

Great apes' strategies to map spatial relations

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Abstract We investigated reasoning about spatial relational similarity in three great ape species: chimpanzees, bonobos, and orangutans. Apes were presented with three spatial mapping tasks in which they were required to find a reward in an array of three cups, after observing a reward being hidden in a different array of three cups. To obtain a food reward, apes needed to choose the cup that was in the same relative position (i.e., on the left) as the baited cup in the other array. The three tasks differed in the constellation of the two arrays. In Experiment 1, the arrays were placed next to each other, forming a line. In Experiment 2, the positioning of the two arrays varied each trial, being placed either one behind the other in two rows, or next to each other, forming a line. Finally, in Experiment 3, the two arrays were always positioned one behind the other in two rows, but misaligned. Results suggested that apes compared the two arrays and recognized that they were similar in some way. However, we believe that instead of mapping the left–left, middle–middle, and right–right cups from

each array, they mapped the cups that shared the most similar relations to nearby landmarks (table's visual boundaries).

Keywords Relational similarity · Spatial cognition · Analogy · Landmark

Introduction

When humans learn about new phenomena, solve novel problems, and construct and reconstruct their knowledge, they more often than not rely on forms of analogical reasoning (Gentner 2003; Leech et al. 2008). Often, humans use analogies to make complex structures intellectually more accessible for themselves and others. For example, the analogy of the solar system can be used to explain the less well-known structure of an atom. In order to form or understand this analogy, one has to recognize the relational (structural) similarity between two domains—objects circling around a central object because of a certain force—and then needs to map the elements from one domain (a base) to another (a target)—sun maps to nucleus and planets map to electrons. Additionally, analogies play a central role in language acquisition (Tomasello 2003) and other human cognitive achievements, such as inductive inference (Holland et al. 1986) and categorization (Ramscar and Pain 1996). This central role in many human cognitive abilities raises the question of whether the ability to recognize and respond to abstract relations between relations might be especially pronounced in humans (Penn et al. 2008), or indeed be the “thing that makes us smart” (Gentner 2003).

The question then becomes, are nonhuman animals capable of analogical reasoning—reasoning about relations between relations? Primates and birds have been shown to

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be capable of reasoning about one relation between items—called “first-order relations” (e.g. Bovet and Vauclair 2001; Flemming et al. 2007; Pepperberg 1987; Vonk 2003; Wright and Katz 2006). However, to be capable of analogical thinking animal would need to be capable of reasoning about the relation between two relations—called “second-order relations”. If an animal is efficient in recognizing first-order relation, it does not automatically mean that she will be able to solve a task that demands reasoning about second-order relations (Flemming et al. 2007). In attempts to answer the above question, most studies have used a so-called relational match-to-sample task (RMTS) (i.e., chimpanzees: Flemming et al. 2008; Thompson et al. 1997; orangutans and gorillas: Vonk 2003; capuchin monkeys: Spinozzi et al. 2004; rhesus monkeys: Flemming et al. 2007, 2008; Guinea baboons: Dépy et al. 1999; Fagot et al. 2001; Fagot and Parron 2010; pigeons: Cook and Wasserman 2007). In the RMTS task, a subject is first presented with a sample consisting of a pair of, for example, identical objects. Then she is presented with two alternative pairs of objects to match to the sample. One of the alternatives matches the sample in the relation between the paired objects (i.e. two identical). In order to solve the RMTS task, the animal has to recognize the relation between the objects in the sample (i.e. sameness) and then find a matching pair that holds the same relation between them (i.e. again sameness); hence, she has to reason about and compare two relations. Given its clear structure and wide applicability across species, RMTS has made a valuable contribution toward understanding nonhuman’s reasoning about relations between relations. However, since all of RMTS studies have used identity/nonidentity relation, they have been criticized by some authors who have suggested that they do not test animals’ ability to recognize and match abstract relations (Penn et al. 2008). Rather, these authors have argued that they could be solved by matching the amount of perceptual variability (entropy) that is depicted in the stimulus arrays (Fagot et al. 2001). For an array with identical objects, the entropy score will be zero and therefore lower than for a nonidentity array (the entropy for two-item array is 1, for 4-items is 2, etc., Fagot et al. 2001)—so subjects only have to pick an alternative array that also has low (or high) entropy. Evidence to support this has come from observations that when the difference between identity and nonidentity arrays’ entropy scores is increased (by increasing the number of items in an array), animal’s performance on RMTS also increases (Fagot et al. 2001).

