

RESEARCH ARTICLE

Great Apes Track Hidden Objects After Changes in the Objects' Position and in Subject's Orientation

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Eight chimpanzees (*Pan troglodytes*), five bonobos (*Pan paniscus*), five gorillas (*Gorilla gorilla*), and seven orangutans (*Pongo pygmaeus*) were presented with two invisible object displacement tasks. In full view of the subject, a food item was hidden under one of three opaque cups resting on a platform and, after an experimental manipulation, the subject was allowed to select one of the cups. In the rotation task, the platform was rotated 180° while the subject remained stationary. In the translocation task, the platform remained stationary while the subject walked to the opposite side from where she saw the reward being hidden. The final position of the food relative to the subject was equivalent in both tasks. Single displacement trials consisted of only one manipulation, either a rotation or a translocation, whereas double displacement trials consisted of both a rotation and a translocation. We also included no displacement trials in which no displacements took place. No displacement trials were easier than single displacements which, in turn, were easier than double displacements. Unlike earlier studies with children, there was no difference in performance between rotation and translocation displacements. Overall, apes performed above chance in all conditions, but chimpanzees outperformed the other species. This study reinforces the notion that the great apes use an allocentric spatial coding. *Am. J. Primatol.* 72:349–359, 2010. © 2010 Wiley-Liss, Inc.

Key words: object permanence; rotations; spatial memory; allocentric spatial coding

INTRODUCTION

Pursuing prey in open ground, following group members to a watering hole, or finding a fruit that has been seen falling from a tree are based on the ability to track the movement of animate and inanimate objects in space. Much of the object trajectories that individuals track are visible, that is, the individual has constant visual access to the successive target positions. However, there are also numerous cases when the target's current trajectory becomes occluded behind some visual obstacle [de Blois et al., 1998; Mendes & Huber, 2004]. For instance, a grey mouse may enter the end of a fallen hollow tree while trying to escape a pursuing fox. It would be advantageous for the fox to be able to anticipate the possible exit location of its prey, based on the nature of the obstacle and its prey's trajectory before disappearance, or, in case the mouse did not go out the expected location, to infer the potential places where it might be relocated.

Keeping track of the positions of objects in space is a challenging task, because even the simplest movement of an object implies the modification of many spatial relations [Sophian, 1984]. Nevertheless,

numerous studies have shown that birds and mammals can cope with displacements in which the trajectory of the object is visible and can recover objects that have disappeared from sight behind opaque barriers [e.g. Call, 2001; Collier-Baker et al., 2004; de Blois et al., 1998; Deppe et al., 2009; Doré, 1986; Dumas, 1992; Fedor et al., 2008; Fiset & Leblanc, 2007; Mendes & Huber, 2004; Natale et al., 1986; Neiworth et al., 2003; Pepperberg & Kozak, 1986; Pepperberg et al., 1997; Pollok et al., 2000; Regolin et al., 1995, 2005; Schino et al., 1990; Zucca et al., 2007]. When perceptual access to the object's trajectory is blocked, the task complexity increases. According to Sophian [1986], this is because individuals must constantly update the *representation* of the unperceived object and its position while

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maintaining a stable representation of the position of those objects that have not moved. However, not all invisible object displacements are equivalent and we can distinguish various types that vary in their difficulty. Filion et al. [1996] found that rhesus macaques were able to anticipate the location where objects moving on a computer screen would reemerge after disappearing behind an obstacle in a computerized task. Just as it was the case for visible displacements, it is very likely that some types of invisible displacement tracking, such as those based on extrapolating the object's trajectory before disappearance, are widespread in the animal kingdom.

There are other types of invisible displacements whose distribution, however, seems much more restricted. The Piagetian stage 6 invisible displacement is a case in point. This displacement entails the target object being placed in full view of the subject inside an opaque container (or the experimenter's closed hand) and moved successively between two or more hiding locations (e.g. containers). For instance, the container with the target object may visit location 1, then location 2, and completely skip location 3. The reward is left inconspicuously in one of the visited locations, and upon the container's displacement, the subject is shown that the container is now empty. Subjects are considered to pass this task when they only search those locations visited by the container, which is where the object could possibly be, and do not search the location not visited by the container. Several control conditions have been devised to detect the use of simpler strategies based on only picking the touched containers or those that are visited first or last [see Fedor et al., 2008]. Several species, including great apes [Barth & Call, 2006; Call, 2001; de Blois et al., 1998, 1999] and psittacids [Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986; Pepperberg et al., 1997], have provided conclusive evidence of their ability to solve this task, whereas the available evidence for other species, such as lesser apes and monkeys, is less convincing [Fedor et al., 2008; Mendes & Huber, 2004; Neiwirth et al., 2003]. Moreover, simple object displacements (i.e. the reward visits one single container) are easier than double displacements (i.e. the reward visits two containers), especially if the two visited containers are nonadjacent [Barth & Call, 2006; Call, 2001; de Blois et al., 1998].

