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Great apes use landmark cues over spatial relations to find hidden food

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Abstract We investigated whether chimpanzees, bonobos, and orangutans encoded the location of a reward hidden underneath one of three identical cups in relation to (1) the other cups in the array—i.e., the relative position of the baited cup within the array; or (2) the landmarks surrounding the cups—e.g., the edge of the table. Apes witnessed the hiding of a food reward under one of three cups forming a straight line on a platform. After 30 s, they were allowed to search for the reward. In three different experiments, we varied the distance of the cups to the edge of the platform and the distance between the cups. Results showed that both manipulated variables affected apes' retrieval accuracy. Subjects' retrieval accuracy was higher for the outer cups compared with the Middle cup, especially if the outer cups were located next to the platform's edge. Additionally, the larger the distance between the cups, the better performance became.

Keywords Landmark use · Spatial encoding · Spatial cognition · Spatial memory · Spatial frames of reference · Spatial relations

Introduction

Encoding and remembering the spatial location of various entities including food sources, conspecifics, and predators is essential for the survival of many animal species. There are several different types of information that animals can use when encoding location, but they fall under two main categories: egocentric information and environmental information. An individual using egocentric spatial coding localizes objects with respect to its own body position (see Newcombe and Huttenlocher 2000; Shettleworth 2010 for reviews), whereas an individual using environmental information uses allocentric spatial coding, which localizes objects in relation to external reference points. These external reference points can be any object or feature of the environment (landmarks), or the geometric shape of the environment that the individual can use to orient and navigate toward its goal (Cheng and Newcombe 2005; Chiandetti et al. 2007; Sovrano et al. 2007). The use of landmarks to find a target location is widespread in the animal kingdom (see Cheng and Spetch 1998; Spetch and Kelly 2006 for reviews).

In the present study, we investigated how great apes encoded the location of a food reward placed underneath one of three identical cups resting on a platform and forming a straight line. As the three cups were identical, subjects needed to use spatial information to locate the baited cup. This information could be egocentric, allocentric—e.g., the cup's distance from an external landmark (e.g., the table edges)—or relational—i.e., the cup's relative position within the array.

In a similar task, cats (Fiset and Dore 1996) and dogs (Fiset et al. 2000) primarily used egocentric (or directional) information about the position of a hiding container (i.e., left or right of their body) to find a food reward. However,

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when egocentric information became unreliable (i.e., they were moved before they were allowed to choose), they used allocentric spatial information. Fiset and Dore (1996) further tested which of the two possible allocentric cues they were encoding: the relative position of the hiding container within the array (i.e., the left, middle, or right container) or the container's distance from the walls. They found that cats used the distance from the walls as cues, rather than the relative positions of the containers. Chickadees (Brodbeck 1994), bumblebees (Church and Plowright 2006), and pigeons (Legge et al. 2009) have all been shown to preferentially encode the global location of a rewarded stimulus. Interestingly, however, chickadees (Brodbeck 1994) and pigeons (Spetch and Edwards 1988) have also been found to use local cues (i.e., the surrounding stimuli) when encoding a reward's position, and chicks have been found to be able to discriminate between two identical boxes by their relative positions (i.e., the left or right box) (Vallortigara and Zanforlin 1986).

In experimental settings, primates have been shown to have very good spatial memory (e.g., Garber and Paciulli 1997; MacDonald 1994; MacDonald and Agnes 1999; MacDonald and Wilkie 1990; Menzel 1973). Moreover, numerous studies have found that nonhuman primates readily use landmark cues to search for hidden food (e.g., Deipolyi et al. 2001; Dolins 2009; MacDonald et al. 2004; Menzel 1996; Poì 2000; Poì et al. 2010; Sutton et al. 2000). Additionally, primates can successfully find a reward that they have seen placed under one of several identical, linearly arrayed opaque containers (Albiach-Serrano et al. 2010; Barth and Call 2006; Call 2001; de Blois and Novak 1994; de Blois et al. 1998; Deppe et al. 2009; Fedor et al. 2008; Mendes and Huber 2004). In most of these studies, comparable retrieval accuracy has been shown for all the containers when a single food reward is hidden (Albiach-Serrano et al. 2010; Barth and Call 2006; Call 2001; de Blois and Novak 1994; de Blois et al. 1998; Deppe et al. 2009; Fedor et al. 2008; Mendes and Huber 2004). However, Beran et al. (2005) reported that when two rewards were hidden in a 5- and 7-container array, chimpanzees were more accurate in retrieving these rewards when the rewards were hidden either in the external positions or in adjacent containers. The authors suggested that the chimpanzees' mistakes were the result of memory errors concerning the exact location of the second hidden item. Furthermore, they argued that it may be easier to remember the location of food hidden in the extreme containers as these containers do not have distracter containers on both sides.

In line with the above prediction, Hoffman and Beran (2006) found similar results when only one food reward was hidden in a 3- or 4-container array. That is, chimpanzees performed worse when the Middle cup(s) contained food

than when either of the two outer cups were baited. In this study, however, after observing a reward being hidden in one of the containers, chimpanzees had to walk around the array, therefore turning 180°. As before, the authors suggested that this worse performance on the Middle cup(s) was likely due either to the distracting foils located on both sides of the Middle cup(s), or to the more salient features that surrounded the outer containers. Interestingly, chimpanzees were equally successful with all cups when they remained and made their choice from the original position. The authors suggested that chimpanzees used both allocentric and egocentric spatial cues when they did not move, but when they moved to a new position—meaning that allocentric and egocentric cues led to different containers—then chimpanzees showed a preference for allocentric cues. Other studies have further supported this notion that great apes prefer allocentric over egocentric coding when they are forced to move (Albiach-Serrano et al. 2010; Haun et al. 2006b). However, none of these studies directly investigated the specific allocentric cues that primates may use to encode a reward's location.

Recently, Hribar et al. (2011) presented chimpanzees, bonobos, and orangutans with a search task in which they had to locate a reward in a 3-cup array, after observing a reward being hidden in a different but identical 3-cup array. To be successful, apes needed to choose the cup in the second array that was in the same relative position as the baited cup in the first array. Apes showed no evidence of using the relative position of the baited cup as a cue to search for the hidden reward. Rather, apes preferentially mapped together the cups from the two arrays that held a similar relation to the table's edge and midpoint (landmarks). Specifically, apes' performance was worst when the Middle cup was baited, which the authors suggested was due to the absence of a differential landmark cue next to that cup. However, it is also possible that apes performed worst on the Middle cup because the cups surrounding it may have exerted a distracting influence, as suggested by Beran et al. (2005).