Moreover, all studies using RMTS require long training periods (i.e. Cook and Wasserman 2007; Fagot et al. 2001) or subjects that have already had experience in the MTS procedure (i.e. Vonk 2003), or in discriminating the identity arrays from nonidentity arrays (i.e. Fagot et al. 2001;

Thompson et al. 1997). Even for children, RMTS appears to be rather difficult (Christie and Gentner 2007; Thibaut et al. 2008). Children are able to recognize and match relations in a RMTS task, which is similar to those presented to animals, only at the age of 8 years (Thibaut et al. 2008), even though at around the third year of life they are already able to reason about relational similarity (depending on the complexity and familiarity of the relations) (i.e. Chen 2007; Goswami 1995; Goswami and Brown 1990; Rattermann and Gentner 1998).

Given these criticisms of a traditional RMTS and the amount of training required in the RMTS paradigm, in the present study we wanted to investigate apes’ ability to reason by analogy using a simpler paradigm in which no training is involved, and where apes are unable to rely on the perceptual similarities between objects to solve it. To this end, we employed a searching task in which apes had to locate a food reward in one array of cups after observing a food reward being hidden in a different, identical array of cups. To locate the food reward, apes needed to infer its position based on the position of the reward in the other array. More precisely, when a reward was hidden underneath the left cup, for example, apes first needed to recognize that in both arrays each of the three cups held a special relation to the other two cups, e.g. the left cup was left of both other two cups. Finally, they needed to select a cup from their array, which held the same relative position within the array as the baited cup in the other array. Our intention was not to train apes to pay attention to specific parts of the task; instead, we wanted to know whether apes spontaneously recognized that the reward was always located in the same relative position in both arrays.

We decided to use such a spatial relational paradigm for two main reasons. Firstly because spatial tasks come rather naturally to great apes thus tapping into a sophisticated set of cognitive abilities that largely match those of humans (Herrmann et al. 2007). Secondly, setups for spatial tasks are simple and require no training and they can be used with a large variety of species.

A similar searching task using spatial relations has previously been used with human children (Haun and Call 2009; Loewenstein and Gentner 2005) and apes (Haun and Call 2009). In Loewenstein and Gentner’s (2005) study, for example, two boxes were vertically arranged that had three possible hiding places for a reward (on the top, in the middle and on the bottom). Children observed the experimenter hide a reward at a given location in the Hiding box and were subsequently asked to search for the same reward in the Finding box. Even the youngest group of children (mean age: 3.8 years) performed at above chance levels, indicating that they found the reward by mapping its corresponding relative location from the Hiding box to the Finding box.

Haun and Call (2009) conducted a similar searching task with children and with four great ape species (chimpanzees, bonobos, orangutans and gorillas). Again, two arrays with three possible hiding places were used, but here the arrays were placed horizontally, one behind the other but misaligned on an inclined table. Additionally, two levels of relational reasoning were tested: causal and abstract spatial relational reasoning (most subjects were tested on both conditions). In the causal condition, the cups in the two arrays were connected with tubes down which a grape could roll from one cup to another. In the spatial relations condition, the two arrays of cups were “connected” by the spatial relational similarity between the arrays, that is, when the left cup in one array was baited, then the subject had to search under the left cup in the other array. Since one of the two arrays was positioned in front of the other on an inclined table, there were three possible strategies that apes could use (for detailed explanation see Haun and Call 2009, p. 150): (1) relational strategy (pick the cup that has the same spatial relations to the other cups within its respective array, as the baited cup in the other array) that led to a success in 100% of time, (2) proximity strategy (pick the closest cup to the baited cup) producing a 66% correct choices, and (3) gravity strategy (pick the cup that is in the line of gravity from the baited cup) that produced 33% correct choices. Their results showed that all four species of great ape and human children could reason about the causal connectedness of the cups, but only older children (4–4.5 years), chimpanzees and bonobos showed evidence of reasoning about the spatial relational similarities between the two arrays of cups. However, since there were three possible strategies to use, it might be harder for apes to pay attention only to the relational strategy and ignore the other two.