The two, mentioned earlier, types of tasks (trajectory anticipation and stage 6 invisible displacements) only involve the displacement of the target. Two other tasks have investigated the simultaneous movement of both the target and the target's potential occluders. In the transposition task, subjects are presented with two or three identical containers forming a straight line and one of them is baited in full view of the subject. Then the position of some or all the containers is switched. In order to choose correctly, the subject has to track the

container where the food has been hidden. Children find this task harder than stage 6 invisible displacements [Barth & Call, 2006; Sophian, 1984]. The four great apes [Barth & Call, 2006; Beran & Minahan, 2000; Call, 2003] and African grey parrots [Pepperberg et al., 1997], unlike cats [Doré et al., 1996] and dogs [Collier-Baker et al., 2004; Fiset & LeBlanc, 2007], can solve this task even when it involves several object transpositions. Those transpositions that involve the container holding the reward are harder than those where the containers moved are empty, and thus the reward remains where the subject last saw it [Sophian, 1984, 1986]. Moreover, just like in stage 6 object displacements, single transpositions (i.e. two containers switch positions once) are easier to solve than double transpositions (i.e. two containers switch positions once and then the same or other containers switch positions again) [Barth & Call, 2006].

Even more demanding than transpositions are rotations, in which the target object is placed in full view of the subject under one of several identical containers and the containers and target object change positions by rotating the platform on which they are located. Although great apes can solve this task [Barth & Call, 2006; Beran & Minahan, 2000; Beran et al., 2005a,b; Call, 2003], they find it harder than transpositions, as happens for human children [Barth & Call, 2006; Call, 2003; Sophian, 1986]. Moreover, the difficulty depends on the amount of rotation. Thus, rotations of 360° are easier than 270° or 90° rotations, which are in turn easier than 180° rotations [Call, 2003; Lasky et al., 1980; but see Beran et al., 2005a]. Okamoto-Barth and Call [2008] studied rotations in 3–9 year old children and apes. They found that both children and apes could solve standard rotations, whereas only children solved a condition where the rotation of the array occurred behind a visual barrier and the location of the food could only be inferred by considering a landmark. These results suggest that the apes rely more on place than on visual cues to locate hidden rewards even though they have this capacity, as was shown in a study by Beran et al. [2005b] where three chimpanzees were able to use landmarks in order to track rotational displacements, regardless of the landmarks being symbolic (representing the hidden food reward) or nonsymbolic. Okamoto-Barth and Call [2008] found that the rotation task differed in difficulty depending on the type of landmark used, with objects placed by the baited container facilitating the task more than the color of the cups or distinctive features on the background. Similarly, Potì [2000] found that two capuchin monkeys (*Cebus apella*) 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.

Unlike the data available for the great apes, there are no studies that have systematically compared each of these three spatial displacement tasks (Piagetian stage 6 invisible displacements, transpositions, and rotations) in other primate species. Moreover, there is no information that we are aware of on transpositions in monkeys and, as far as we know, there is only data on Piagetian stage 6 invisible displacements for the lesser apes [Fedor et al., 2008]. Also, there is need for more data on other even less studied invisible object displacement tasks. For example, not much is known about how great apes (and other animals) cope with invisible changes in the relative rather than the absolute position of objects owing to the subject's own movement (the so-called translocations).

Unlike those object displacements that entail changes in the absolute location of objects, translocations entail a change in the subject's position relative to the object while the object remains stationary. For instance, the subject may take a position just opposite to her original location, which would result in the same effect as a 180° rotation. Few studies have investigated the ability of primates to solve translocations. Tinklepaugh [1928] found that one Philippine monkey (*Macacus cynomologos*) and one rhesus macaque (*Macaca mulatta*) could retrieve a piece of food that they had seen hidden under one of two cups, after walking around the array of cups and facing them from the opposite side. The Philippine monkey also performed correctly when a visual barrier prevented him to keep track of the position of the food during walking. Visalberghi [1986] investigated the ability of an infant gorilla to track the location of a food reward within a spatial array of four containers, after being carried around the array. The gorilla was successful as long as she remained stationary or when, after 360° translocations, she could choose from the same place where she had witnessed the baiting, but failed when she had to retrieve the food from one side (90°) or from the opposite side (180° translocations). More recently, Hoffman and Beran [2006] reported that two adult chimpanzees were capable of locating a reward that had been hidden under one of four containers, after undergoing a 180° change of orientation with respect to their original location and the location of the containers. One of these chimpanzees also performed above chance when the experimenters placed a visual barrier, so that she could not visually track the location of the food during her movement around the spatial array. The authors concluded that chimpanzees were capable of using allocentric cues during their spatial searches.

In an allocentric frame of reference, the location of an object is specified with reference to other objects, whereas in an egocentric frame of reference, the location of an object is specified with reference to

the subject's body. Haun et al. [2006] also investigated the use of spatial frames of reference in humans and apes. They presented human children and adults from two cultures and representatives of each of the nonhuman great apes with two platforms facing each other but separated by an opaque barrier. Each platform had a set of three aligned containers placed on it. While the subject was facing platform 1, she witnessed the experimenter placing a reward under one of its cups. Then the subject moved around the platform to a position just opposite of her initial location and while she was facing platform 2 (platform 1 lay beyond the opaque barrier), she was allowed to select one of the cups available. Haun et al. [2006] found that apes used an allocentric rather than an egocentric frame of reference. Moreover, the widespread preference for the allocentric frame of reference across species belonging to the same phylogenetic clade led the authors to conclude that such a preference was likely to reflect a common phylogenetic inheritance from the common ancestor shared by all four genera.