The goal of the current study, therefore, was to investigate whether apes encoded the location of a hidden reward in relation to (1) the other cups in the array (i.e., the relative position of the baited cup within the array) or (2) the landmarks surrounding the array (e.g., the edge of the table). In addition, we examined whether apes might be using egocentric information as well (i.e., left or right of their own body). Apes witnessed the hiding of a food reward under one of three cups which rested on a platform and formed a straight line. After 30 s, the apes were allowed to search for the reward from their original position. We imposed a time delay because previous studies have shown near ceiling performance when using a 3-cup array (including the Middle cup) and no delay, and a

marked decrease in performance when using a 3-cup array and a 30-s delay (Barth and Call 2006). In addition, the experimenter lured subjects away from the array to break their visual contact with the cups for a short time, which has also been shown to interfere with their performance (Hoffman and Beran 2006). In order to make them leave the array, apes were offered a low-value food at a different location, and this interaction with the experimenter probably represented additional distraction for them. In three experiments, we varied the distance between the cups and the distance of the array to the edge of the table. We tested chimpanzees, bonobos, and orangutans to investigate interspecies differences. Previous studies have shown that chimpanzees outperform orangutans in some spatial tasks (Albiach-Serrano et al. 2010; Barth and Call 2006; Herrmann et al. 2007). In the present study, we tested the putative superiority of chimpanzees over orangutans in spatial cognition in the absence of displacements.

Experiment 1

In Experiment 1, apes observed a food reward being hidden underneath one of three physically identical cups standing next to each in a straight line. After 30 s, the ape was allowed to search for the reward. Here, we wanted to examine whether apes would be more successful in finding the reward when it was hidden underneath the Left and Right cups than when it was hidden underneath the Middle cup.

Methods

Subjects

Six chimpanzees (*Pan troglodytes*), five bonobos (*Pan paniscus*), and five orangutans (*Pongo pygmaeus*) housed at the Wolfgang Köhler Primate Research Centre, Zoo Leipzig, participated in this study (see Table 1). Their ages ranged between 7 and 35 years. There were 11 females and 5 males. Three chimpanzees, three bonobos, and two orangutans were nursery reared, and the rest were mother reared. The apes live with their conspecifics in spacious indoor and outdoor areas (combined space: chimpanzees: 1,740 m², bonobos: 2,620 m², orangutans: 1,999 m²). They are fed several times a day, and they were never food deprived during our study. Water is available to them ad libitum, as well as during testing. They were tested individually in their sleeping rooms, except for five mothers that were accompanied by their infants. Most of the apes have previously participated in various experiments concerning spatial encoding (Haun et al. 2006a, b; Kanngiesser and Call 2010), episodic-like memory (Martin-Ordas et al.

Table 1 Apes tested in this study

Name	Sex	Age (years) ^a	Rearing	Experiment
Chimpanzees				
Jahaga	F	16	Mother	1, 2, 3
Fifi	F	16	Mother	1, 2, 3
Trudi	F	16	Mother	1, 2, 3
Alexandra	F	9	Nursery	1, 2, 3
Annett	F	9	Nursery	1, 2, 3
Alex	M	8	Nursery	1, 2, 3
Bonobos				
Luiza	F	5 ^b	Mother	3
Ulindi	F	15	Mother	1, 2, 3
Yasa	F	11	Mother	1, 2, 3
Limbuko	M	13	Nursery	1, 2, 3
Kuno	M	12	Nursery	1, 2, 3
Joey	M	27	Nursery	1, 2, 3
Orangutans				
Raaja	F	6 ^b	Mother	3
Kila	F	9 ^b	Mother	3
Dunja	F	36	Nursery	1, 2
Padana	F	11	Mother	1, 2, 3
Pini	F	20	Mother	1, 2, 3
Dokana	F	21	Mother	1, 2, 3
Bimbo	M	28	Nursery	1, 2, 3

^a Age at the time of Exp1; Exp2 was done six and Exp3 15 months after Exp1

^b Age at the time of Experiment 3

2010) and spatial mapping (Haun and Call 2009; Hribar et al. 2011).

Materials

We used one array consisting of three identical plastic cups ($d = 8$ cm) arranged in a straight line on a blue tray (31 cm \times 14 cm). This array always rested on the left half of a sliding table (80 \times 35 cm) from the experimenter's viewpoint (see Fig. 1a). The outer cups were situated next to the edges of the tray, and the distance between the cups was 3.5 cm. The distance of the left-most edge of the tray (and therefore of the Left cup) from the table's edge was 8 cm. As a low-value food, we used small slices of carrot for all subjects. With the exception of one orangutan where banana pellets were used, grapes served as a high-value food for the subjects.

Procedure

The sliding table was fixed to a mesh panel (70 cm \times 50 cm) through which apes could observe and

