In contrast, apes solved transpositions and the object permanence task equally well in the current study, and some previous studies have even indicated that transpositions are easier for apes than object permanence displacements (Beran & Minahan, 2000; Call, 2001).

Although the results on transpositions do not perfectly fit the hypothesis of an inverse relation between performance and the number of elements that change location in the displacement, it is still possible to argue that apes and children have different thresholds for the number of elements that they can track during displacement tasks. Thus, 30-month-old children can cope with transformations in one element, whereas apes can cope with transformations in up to two elements. The alternative to this hypothesis is that some types of displacements are intrinsically harder than others regardless of the number of elements that undergo spatial changes. For instance, apes found 180° rotations in which the reward did not change locations (because it was under the center container) significantly harder than transpositions in which the reward changed location, even though in both tasks, two elements changed their initial locations. Conversely, children found that kind of rotation easier than that kind of transposition.

Thus, there may be at least two factors related to attention and memory that influence apes' performance in displacement tasks. One is the number of elements involved in the transformation, and the other is the type of transformation taking place. The more elements change locations, the more difficult the task becomes for both apes and children. Moreover, young children find tasks in which the containers change locations particularly difficult, whereas apes find tasks in which a rotation is performed with the platform on which three or more containers rest particularly difficult. Note that apes performed well on various rotations with two, three, or five containers (Beran et al., 2005; Call, 2003).

We can also draw some conclusions from comparing the performance of the various species. The tasks used in the current study revealed far more similarities than differences among species. Only the transposition task uncovered systematic differences not just between children and apes but also within ape genera. In particular, chimpanzees and bonobos performed better on spatial transpositions than gorillas and orangutans. Motivation alone cannot explain our results because members of the genus *Pan* were not different from gorillas or orangutans in certain tasks. Besides, if

motivation alone could explain species differences, one would expect to find more consistent interspecies differences across tasks. It is also not the case that the particular chimpanzees that we tested were simply smarter than the latter, because other studies conducted on the same group of individuals have shown no substantial differences between species and have in fact produced the opposite pattern of results to the current study (Call, 2004; Suda & Call, 2004). For instance, Suda and Call (2004) found that orangutans performed better than chimpanzees and bonobos in Piagetian liquid conservation tasks. This suggests that interspecies differences are task dependent and points to the wholly unsurprising (but often ignored) conclusion that ape cognition is not monolithic but is open to specialization in each species. One important task for the future will be to map where the similarities and the differences across species reside.

Another important issue is the comparison between apes and other species. The data available suggest that apes differ from cats and dogs in displacement tasks (Collier-Baker, Davis, & Suddendorf, 2004; Doré et al., 1996). Doré et al. (1996) reported that cats and dogs failed transposition problems comparable with those that apes solved in the current and previous studies (e.g., Beran & Minahan, 2000; Call, 2003). Likewise, Collier-Baker et al. (2004) found that dogs solved invisible displacements using the proximity to certain items compared with apes that used representational strategies.

Parrots and corvids perform better than cats and dogs and appear capable of solving various types of invisible displacements (Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986; Pollok, Prior & Güntürkün, 2000). However, these results are not uncontroversial because they are based on the Uzgiris–Hunt scale to measure object permanence. Several authors have criticized this scale because correct responses are scored according to the order of searches rather than on whether subjects search only in possible places (e.g., Doré et al., 1996; Sophian, 1985). For instance, in the last (and presumably most demanding) task of this scale (i.e., three consecutive invisible displacements), subjects are credited with passing this task if they search under the last cover visited by the experimenter or if they search in the reverse order to the trajectory described by the object. However, it is not clear that searching under the first cover first is incorrect. If the subject has a representational notion of objects, the objects could be under any of the covers and the search order is irrelevant. Searching all covers irrespective of order should be acceptable. But this raises another problem. If one disregards the search sequence, subjects could solve the problem using a nonrepresentational strategy consisting of searching under all locations until finding the object. The solution to this second problem, which a number of researchers have adopted, is to displace the object only under two of the three available containers (Natale et al., 1986; Sophian, 1985) and scoring searches to the nonvisited container as incorrect. Recently, Pepperberg et al. (1997) found that 2 African grey parrots not only solved this kind of displacement but also a transposition displacement.

There is also some evidence that apes perform better than monkeys in invisible displacement tasks (e.g., de Blois et al., 1998). However, caution is needed in establishing broad comparisons across taxa because only a few monkey species have been investigated under controlled situations. There are indeed some studies that found no differences between monkeys and apes in

several invisible displacements such as single displacements (de Blois & Novak, 1994; Neiworth et al., 2003). Neiworth et al. (2003) even found that cotton-top tamarins solved double invisible displacements above chance. However, their methodology was based on allowing subjects to choose only one of the containers. Because subjects showed a marked tendency to touch the last container visited by the experimenter, one may interpret this in terms of a recency effect (see also Beran et al., 2005), which, as the authors indicated, did not appear in visible displacements. Allowing subjects to select two containers and varying the final location of the reward between the first and second container visited may have helped to disambiguate this result. It is therefore still unclear whether apes and monkeys differ substantially in object permanence or any other type of displacement, for which there is little data available to compare species.

In conclusion, apes and young children solved most kinds of object displacements and performed at comparable levels in all tasks except the transpositions task, in which apes performed better than children. The different ape species also showed more similarities than differences. The only reliable difference arose in single transpositions, in which chimpanzees and bonobos performed better than gorillas and orangutans. This series of object displacement tasks proved to be a sensitive and easily applicable tool (using a small number of trials per task) for measuring the ability to track object displacements in great apes and young children. One of the most promising avenues for future research is the use of batteries of tasks like this as standardized tests across several labs. Results from different populations could then be compared and would provide interesting insights into variables such as rearing history and sex differences that are usually unaddressed in comparative studies because of low number of subjects.

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