Besides the paucity of data on translocations, there is also little known about how translocations compare to other object displacements. Although similar skills are required for solving both rotations and translocations, as would be the case of visual perspective taking which happens to be good in both children [Call & Carpenter, 2001] and chimpanzees [Krachun & Call, 2009], several studies with children have found differences in performance between the two tasks. Bremner [1978] found that 9 month old human infants found 180° translocations easier than 180° rotations. Furthermore, Lasky et al. [1980] tested children of several ages, comparing different degrees of rotations and translocations with a four-cup array and found that, whereas translocations were solved by 2–4 year old children, rotations were only consistently solved at around 7 years of age. These results suggest that as infants begin to crawl, they improve their searching abilities first in a condition where they move among stable objects than in a condition where the objects move while they remain stable [Okamoto-Barth & Call, 2008]. Thus, it seems that translocations, at least in human infants, are easier than rotations.

In brief, rotations and translocations are tasks aimed at investigating the cognitive representation of hidden objects and their movement, and they have proven difficult to solve, possibly because in these tasks every element of the problem changes positions with respect to the subject, which may complicate the tracking of the goal object. These tasks are, therefore, useful to explore possible differences between species, which could be owing to different social or ecological factors, and can help us to reconstruct the evolution of object-tracking abilities. Moreover, the performance of subjects on translocations gives us

information about the type of spatial representation used by the species. Finally, and despite the fact that the capabilities required to solve both tasks are similar, it has been found that translocations are easier to solve than rotations for children. This could have an ontogenetic explanation: humans face more often and from an earlier age a situation where they move in space to find still objects than the other way around. It would be interesting to know if this is true for other species as well.

In conclusion, there are two key pieces of information that are currently missing in the nonhuman literature. First, all the data available on ape translocations are exclusively based on two chimpanzees and one infant gorilla. Also, missing data on the other great apes is problematic because it prevents us from being able to attempt a reconstruction of the evolution of object tracking and spatial representation in the great apes. Second, there exists no direct comparison of the performance of apes in rotations (i.e. changes in the objects position in relation to a stationary subject) compared with translocations (i.e. changes in the subjects position in relation to a stationary object). The aim of this study was to remedy this situation by comparing the performance of chimpanzees, gorillas, bonobos, and orangutans in translocations and rotations. Subjects were presented with three aligned opaque containers resting on a platform and witnessed the experimenter hide food under one of the containers. In the slide condition, the experimenter slid the platform away from the subject against a window opposite their location. To retrieve the reward, subjects had to walk to the opposite side from where they had witnessed the baiting and select the correct container. We compared this condition to the rotate condition, in which the subject remained stationary and the platform (and the containers) changed their orientation by 180°, thus making the location change of the reward comparable to that in the slide condition. We also administered two other conditions in which subjects experienced a combination of a rotation and a translocation (rotate–slide) or a translocation and a rotation (slide–rotate), in order to compare the relative difficulty of single and double displacements, and a condition (baseline) where no movement was applied to any part of the experimental setup.

METHOD

Subjects

Eight chimpanzees (*Pan troglodytes*), five bonobos (*P. paniscus*), five gorillas (*Gorilla gorilla*), and seven orangutans (*Pongo pygmaeus*) participated in this study. Our sample included 7 males and 18 females. There were five juveniles (5–8 years of age) and 20 adolescents and adults (> 8 years of age).

The mean age was 14.2 years (range: 5–31). All subjects were socially housed at the Wolfgang Köhler Primate Research Center, located at the Leipzig Zoo, Germany. Each group had access to spacious indoor and outdoor areas furnished with natural vegetation, climbing structures, and visual barriers. They were fed three times a day with their species typical diets of vegetables and fruit. Water was available ad libitum. All subjects were tested individually in testing rooms adjacent to their indoor areas. They were not deprived of food or water at any time. All subjects had earlier participated in object displacement tasks [Barth & Call, 2006], including a delayed response task and a rotations task, however, not involving subject movements as a task variable. For a detailed overview of their age, sex, and rearing history, see Table I. All research reported in this manuscript adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates as well to as all German laws regarding animal holding and testing (German “Tierschutzgesetz”).