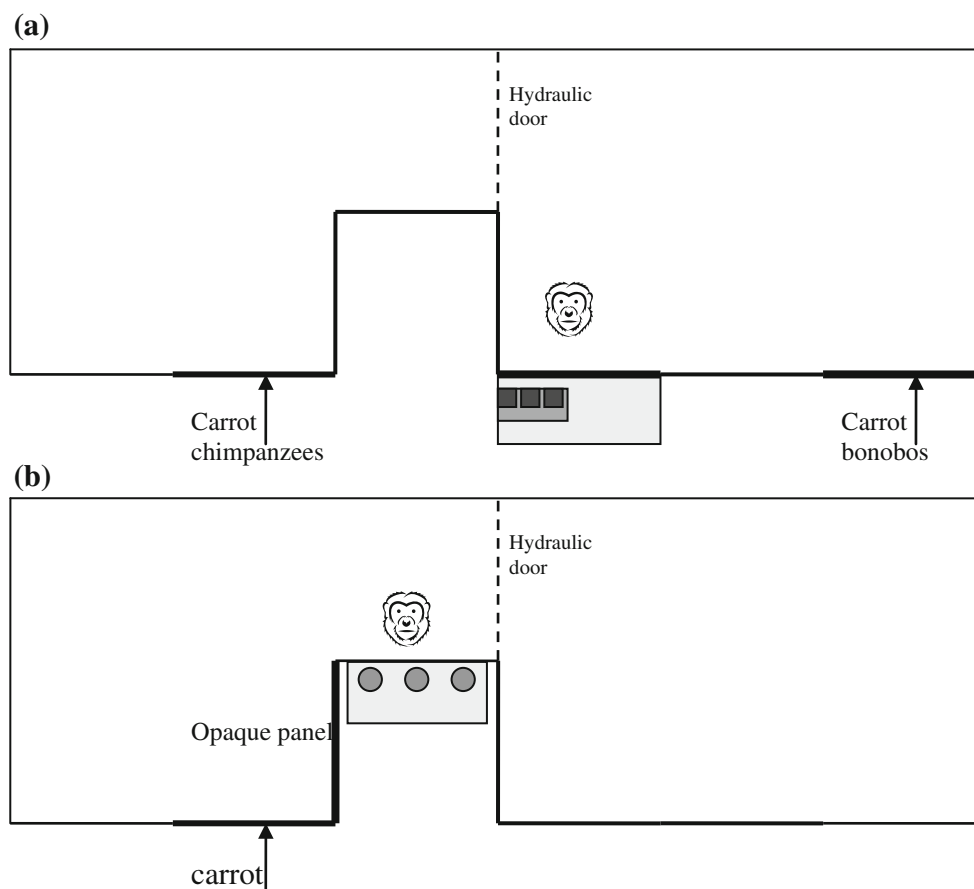


Fig. 1 Experimental setup for **a** Experiments 1 and 2. Depicted is a testing room with a setup for the bonobos and chimpanzees (with one difference—the bonobos had to walk to the *right panel* and the chimpanzees to the *left panel* to get carrot). For the orangutans, a

room and a setup were an exact mirror picture of the bonobos' setup. **b** Experiment 3. The setup was the same for all species. The *arrows* indicate the second panel where the apes were offered a piece of carrot

point to the cups. At the beginning of each trial, all cups lay on their sides with the opening facing toward the subject. Initially, apes observed the cups being overturned (“closed”) while a food reward was placed underneath one of the cups. At this point, the timer was started. After 5 s, the experimenter got up and went to a second panel (approx. 2 m away) either to the left (for the orangutans and the chimpanzees) or to the right (for the bonobos) and offered subjects a small piece of carrot. While some subjects did not always eat the piece of carrot, it was always the case that subjects approached the experimenter. When the subject followed the experimenter to receive a carrot, she had to let the baited cup out of her sight. The experimenter then waited 20 s at the second panel before returning to the table. When 30 s had elapsed, she pushed the table forward and the subject could point through the mesh to the chosen cup. Each subject received one session of 12 trials. Each cup was baited four times in a semi-random order; the same cup could only be baited twice in a row.

Scoring and data analysis

We filmed all sessions, and scoring was done live as well as subsequently from the videos. We scored which cup (Left, Middle, Right) apes chose, and the dependent measure was the percentage of correct trials. A second coder scored 20% of trials (approx. 20% for each species) to assess inter-observer reliability, which was excellent (Cohen's kappa = 0.96). Preliminary analyses showed no sex differences in performance on any of the cups, and as such, we did not include this variable in the subsequent analyses. To test whether there was a difference in performance in the three cups, and whether there were any species differences, we conducted a mixed 3 (Cups) \times 3 (Species) analysis of variance (ANOVA), with Cups as the within-subjects variable and Species as the between-subjects variable. Performance on each cup was also compared against chance level using a one-sample *t* test. As apes could choose from three cups, chance level was set at 33.3% correct.

Results and discussion

Figure 2 presents the percentage of correct trials as a function of the baited cups' position and species. On average, apes correctly selected the Left and Right cups in 90% and 82.5% of trials, respectively, which was above chance ($T_{15} > 9.070$, $P < 0.001$, in both cases). In contrast, the Middle cup was correctly selected in only 48% of trials, which was not significantly above chance ($T_{15} = 1.829$, $P = 0.087$). ANOVA revealed main effects of Cups ($F_{2, 26} = 15.135$, $P < 0.001$) and Species ($F_{2, 13} = 7.908$, $P = 0.006$), but no interaction between these factors ($F_{4, 26} = 2.015$, $P = 0.122$). Bonferroni-corrected post hoc tests revealed that the apes found the reward significantly more often when it was hidden under the Left cup ($P < 0.001$) and the Right cup ($P = 0.011$) than when it was hidden under the Middle cup. There was no difference in apes' performance on the Left and the Right cups ($P = 0.965$). Orangutans performed significantly worse than chimpanzees ($P = 0.005$), but no significant difference was found when their performance was compared with bonobos' ($P = 0.087$). There was no significant difference between chimpanzees' and bonobos' performance ($P = 0.565$).

In summary, apes had greater difficulty in retrieving a reward hidden underneath the Middle cup compared with the outer two cups. In the next experiment, we tested two possible explanations for this difference. The first explanation is that each cup was encoded by way of the two relations it held with the other two cups. The Left cup is left of the other two cups; the Right cup is right of the other two cups; and the Middle cup is left of the Right cup and right of the Left cup. Note that this might explain the decreased performance in the Middle cup, as both the Left and Right cups (by virtue of being at the extremities) hold the same relation with the other two cups, whereas the

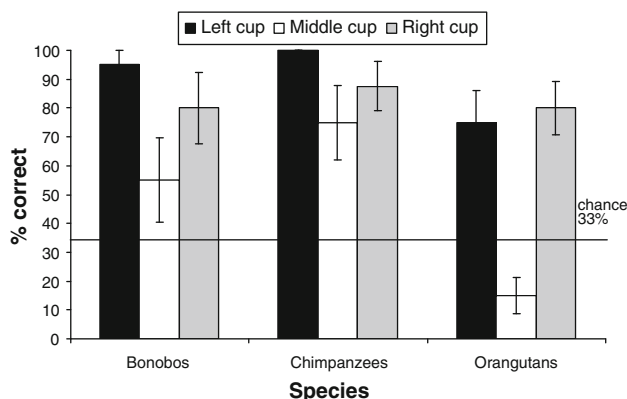


Fig. 2 Experiment 1: apes' percentage correct for each cup as a function of species. Bars represent *standard error*

Middle cup's position is in between the other two cups, meaning it holds two different relations with the other cups. The second explanation is that apes encoded the three cups in relation not to the other cups, but to external reference points. These external reference points, or landmarks, could be the edges of the tray on which the cups rested, the edges of the table, or possibly, the middle of the table. Edges of a platform and boundaries have been found to be quite salient landmarks for nonhuman animals (Cheng and Sherry 1992; Hoffman and Beran 2006; Kubo-Kawai and Kawai 2007). Humans' spatial recall is also affected by visual boundaries (Bullens et al. 2010; Huttenlocher et al. 1994) and by symmetry axes, such as an invisible middle line dividing a space into two halves (Huttenlocher et al. 1994). Hribar et al. (2011) also suspected that apes in their study might be using the middle of the table as a reference point. The Left and Right cups therefore had an obvious landmark next to them, whereas the Middle cup was somewhere between the edge and the middle of the table. As such, it did not have a specific landmark of its own next to it, but it had to be defined by two landmarks, which previous studies have shown is a demanding task for primates (MacDonald et al. 2004; Marsh et al. 2011; Potì et al. 2005, 2010; Sutton et al. 2000).