TABLE I. Sex (F, Female; M, Male), Age (in years), and Rearing History of the Subjects That Participated in the Study

Species	Name	Sex	Age	Rearing
Chimpanzee (<i>Pan troglodytes</i>)	Fraukje	F	27	Nursery
	Jahaga	F	10	Mother
	Gertruida	F	9	Mother
	Fifi	F	9	Mother
	Riet	F	25	Nursery
	Sandra	F	9	Mother
	Frodo	M	9	Mother
	Dorien	F	22	Nursery
Bonobo (<i>Pan paniscus</i>)	Ulindi	F	9	Mother
	Joey	M	20	Nursery
	Limbuko	M	7	Nursery
	Kuno	M	6	Nursery
	Yasa	F	10	Mother
Gorilla (<i>Gorilla gorilla</i>)	N’Diki	F	25	Unknown
	N’Kwango	M	6	Mother
	Bebe	F	23	Unknown
	Ruby	F	5	Mother
	Viringika	F	12	Mother
Orangutan (<i>Pongo pygmaeus</i>)	Bimbo	M	22	Mother
	Walter	M	13	Mother
	Dunja	F	31	Mother
	Toba	F	9	Mother
	Pini	F	14	Mother
	Padana	F	5	Mother
	Dokana	F	18	Mother

The nursery-reared subjects were bottle-fed by humans during approximately their first two years of life. In the case of the chimpanzees, this happened in a biomedical research center, with peer cohorts. The bonobos were raised by keepers from zoos other than the Leipzig Zoo.

Materials

A table (82 cm × 60 cm) connected two testing windows that faced each other in the booth of a testing unit (see Fig. 1A, B). A platform (82 cm × 30 cm) rested orthogonally on the table and could be slid from one window to the other with the help of two small handles attached to the outer sides of the platform for allowing a controlled standardized movement of it. Three identical opaque square cups (11 cm wide, 8 cm high) were placed in a row on the platform. The windows consisted of a Plexiglas panel with three circular holes at the bottom that permitted the subject to choose among the three cups on the platform by touching them. All subjects were very familiar with this interaction. The door connecting the two contiguous enclosures that had the two testing windows was left open during the test to allow the free movements of the subjects between them. Grapes and banana slices were used as rewards.

Procedure

The experimenter sat behind the table facing the booth (Fig. 1A, B). The subject sat behind the Plexiglas window 1 (see Fig. 1B). At the onset of each trial, the experimenter placed the square cups on their side, so that the open sides were facing the subject, next to each other on the platform. The platform was in a slide-back position to prevent the subjects from making any premature choices. The experimenter then, in full view of the subject,

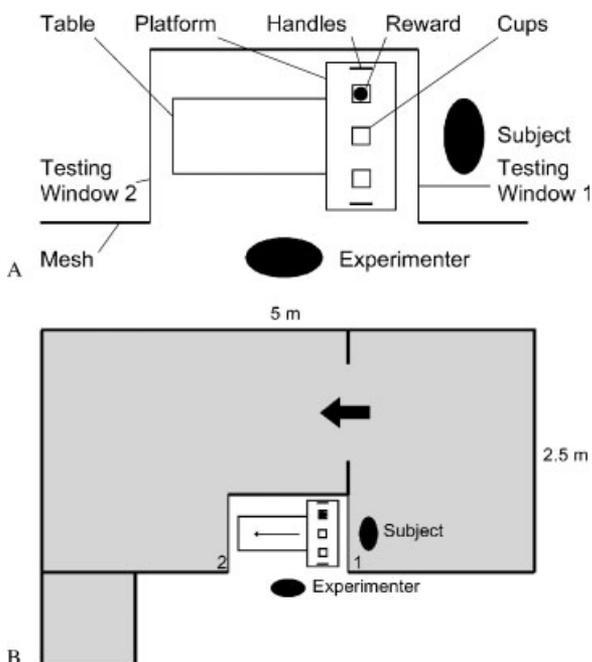


Fig. 1. (A) Experimental setup. (B) Diagram of the testing unit. See text for details.

placed a piece of food in front of one of the cups and placed all the cups upside down concealing the reward (see Fig. 2). The experimenter then administered one of the five conditions listed below and pushed the panel against the Plexiglas window, allowing the subject to choose any of the cups. The first cup the subject touched was scored as the choice. If the subject chose the baited cup, she received the reward and verbal praise. If the subject chose an empty cup, the experimenter just lifted the cup showing the subject that it was empty and then lifted the other two cups to show their content, and a new trial was started. There were five conditions (Fig. 3):

Baseline

The experimenter simply pushed the platform against window 1 so that the subject could choose one of the cups. Because there was no displacement of any kind, the reward remained where the experimenter had initially deposited it. This condition provided an assessment of the subjects' motivation to participate and the general understanding of the task.

Rotate

The experimenter rotated the platform 180° and then pushed it against window 1. Specifically, the experimenter lifted the platform and made two 90° rotations with it. 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. After the rotation was completed, the reward was located at the opposite side of the platform if the reward was hidden under either one of the outer cups (left or right). On trials where the reward was placed under the middle cup it remained in the middle position.

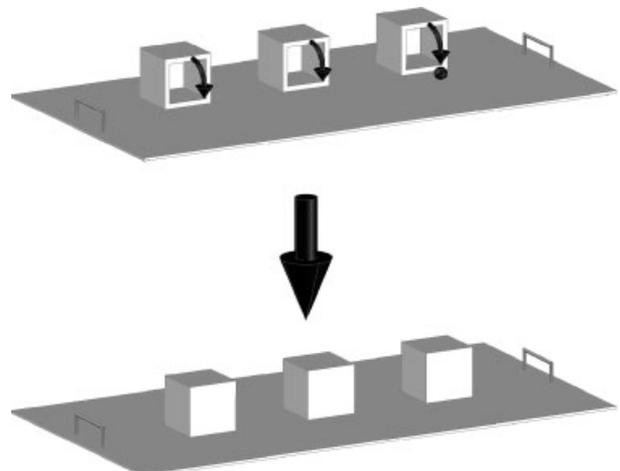


Fig. 2. Conceal of the reward. See text for details.