Experiment 2

In Experiment 2, we placed the three cups over the whole length of the table (Full table condition), so that the Left and Right cups stood next to the table's edges and the Middle cup occupied the position in the middle of the table. Thus, all three cups were located near a salient landmark—table's edges and the middle of the table. The predictions are that if the apes encode the cups by their relation to nearby landmarks, then their performance on the Middle cup will now not differ from their performance on the other two cups. However, if the apes encode the cups using their spatial relation within the array, then once again they should perform worse on the Middle cup. We wanted to compare the results from the Full table condition with the results from Experiment 1, but since it was conducted 6 months after Experiment 1, we decided to run Experiment 1 (henceforth Half table condition) again, so as to make sure that the apes' performance on the original spatial memory task did not change during this time.

Subjects

Subjects were the same as in Experiment 1.

Materials

Materials were exactly the same as in Experiment 1.

Procedure

There were two conditions: the Half table and the Full table condition. The Half table condition was identical to Experiment 1. In the Full table condition, the three cups were placed directly on the table, spread out over its whole length. The cups were separated by a distance of ca. 17 cm. The rest of the procedure was exactly the same as in the Half table condition. All subjects participated in both conditions, which were blocked in 12 trials and presented on separate days. Half of the subjects started with the Half table condition, and the other half of the subjects started with the Full table condition. The position of the food reward was semi-randomized; the same position (cup) was not baited on more than two consecutive trials. All subjects walked over to the experimenter when she offered them a piece of carrot at the second mesh (again some did not eat it) except one bonobo. This one bonobo chose to stay in front of the cups in some trials, but he did not look at the cups continuously during the 30-s interval.

Scoring and data analysis

Scoring was done in the same way as in the previous experiment. Inter-observer agreement was 100% (Cohen's kappa = 1). Preliminary analyses showed no sex differences in performance on any of the cups, and as such, we did not include this variable in the subsequent analyses. To investigate the effect of the baited cups' position in the two conditions, we conducted a 3 (Cups) \times 2 (Condition) \times 3 (Species) analysis of variance (ANOVA), with Cups and Condition serving as within-subjects variables, and Species serving as a between-subjects variable. To compare the two conditions on each cup separately, we conducted paired-samples *t* tests (two-tailed).

Results and discussion

Figure 3 separately presents the percentage of correct trials as a function of the baited cups' position and species for both conditions. ANOVA revealed main effects of Cups ($F_{2, 26} = 14.228$, $P < 0.001$), Condition ($F_{1, 13} = 18.670$, $P = 0.001$), and Species ($F_{2, 13} = 7.286$, $P = 0.008$). There were also two significant interactions: Cups \times Condition ($F_{2, 26} = 7.344$, $P = 0.003$) and Cups \times Condition \times Species ($F_{4, 26} = 3.381$, $P = 0.024$).

The effect of species was due to the lower performance of the orangutans compared with the chimpanzees ($P = 0.018$) and the bonobos ($P = 0.015$). There was no

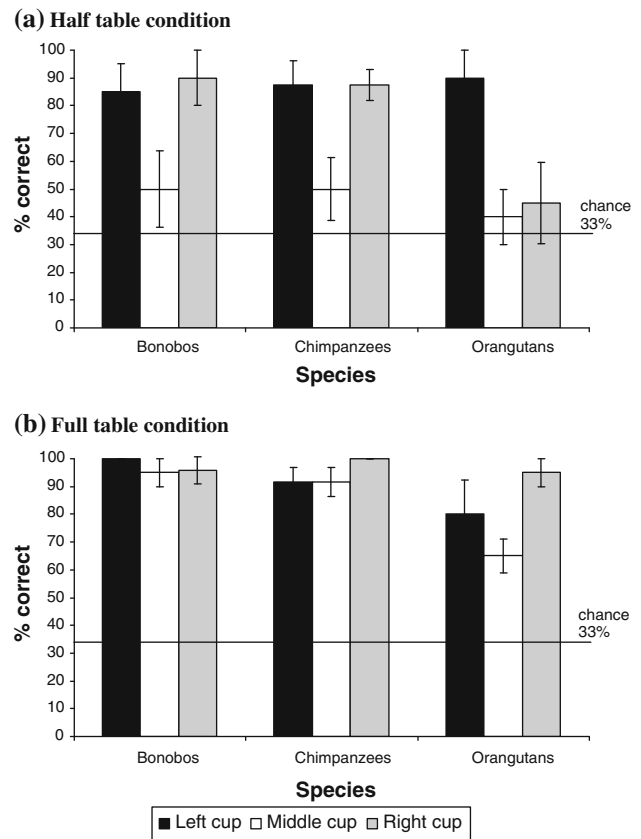


Fig. 3 Experiment 2: percentage of correct responses for each cup as a function of species in **a** Half table condition, **b** Full table condition. Bars represent *standard error*

significant performance difference between the chimpanzees and the bonobos ($P > 0.05$).

Because the key variable of interest was Condition, we investigated the pattern of the three-way interaction by conducting a mixed 3 (Cups) \times 3 (Species) ANOVA separately for each condition. In the Half table condition, we found a main effect of Cups ($F_{2, 26} = 13.470$, $P < 0.001$) but not of Species ($F_{2, 13} = 1.943$, $P = 0.183$), and the interaction between these factors was not significant ($F_{4, 26} = 2.007$, $P = 0.123$). Bonferroni-corrected post hoc tests revealed that the main effect of Cups was due to the apes' significantly lower performance on the Middle cup (47%), relative to the Left (87.5%, $P = 0.001$) and the Right cups (74%, $P = 0.024$). These results replicate the results of Experiment 1: The apes were significantly impaired in remembering where the reward was hidden when it was underneath the Middle cup.

In the Full table condition, we found a main effect of Species ($F_{2, 13} = 6.657$, $P = 0.010$), a marginal effect of Cups (Greenhouse-Geisser corrected, $F_{1, 363, 17.714} = 3.771$, $P = 0.057$), and no reliable interaction between these factors ($F_{4, 26} = 1.978$, $P = 0.128$). Bonferroni-corrected post hoc tests again showed that the orangutans

performed significantly worse than the chimpanzees ($P = 0.030$) and the bonobos ($P = 0.016$). The apes performed better on the Right cup compared with the Middle cup ($P = 0.009$), but there was no difference between the Left and the Middle cups or between the Left and the Right cups ($P > 0.05$).

We further compared apes' performance on the three cups in the Half table condition with their performance on the three cups in the Full table condition. Apes performed significantly better on the Middle cup ($T_{15} = 4.743$, $P < 0.001$) and the Right cup ($T_{15} = 2.671$, $P = 0.017$) in the Full table condition, but there was no significant difference between conditions on the Left cup ($T_{15} = 0.522$, $P = 0.609$). Finally, we compared the results from Experiment 1 with the results from the Half table condition of Experiment 2 to investigate whether apes' performance had changed with additional experience. It had not: The apes' performance in the two experiments did not significantly differ on any of the three cups ($T_{15} < 1.05$, $P > 0.31$, in all cases).

To summarize, apes performed significantly better on the Middle cup when it stood in the middle of the table (Full table), compared with when it did not (Half table). Additionally, subjects also performed significantly better on the Right cup when it stood near the edge of the table (Full table), compared with when it stood in the middle of the table (Half table). Since the relations between the cups are the same in both table conditions, these data fail to support the idea that subjects were using the relative spatial position of the cups to encode food location. Instead, it appears that apes encoded each cup separately in relation to a specific landmark.

Apes' high performance on the cups located near the table's edges suggests that edges are important landmarks for the encoding of spatial location. Of course, in the Half table condition, apes could have potentially used the tray edge as a landmark cue. However, the observed decrease in performance in the Half table condition when the Right cup was moved away from the table's edge suggests that they did not use the tray edge, but rather the table edge and/or the middle of the table. Indeed, the difference in performance on the Middle cup between the Full and the Half table conditions suggests that the middle of the table was likely used as a landmark.

However, it is still possible that apes may have ignored the middle of the table as a landmark, focusing solely on the table's edges as landmark cues. If true, this would mean that the closer a cup is to one of the table's edges, the easier it will be for apes to remember that a reward is located underneath that cup. Thus, the difference between the conditions in the performance on the Middle cup may not be due to its different position within each condition, but rather to the distance between the cups within each array.

Note, in the Full table condition, the cups were further apart than in the Half table condition, and as such, it might have been easier for the apes to remember under which cup the reward was hidden. In the next experiment, we sought to disentangle these possibilities.

Experiment 3

Experiment 2 suggested that apes encoded the location of the baited cup with regard to external landmarks based on geometric cues (middle of the table) or physical properties of the environment (table's edge). In the current experiment, we examined how distance to the landmarks and distance between cups affected subjects' choices.

Methods

Subjects

Six chimpanzees, six bonobos, and six orangutans socially housed at the Wolfgang Köhler Primate Research Centre, Zoo Leipzig, participated in this experiment (see Table 1). There were 13 females and 5 males ranging in age between 4 and 28 years. Subjects were tested individually in their sleeping rooms, except for six mothers that were accompanied by their infants.

Materials

We used an array of three identical metal round cups ($d = 6$ cm) and three testing tables (Small: 26.5×35 cm; Medium: 45×35 cm; Large: 82×35 cm). Cups were placed on a moving platform which was the same length as the table, but 10 cm narrower. As a low-value food we again used small slices of carrot, and as a high-value food we used grapes, except for one orangutan that received banana pellets.

Procedure

We followed the same basic procedure as in previous experiments. First, we placed the 3-cup array on a platform in front of the mesh panel (83 cm \times 50 cm). All tables with the corresponding platforms were always positioned in the center of the testing mesh panel. Each trial started with all three cups being "opened" (right way up). The experimenter "closed" (upturned) two of the cups and then placed a food reward underneath the last cup. After 5 s, the experimenter got up and walked to a mesh panel to her left, where she offered the subject a small piece of carrot. All subjects walked over to the experimenter when she offered them the piece of carrot (some did not eat it), except two

bonobos that chose to stay in the place where they had observed the hiding in some trials. As soon as the subject approached the experimenter to take the carrot, an opaque panel forced the subject to break eye contact with the cups (see Fig. 1b). After 20 s, the experimenter went back to the testing table, and after 30 s, she pushed forward the platform on which the cups rested, so the subject could point to one of them. There were four conditions that differed in the positioning of the cups on the table (either occupying one half of the table or the full table) and in the distance between the cups (which could either be small or large) (Fig. 4).

1. *Full table Near* The cups occupied the whole length of the Small table such that the Left cup rested 1 cm from the left edge of the table, the Right cup rested 1 cm from the right edge of the table (Edge cups), and the third cup was positioned between them in the middle of the table (Middle cup). The distance between adjacent cups was 3.25 cm.
2. *Full table Far* This condition was identical to the Full near condition except that we used the Medium table. This resulted in a distance between adjacent cups of 12.5 cm.
3. *Half table Near* The cups occupied only half of the Medium table. This meant that one cup always stood 1 cm from the table's edge (Edge 1 cup), one cup always stood in the middle of the table (Edge 2 cup), and one cup always stood between the Edge 1 and Edge 2 cups (Middle cup). In the first half of trials, the cups were placed on one side of the table, and in the second half of trials, the cups occupied the other side

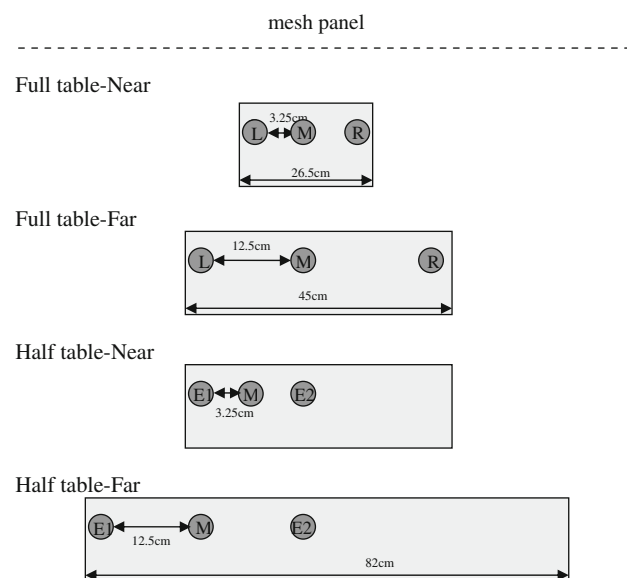


Fig. 4 The positioning of the cups for the four conditions. *L* Left cup, *M* Middle cup, *R* Right cup, *E1* Edge1 cup, *E2* Edge2 cup

of the table. The starting side (left or right half of the table) was counterbalanced across subjects. The distance between adjacent cups was 3.25 cm.