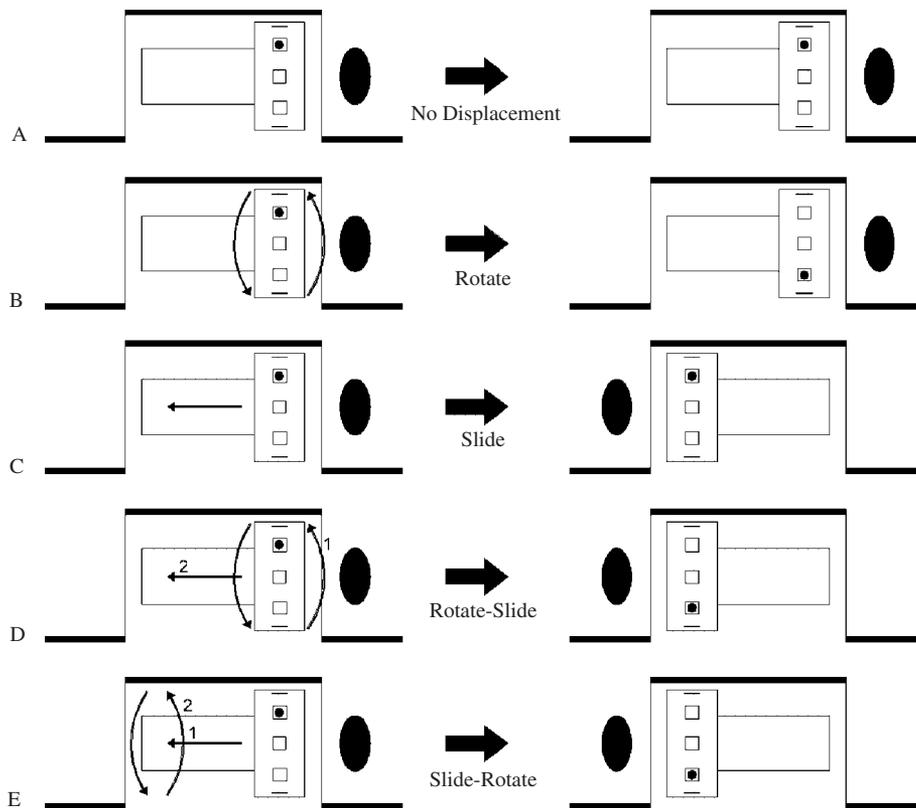


Fig. 3. Conditions. Once the reward concealed, the experimenter could (A) directly offer the cups for the subject to choose (No Displacement), (B) rotate the platform 180 degrees (Rotate), (C) slide the platform to the opposite window (Slide), (D) first rotate and then slide the platform (Rotate-Slide), or (E) first slide and then rotate the platform (Slide-Rotate). After these manipulations, the subjects could choose one of the cups by touching it, either from window 1 or window 2, depending on the condition.

Slide

The experimenter displaced the platform from its original position (window 1) toward the opposite side (window 2), so the subject had to move from window 1 to window 2 to make a choice. Although the reward stayed on the same side of the platform, the subject had to take into account her own movement to choose correctly. That is, if the reward was first located to the subject's right it was now located to the subject's left when the subject had to make a choice.

Rotate+Slide

The experimenter first performed the rotation as indicated in the Rotate condition and then slid the platform toward the opposite window as indicated in the Slide condition.

Slide+rotate

The same as the Rotate-Slide condition except that the order of the displacements was reversed.

Those conditions that involved a translocation (slide, rotate+slide, slide+rotate) forced the subject to lose sight of the containers momentarily when she moved to the other cage to select one of the containers. The subjects received three trials per

condition (15 trials in total) administered in blocks of five trials (one trial per condition). We administered one to three blocks of trials per session, depending on the subject's motivation to participate in the experiment. If the subject did not complete all three blocks in one session, she received the remaining trials the next day. The order of the conditions was random within each block of trials. The locations of the reward were randomly and exhaustively assigned to the left, middle, and right cup.

Scoring and Data Analysis

All trials were recorded on digital video and scored live on code sheets. Two independent raters viewed the video recordings and scored for each trial which cup the subject touched first. One rater coded all trials of all subjects while the second rater coded all trials of six randomly selected subjects (90/375, 24% of all trials). Interobserver reliability was excellent (Cohen's $\kappa = 0.90$). Our dependent measure was the percent of correct trials. We used non-parametric statistics to assess the effect of sex, rearing history, species (Kruskal-Wallis and Mann-Whitney tests), age (Spearman correlation), and condition (Friedman and Wilcoxon tests) on the percent of correct trials. We also used a Wilcoxon test

to measure deviation from chance ($P = 0.33$). Finally, we analyzed the subjects' choices as a function of the baited cup and condition. This allowed us to explore in more detail where subjects allocated their choices and detect potential biases. For each condition in which the reward changed location at some point during the trial (this excluded all baseline trials and those trials in other conditions in which the baited cup was the middle one), we contrasted the percent of trials in which subjects chose the same side that they had seen baited with the opposite side. To reduce the number of statistical tests, we added the values appearing on the opposite corners of each of the matrices, shown in Table III, for each subject and compared them to each other with a Wilcoxon test. All tests were two-tailed.