4. *Half table Far* This condition was identical to the Half near condition except that we used the Large table, resulting in a distance between adjacent cups of 12.5 cm.

The only difference between the Full table Near and the Full table Far conditions, and between the Half table Near and the Half table Far conditions, is the distance between the cups. Therefore, if apes performed better on the Far conditions than on the Near conditions, this would be a strong evidence that inter-cup distance affects apes' performance. Similarly, there is only one difference between the Full table Near and the Half table Near conditions, and between the Full table Far and the Half table Far conditions. Specifically, the Full table conditions have two cups directly located at the table edges, and the Half table conditions have only one cup directly located at a table edge. As such, if apes performed differently on the outside (Left or Right cups) cups that were directly located at the table's edge and the outside cups that were in the middle of the table, then this would be a strong indication that apes were using landmarks—table edge to encode the location of the baited cup—and not egocentric cues, such as the angle and the distance from their body to the baited cup. Additionally, by comparing performance on the Middle cup in the Full table Near and Half table Near conditions, and in the Full table Far and Half table Far conditions, we can test whether the apes were using the middle of the table as a landmark.

Subjects received four 12-trial sessions (one session per condition). Starting condition was counterbalanced across subjects, and the order of the conditions was different for every subject. The position of the reward was semi-randomized; the same position (cup) was not baited on more than two consecutive trials.

Scoring and data analysis

Scoring was done in the same way as in the previous two experiments. Inter-observer reliability was excellent (Cohen's kappa = 0.99). Preliminary analyses showed no sex differences in performance on any of the cups, and as such, we did not include this variable in the subsequent analyses. Variables of interest were the distance between cups (far or near), the positioning of the array (over the whole table or over one half of the table), and the cups' position on the table. Due to the fact that the outer two cups in the Full table conditions were both Edge 1 cups (i.e., placed directly at a table's edge), but in the Half table conditions the two outer cups were two different types of

Edge cups—one at the edge and the other in the middle of the table—we analyzed the Half and Full table conditions separately. Therefore, a mixed 2 (Distance) \times 3 (Cups) \times 3 (Species) analysis of variance (ANOVA), with Distance and Cups as within-subjects variables, and Species as a between-subjects variable, was conducted separately for each condition. In addition, to compare each condition's performance against chance (33.3%), we conducted one-sample *t* tests. Moreover, we compared individual cups between conditions with paired-samples *t* tests.

Results and discussion

Figures 5 and 6 present the percentage of correct responses for each cup as a function of species for all four conditions. Overall, apes found the hidden food reward above chance levels (33%) in all conditions (Full table Near: 65%, $T_{17} = 9.25$, $P < 0.001$; Full table Far: 81%, $T_{17} = 7.29$, $P < 0.001$; Half table Near: 62%, $T_{17} = 13.15$, $P < 0.001$; Half table Far: 76%, $T_{17} = 12.68$, $P < 0.001$).

ANOVA for the Full table conditions revealed main effects of Distance ($F_{1,15} = 19.636$, $P < 0.001$), Cups (Greenhouse-Geisser corrected, $F_{1,223,18,338} = 41.948$,

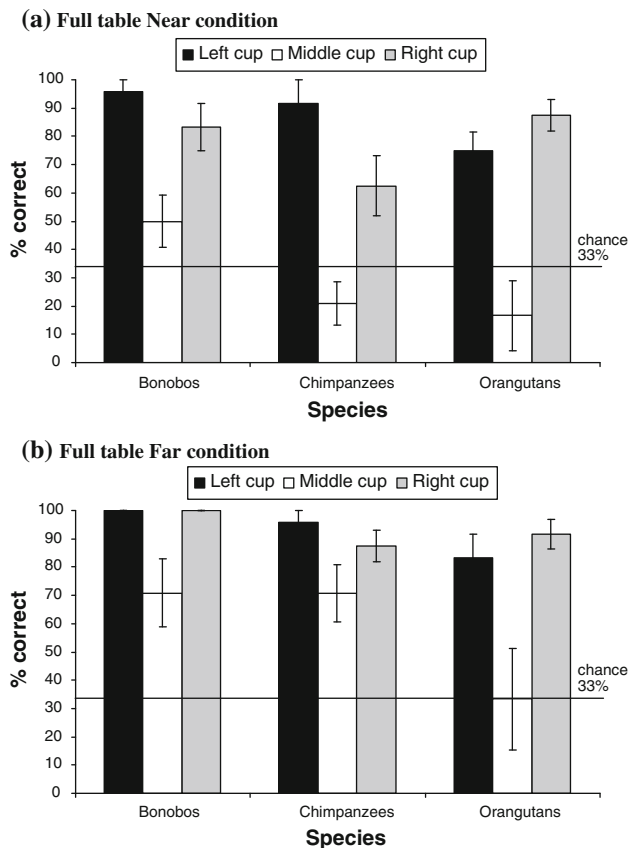


Fig. 5 Experiment 3: percentage of correct responses for each cup as a function of species in **a** Full table Near condition, **b** Full table Far condition. Bars represent *standard error*

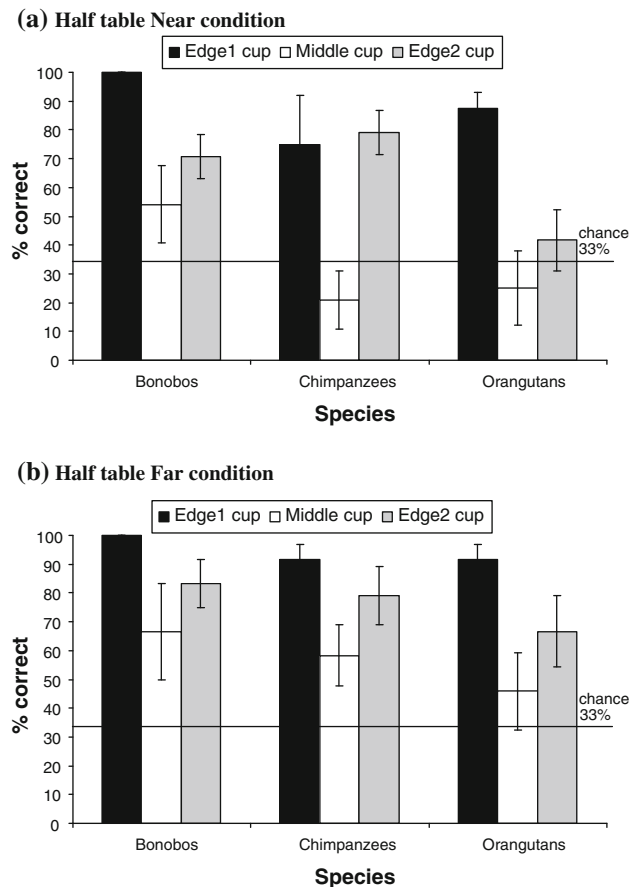


Fig. 6 Experiment 3: percentage of correct responses for each cup as a function of species in **a** Half table Near condition, **b** Half table Far condition. Bars represent *standard error*

$P < 0.001$), and Species ($F_{2,15} = 5.157$, $P = 0.020$). Apes found the reward more often in the “Far” condition (81.5%) than in the “Near” condition (65%). Bonferroni-corrected post hoc tests revealed that apes’ success was higher on the Left and Right cups (the Edge cups) compared with the Middle cup (both P s < 0.001), and that the bonobos performed better than the orangutans ($P = 0.019$). There were no other species differences. There was also a significant interaction between Distance and Cups (Greenhouse-Geisser corrected, $F_{1,385,20,769} = 4.506$, $P = 0.035$). To investigate this interaction, we compared the three cups in the Near and Far conditions separately. In both conditions, apes’ success varied on the three cups (Near: $F_{2,34} = 15.421$, $P < 0.001$; Far: $F_{2,34} = 37.155$, $P < 0.001$). Bonferroni-corrected post hoc tests showed that, in both conditions, apes’ success was higher on the Left and Right cups than on the Middle cup (all P s < 0.002). However, this difference was more pronounced in the Near condition (87.5%, 29.2%, 77.5%, Left, Middle, Right cup, respectively) than in the Far condition (93.1%, 58.3.1%, 93.1%, Left, Middle, Right cup, respectively).

ANOVA for the Half table conditions also revealed main effects of Distance ($F_{1,15} = 16.399$, $P = 0.001$,

Cups ($F_{2, 30} = 19.203$, $P < 0.001$), and Species ($F_{2, 15} = 4.435$, $P = 0.031$). Bonferroni-corrected post hoc tests revealed that apes performed better on the Edge 1 cup (91%) than on both the Edge 2 cup (70%, $P = 0.013$) and the Middle cup (45%, $P < 0.001$). Additionally, apes' success was higher on the Edge 2 cup than on the Middle cup ($P = 0.024$). Again, apes located the food reward more often in the "Far" condition (76%) than in the "Near" condition (62%), and bonobos outperformed orangutans ($P = 0.029$). There were no significant interactions between factors.

In both analyses, there was an effect of Distance: Apes' success was higher when the cups in the array were put further apart. By examining Figs. 5 and 6, we see that in the Full table and Half table conditions this effect was highest for the Middle cup. We were also interested in whether this was true for the outer cups too. As such, we compared the two Full table conditions on the Left, Middle, and Right cups, and we compared the two Half table conditions on the Edge 1, Middle and Edge 2 cups. There was a significant difference between the two Full table conditions in all three cups, with performance on the Far condition being higher (Left cups: $T_{17} = 2.204$, $P = 0.042$; Middle cups: $T_{17} = 3.580$, $P = 0.002$; Right cups: $T_{17} = 2.500$, $P = 0.023$). However, in the Half table conditions, apes performed differently only on the Middle cup ($T_{17} = 3.449$, $P = 0.003$).

We further wanted to examine whether the apes found the reward that was hidden underneath the Middle cup more often when it stood in the middle of the table compared with when it did not. Consequently, we compared the Full table Near condition with the Half table Near condition, and the Full table Far condition with the Half table Far condition. There were no significant differences in either of these comparisons ($T_{17} > 0.170$, $P > 0.5$, both cases).

Even though the above results already suggest that apes did not use egocentric information to find the hidden reward (i.e., apes performed equally well on the Left and Right cups in the Full table conditions, but not on the Edge 1 and Edge 2 cups in the Half table conditions), we investigated in more detail the possibility that apes used egocentric cues. One indication whether apes were using egocentric cues would be if they systematically used their left hand to point to the Left cup, and their right hand to point to the Right cup. We examined apes' choices in all four conditions. In the Full table Near, Half table Near, and Half table Far conditions, only one subject (a different one in each condition) consistently indicated to the Left and Right cups with their left and right hands, respectively. In the Full table Far condition, three subjects indicated to the Left and Right cup with the corresponding hand 100% of the time (one additional subject in 7/8 times). Eight subjects always used the same hand to point with (6 with the

left hand and 2 with the right), and the rest of the subjects did not show any preference. The low number of subjects that consistently used the corresponding hand indicates that apes did not use their body cues to encode location. However, if pointing to the cups with the corresponding hand did help the apes to better recall the position of the hiding cup, then we should expect higher performance on the Left and Right cups for those subjects who consistently used the corresponding hand than for those who always used the same hand. We performed this analysis only for the Full table Far condition, and we found no significant differences between the groups (Mann–Whitney test: $Z < 0.41$, $P = 1.0$, $N = 12$, both cups).

In summary, there were four main results: apes had most trouble remembering the reward's location when it was placed underneath the Middle cup, no matter what its position on the table. In other words, we did not find any evidence that apes were using the middle of the table as a landmark. Second, apes' success was higher when the distance between the cups was larger; however, this effect was more pronounced for the Middle cup. Third, we did not find any evidence that the apes were using egocentric cues. Finally, the apes were most successful when the reward was hidden underneath a cup that was located at the very edge of the table, suggesting that the apes used the table edges as landmarks.

General discussion

We investigated how chimpanzees, bonobos, and orangutans encoded the location of a reward hidden underneath one of three identical cups that formed a straight line on a platform. Two main factors were found to affect apes' retrieval accuracy: the distance between the cups and the position of the cups in relation to the platform's edge. The larger the distance between the cups, the better performance became. Additionally, subjects' retrieval accuracy was higher for the outer cups than for the Middle cup, particularly when the outer cups were located next to the platform's edges. Although the pattern of responses was the same for all three species in all experiments, chimpanzees and bonobos outperformed orangutans in every cup constellation except in the Half table condition of Experiment 2.

Our results offer no support for the relational hypothesis (i.e., that the apes encoded the position of the baited cup in relation to the other two cups in the array). This hypothesis predicts that apes should have performed equally well in all three experiments, given the fact that the cups maintained the same relations in all experiments, despite changes in the proximity between cups and with respect to the table's edges. Contrary to this prediction, our results showed that

both manipulations substantially affected apes' retrieval accuracy. Specifically, apes' superior retrieval accuracy for cups located near the edges of the table strongly suggests that apes used these as landmarks, thus supporting the landmark-coding hypothesis (i.e., that the apes encoded the position of the baited cup in relation to a nearby landmark).