RESULTS

We found no evidence that performance varied as a function of sex (Mann–Whitney test: $z = 0.03$, $P = 0.976$), rearing history (Kruskal–Wallis test: $\chi^2(2) = 1.05$, $P = 0.592$) or age (Spearman correlation: $r_s = -0.046$, $P = 0.827$). Therefore, we did not consider these variables in subsequent analyses.

Table II presents the mean percentage of correct trials per species for each condition. Although apes overall performed significantly above chance in all conditions (Wilcoxon tests: $z > 3.70$, $P < 0.001$; see Fig. 4), there were significant differences between conditions (Friedman Test: $\chi^2(4) = 32.42$, $P < 0.001$). Post hoc tests indicated that subjects performed significantly better in the baseline compared with all other conditions (Wilcoxon tests: $z > 3.05$, $P < 0.005$). Subjects also performed significantly better in the rotate compared with the slide–rotate (Wilcoxon tests: $z = 2.00$, $P = 0.045$) and rotate–slide conditions (Wilcoxon tests: $z = 2.13$, $P = 0.033$). Pooling together the conditions with a single displacement and comparing them to those with two displacements revealed that apes performed significantly better after one compared with two displacements (Wilcoxon test: $z = 2.74$, $P = 0.006$; see Fig. 5).

TABLE II. Percentage of Correct Choices as a Function of Condition and Species

Species	Condition					Mean
	ND	R	S	R–S	S–R	
Chimpanzee	96	71	92	62	67	78
Bonobo	100	73	53	53	33	63
Gorilla	94	39	33	28	50	52
Orangutan	81	57	48	48	38	54
Mean	92	63	61	49	49	63

ND, No Displacement; R, Rotate; S, Slide; R–S, Rotate–Slide; S–R, Slide–Rotate.

There were significant differences between species on the overall score (Kruskal–Wallis test: $\chi^2(3) = 9.88$, $P = 0.02$). Post hoc tests indicated that chimpanzees performed significantly better than gorillas (Mann–Whitney test: $z = 2.58$, $P = 0.010$) and orangutans (Mann–Whitney test: $z = 2.56$, $P = 0.01$) but not better than bonobos (Mann–Whitney test: $z = 1.48$, $P = 0.139$). No other differences between species were found (bonobo–gorilla: $z = 1.16$, $P = 0.248$; bonobo–orangutan: $z = 0.99$, $P = 0.324$; gorilla–orangutan: $z = 0.25$, $P = 0.806$; see Fig. 6).

Within conditions, there were significant species differences in slide (Kruskal–Wallis tests: $\chi^2(3) = 10.42$, $P = 0.015$) and in slide–rotate ($\chi^2(3) = 8.04$, $P = 0.045$) but not in the rest of the conditions (baseline: $\chi^2(3) = 3.90$, $P = 0.273$; rotate: $\chi^2(3) = 3.94$, $P = 0.268$; and rotate–slide: $\chi^2(3) = 5.48$, $P = 0.139$). Post hoc tests revealed that chimpanzees significantly outperformed bonobos in slide (Mann–Whitney test: $z = 2.10$, $P = 0.035$) and slide–rotate

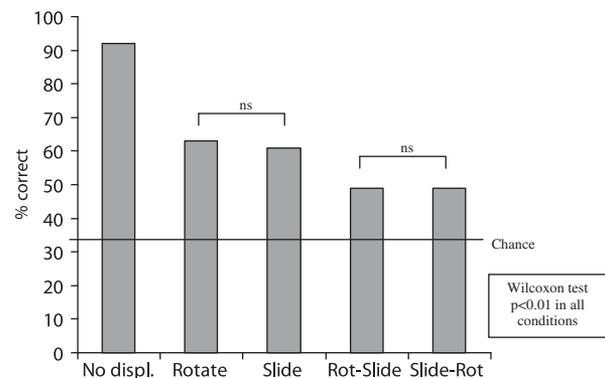


Fig. 4. Mean percent of correct answers as a function of condition for all apes. Overall apes performed above chance in all conditions. No significant differences were found between Rotate and Slide (single displacement conditions) and between Rotate–Slide and Slide–Rotate (double displacement conditions).