Following the landmark hypothesis, the apes encoded the cups' positions with regard to their relation to the table's edge. The outer cups (the Left cup and the Right cup) were both defined by a single relation—i.e., being near to an edge of the table—whereas the Middle cup could be defined as either the second cup to one edge of the table, or the cup situated between the two edges of the table. It is conceivable, therefore, that apes' retrieval accuracy on the Middle cup was lowest due to the requirement that two relations needed to be encoded. Not surprisingly, having to encode a location in relation to two landmarks is cognitively more demanding than encoding that location in relation to only one landmark. For example, children are able to guide their search behavior in relation to one landmark much earlier (at 2 years of age) (DeLoache and Brown 1983) than they are able to guide their search behavior in relation to two landmarks (at 4 years of age; e.g., when having to find a reward in the middle of two landmarks) (Simms and Gentner 2008; Uttal et al. 2006). Similarly, there are numerous reports that while nonhuman animals can use single landmarks to effectively find food, they struggle when they have to use two or more landmark cues relationally (MacDonald et al. 2004; Marsh et al. 2011; Potì et al. 2005, 2010; Sutton et al. 2000).

We also considered the possibility that subjects used a geometric landmark, such as the middle of the table. However, this possibility was not supported by the data. Specifically, placing the Middle cup in the middle of the table, as opposed to placing it to one side, did not affect apes' retrieval accuracy. Moreover, the lack of a difference between these conditions also suggests that the edge of the table was used as a landmark only for the cup closest to that edge. Interestingly, the Middle cup in the Half table condition was closer to one edge than the other, just like the outer cups were closer to one edge than to the other. However, no difference between these cups was detected, and this may suggest that edges lose their benefits when another cup is closer to them.

Despite the advantage afforded by the use of edge information for accurate food retrieval, edge information alone is not sufficient to explain the subjects' success, as in some conditions both the far left and the far right cups were near edges. In order to choose accurately, subjects also needed to encode some information to identify the correct edge—i.e., the left or the right edge. Humans and animals usually do not encode locations using only one fixed strategy. Instead, they apply different strategies in different

situations, depending on what information is available to them (Burgess 2006; Cheng and Newcombe 2005; Kanngiesser and Call 2010). Even though, we did not find any evidence that the apes were predominantly using egocentric cues, apes may still have encoded egocentric cues and then combined these cues with the allocentric cues (e.g., the cup at the edge on my “left” side). Data from transposition tasks lend support to this possibility, showing that apes encode both egocentric and allocentric cues (Albiach-Serrano et al. 2010; Hoffman and Beran 2006). In these transposition tasks, apes first observed an experimenter hide a reward in one container and then they had to walk around the array before they were allowed to choose. This manipulation, therefore, changed the apes' perspective by 180° from their original location. Consequently, egocentric information was no longer reliable, whereas allocentric information was. Apes performed worse on such transposition tasks (i.e., when they had to move around the array) than when they could choose from their original position, where both types of information were viable (Albiach-Serrano et al. 2010; Hoffman and Beran 2006).

One further possibility with regard to how apes kept apart the left and the right edges could be that apes encoded, together with the table edge, some additional landmark, subsequently using these landmarks hierarchically. In the natural environment, there are always multiple landmarks or cues that an animal can potentially use to encode the location of something. Animals and humans have been shown to encode multiple spatial cues and use them hierarchically (e.g., Brodbeck 1994; Cheng and Sherry 1992; Fiset and Dore 1996; Fiset et al. 2000; Gibbs et al. 2007; Gouteux et al. 2001; Legge et al. 2009; Spetch and Edwards 1986; Uttal et al. 2006). Furthermore, they prefer the closest (Cheng and Sherry 1992; Goodyear and Kamil 2004), more stable (Biegler and Morris 1999; Learmonth et al. 2001), and larger landmarks (Bennett 1993; Gouteux et al. 2001) that are part of the environment. We can only speculate, which this additional landmark could be: maybe an adjacent cage or the side to which they had to walk to get a carrot.

In the current study, absolute positioning of the cups was stable; hence, their relations with the surrounding environment also remained stable. This fact is a key reason why we believe the landmark strategy, and not the egocentric or the relative strategy, emerged as a predominant strategy in the apes tested here. One could argue that apes' own position to the baited cup was the same at the time of baiting and at the time of choosing and that it is therefore surprising that the egocentric strategy was not the preferred one. However, subjects' position did not remain stable throughout the trials—they moved to a different position to receive a carrot and they did not (always) return to exactly the same place. This would also explain the discrepancy

between the chimpanzees' almost perfect performance in the Hoffman and Beran's study (2006)—when a visual barrier was placed between them and the array but they did not need to move—and the less than perfect performance of the apes in our study.

Our data are consistent with the previous reports showing that chimpanzees and bonobos outperform orangutans in spatial cognition tasks that involve displacements (Albiach-Serrano et al. 2010; Barth and Call 2006; Herrmann et al. 2007). The current study shows that these differences in spatial cognition can also be extended to a task without reward displacements. As things stand at the moment, we do not have a good explanation for why these species differences in spatial cognition exist, and we can only speculate at this point. We can rule out that this difference is related to diet, as both chimpanzees and orangutans are fruit specialists. Moreover, we can rule out the idiosyncrasy of the Leipzig populations as a potential explanation, because two other studies on different (and larger) ape populations also found differences between chimpanzees and orangutans in spatial cognition (Haun and Call 2009; Herrmann et al. 2007). It is possible, therefore, that other factors, such as the level of sociality and/or terrestriality, might help explain the observed inter-species differences in spatial cognition. In particular, chimpanzees and bonobos, by virtue of their higher degree of sociality than orangutans, may have a greater capacity to keep track of the movements and locations of their group members than orangutans. Another possibility for the observed differences might be that orangutans, by virtue of being more arboreal than chimpanzees and bonobos, are less skillful than the African apes at encoding precise spatial information based on landmarks. These hypotheses, however, require empirical verification.

In conclusion, we found that apes encoded the location of a reward by referencing each cup with a different landmark (e.g., the left and the right edges of the table). Although the reduced retrieval accuracy for the Middle cup has been reported in the previous studies (Beran et al. 2005; Hoffman and Beran 2006; Hribar et al. 2011), this study links this deficit in performance with the position of the cups in relation to the landmarks provided by the table's edges. Moreover, this study also demonstrates that reducing the distance between cups, irrespective of their relation to key landmarks, also substantially reduces retrieval accuracy.

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