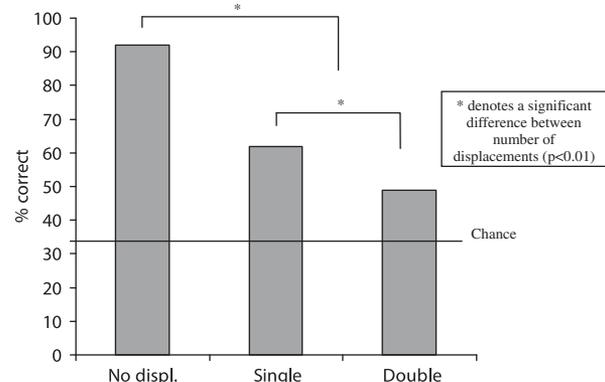


Fig. 5. Mean percent of correct answers as a function of number of displacements for all apes. Apes performed significantly better in the No Displacement condition than in those conditions where there was displacement. Within those conditions with displacement, single displacements were easier to solve than double displacements.

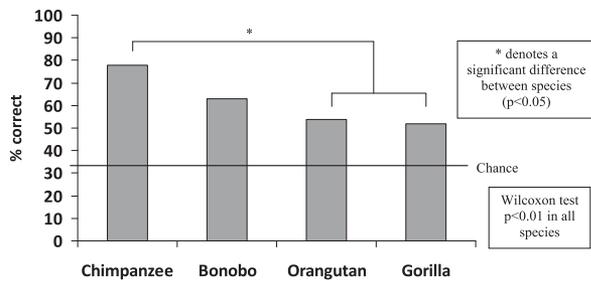


Fig. 6. Mean percent of correct answers as a function of species. Chimpanzees performed better than Orangutans and Gorillas, but not than Bonobos.

($z = 2.02$, $P = 0.043$), gorillas in slide ($z = 2.82$, $P = 0.005$), and orangutans in slide ($z = 2.60$, $P = 0.009$) and slide-rotate ($z = 2.31$, $P = 0.021$).

Chimpanzees were the only species that performed above chance levels in every condition (Wilcoxon tests: baseline: $z = 2.71$, $P = 0.007$; rotate: $z = 2.42$, $P = 0.015$; slide: $z = 2.64$, $P = 0.008$; rotate-slide: $z = 2.55$, $P = 0.011$; slide-rotate: $z = 2.56$, $P = 0.011$). Bonobos performed above chance levels in baseline ($z = 2.24$, $P = 0.025$), rotate ($z = 2.12$, $P = 0.034$), and rotate-slide ($z = 2.06$, $P = 0.039$). Gorillas performed above chance levels in baseline ($z = 2.12$, $P = 0.034$), rotate ($z = 2.07$, $P = 0.038$), and slide-rotate ($z = 2.07$, $P = 0.038$). Orangutans performed above chance levels in baseline ($z = 2.41$, $P = 0.016$) and slide-rotate ($z = 2.53$, $P = 0.011$).

Table III presents the percentage of trials in which subjects selected each of the cups as a function of the position of the baited cup and the condition. In those conditions in which the initial and the final position of the reward, with respect to the subject, coincided, subjects concentrated their choices on the main diagonal. In contrast, in those conditions in which the initial and final position of the reward, with respect to the subject, differed, subjects concentrated their choices on the inverse main diagonal. Focusing on those trials in which the reward underwent some sort of displacement (i.e. dropping the baseline condition and all trials in the remaining conditions in which the experimenter baited the middle cup), produced comparable results. Subjects selected the cup on the same location where they had seen the experimenter bait the cup in the rotate-slide (Wilcoxon test: $z = 2.74$, $P = 0.006$) and slide-rotate conditions (Wilcoxon test: $z = 2.44$, $P = 0.015$). In contrast, subjects selected the location opposite the place where they had seen the cup being baited in the rotation (Wilcoxon test: $z = 2.72$, $P = 0.007$) and slide conditions (Wilcoxon test: $z = 3.53$, $P < 0.001$).

DISCUSSION

Overall, apes performed above chance in all conditions, although there were marked differences between conditions. Double displacements were harder than single displacements which were in

TABLE III. Percentage of Choices Directed at Each of the Three Cups as a Function of Condition and Cup Baited Initially for all Apes

Condition Baited cup	Selected cup		
	Left	Middle	Right
Baseline			
Left	88 ⁺	12	0
Middle	4	96 ⁺	0
Right	0	8	92 ⁺
Rotate			
Left	20	28	52 ⁺
Middle	12	84 ⁺	4
Right	52 ⁺	28	20
Slide			
Left	8	32	60 ⁺
Middle	28	56 ⁺	16
Right	68 ⁺	16	16
Rotate-Slide			
Left	44 ⁺	44	16
Middle	28	56 ⁺	16
Right	16	36	48 ⁺
Slide-Rotate			
Left	32 ⁺	32	36
Middle	16	52 ⁺	32
Right	8	28	64 ⁺

⁺ Indicates the Correct Cup.

turn harder than no displacements. In contrast, the type of displacement (rotate vs. slide) had no effect on performance, neither when presented alone nor in combination with each other. In general, chimpanzees obtained the highest scores and outperformed other species, in particular in those conditions that included slide as one of the displacements.

This study confirms that chimpanzees can track invisible displacements of objects both when it is the objects that are moving and also when this entails the subjects changing their initial position [Hoffman & Beran, 2006]. Additionally, this study indicates that this skill is also present in the other nonhuman great ape species. Thus, this study reinforces the notion that the great apes use an allocentric spatial frame of reference [Haun et al., 2006; Hoffman & Beran, 2006], although only chimpanzees solved all conditions. The difference between chimpanzees and non-chimpanzees was particularly striking when subjects had to move in space while objects remained stationary (i.e. slide condition). One possible interpretation of this result is that non-chimpanzees relied more heavily than chimpanzees on an ego-centric strategy even though such a tendency was not too strong, because otherwise they would have performed below chance levels in this condition.

In general, our results show that gorillas and orangutans may be less skilful in solving these tasks than members of the genus *Pan*, confirming those results of earlier studies using spatial displacement tasks in which chimpanzees and bonobos

outperformed gorillas and orangutans [Barth & Call, 2006; Herrmann et al., 2007]. Therefore, with regard to the evolution of object tracking, the current evidence suggests that all great apes share a basic ability to track invisible object displacements, but chimpanzees and bonobos consistently outperform gorillas and orangutans. It is conceivable that this could be related to some aspects of each species' socioecology. For instance, Amici et al. [2008] found that species with high fission–fusion dynamics performed better in a battery of tasks on inhibitory control compared with species with low fission–fusion dynamics. This could explain the difference between gorillas and members of the genus *Pan* in this study, with the latter being better able to inhibit the tendency to reach for the last place where they saw the reward (which changed after the displacement). However, it cannot explain the orangutans' results because orangutans, which are also considered a fission–fusion species, performed worse than *Pan* and at the same level as gorillas. Additionally, Amici and co-workers (unpublished data) showed that spider monkeys, who also display fission–fusion dynamics, do not perform well in transposition tasks. More research should be done in order to find a better explanation for these results. It is important to emphasize that our current finding should not be taken as an indication that chimpanzees and bonobos outperform gorillas and orangutans in every task. On the contrary, orangutans outperform chimpanzees and bonobos in several tasks, including Piagetian conservation and some problem solving tasks [Hanus et al., 2009 (submitted for publication); Vlamings et al., 2009 (submitted for publication)]. Moreover, the limited number of studies and the relatively small samples used, together with the fact that captive populations may be somehow biased with respect to the wild populations in some cognitive aspects, require that we are cautious when generalizing results from our samples to the species level.

A second goal of our study was to compare translocations and rotations. Unlike earlier studies with children, we found no evidence that displacements in which the subject remained stationary and tracked the movement of containers were any harder than those that required the subject to change her position in space. This is perhaps a surprising finding given that, although these subjects had some experience with rotations, individuals encounter translocations much more often than rotations in their everyday lives. One possible explanation might be that, whereas in the rotation task subjects could perform just by visually tracking the baited cup, performance in the translocation task involved more difficulty because subjects momentarily lost sight of the stimuli when they moved between cages, which did not happen in the studies that compared rotations and translocations in children. Also, we would like to note that although one could question the administration of the rotation task on

ecological validity grounds, from a cognitive point of view this is an interesting task because it reveals capabilities that go beyond the species-specific behavior and gives information about the kind of mental representation that is deployed to locate hidden objects after some spatial transformation has taken place. Anyway, here the putative higher ecological validity of translocations compared with rotations (apes probably encounter rotation problems less often than translocations in their natural habitats) did not translate into a differential performance between tasks.

With regard to other object invisible displacement tasks, given that rotations are harder than both transpositions and object permanence invisible displacements [Barth & Call, 2006], we can venture an opinion that translocations may be harder than those other displacements as well. Also, if we take into consideration that 180° rotations have proved to be more difficult to solve than 360, 27, or 90° rotations [Call, 2003; Lasky et al., 1980; Visalberghi, 1986], it is conceivable that the translocation task is harder to solve than these types of rotation too. In line with Visalberghi [1986], it would be interesting to investigate 360, 27, and 90° subject translocations in apes, in order to compare the results with those of the rotations studies. Regarding the significant differences we found between those conditions that involved either a slide or a rotation and those conditions that involved both a slide and a rotation, following Barth and Call [2006], we suggest that the more complex sequence of movements, which led to a higher demand for information updating and a more likely confusion between relevant and irrelevant containers, was the reason for the higher difficulty experienced by subjects in double compared with single displacements.

Future studies should be devoted to investigating the tracking of visible and invisible displacements in a variety of primate and non-primate species, in an attempt to reconstruct the evolution of representational abilities in animals [see Haun et al., 2006]. These studies should include not just stage 6 invisible displacements but also transpositions, rotations, and translocations, to have a better picture of which are the variables that are influencing subjects' performances. Given that the ability to infer the hidden movements of an object may be differentially elicited depending on the testing paradigm, new paradigms should be explored, including tasks of different ecological validity and tasks that require less interaction between the subject and the experimenter, which may help in testing some species, for example, monkey species [de Blois et al., 1998]. Finally, the role of prospectiveness and retrospectiveness in invisible displacement tasks should also be investigated, given that even most tasks used up to date are retrospective (i.e. the subject has to reconstruct the path followed by the object), there is some evidence that prospective tasks (i.e. the subject has to predict the path of the object) may be easier to solve [Filion

et al., 1996], although additional data is needed to confirm this point.

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