In the present study, therefore, we sought to further explore the spatial relational reasoning in our closest living relatives, the other great apes. In Experiment 1, there were two main modifications compared to Haun and Call’s study. First, the two 3-cup arrays were placed on a flat table instead of an inclined one, and therefore a possibility of gravity bias was eliminated. Second, the two arrays were positioned next to each other forming a line, and therefore all three cups could be solved only by using the relational strategy. In Experiment 2, we further addressed the issue of flexibility in spatial relational mapping, by altering the constellation of the two arrays of cups. Specifically, these arrays were either placed next to each other, forming a line, or were aligned perfectly one behind the other. In Experiment 3, we investigated an effect of proximity bias on apes’ relational mapping ability.

Although in all three experiments apes were rewarded only when they chose the spatially relationally equivalent cup in the Search array to the baited cup in the Hiding

array, we noticed that when in Experiment 2 the two arrays were placed next to each other forming a line, some individuals might have used a different strategy. In particular, apes seemed to select the cup at the table edge (L cup) in the Search array when the cup at the other table edge (R cup) was baited in the Hiding array. Additionally, they chose the cup in the middle of the table (R cup) in the Search array when the cup in the middle of the table (L cup) was baited in the Hiding array (see Fig. 1c for better understanding). Because we suspected that the apes were mapping together the cups that were placed next to the same landmark (i.e. table’s visual boundary), we called this strategy a “landmark strategy”. Therefore in the first two experiments, where the two arrays were positioned next to each other in one line, we additionally assessed whether the apes tended to choose the cups after this strategy.

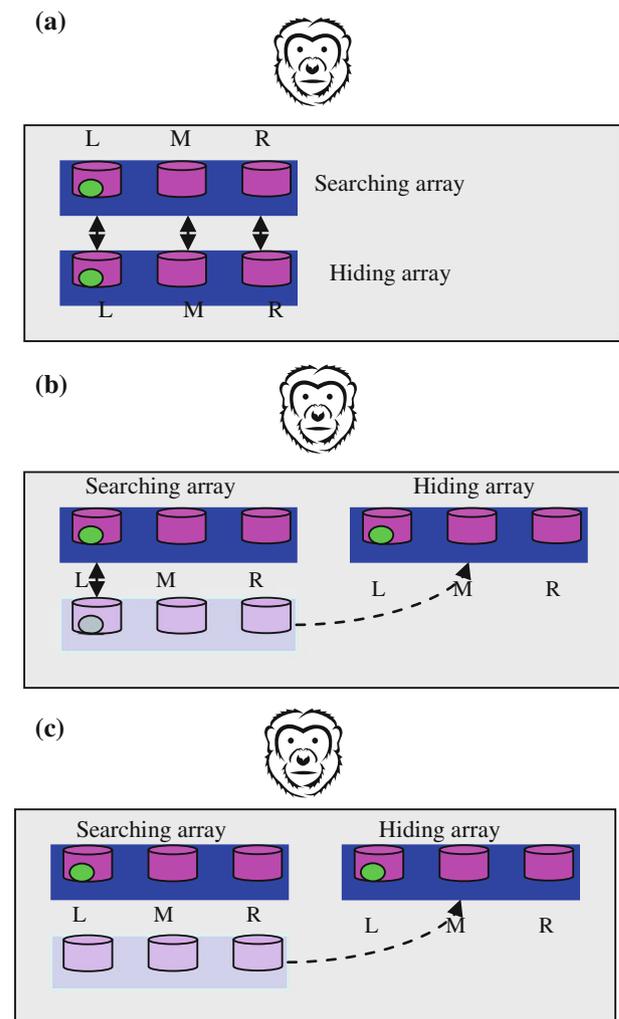


Fig. 1 Position of the two arrays for **a** Two rows, **b** Transition and **c** One line conditions in Experiment 2

Experiment 1: retrieving and searching

Prior to Experiment 1 we conducted a pilot study with three 15-year-old chimpanzees. The procedure was almost identical to the procedure of Exp 1 except that the chimpanzees were allowed to choose only from the Search array. Results showed that none of the chimpanzees was able to select the baited cup at above chance levels. A number of possible explanations exist for this outcome: First, apes may simply not possess the necessary cognitive requisites that are required to appreciate the spatial relations that would lead to successful responding in our task. It is also possible, however, that subjects simply did not pay attention to the baiting of the Hiding array because they never got to choose from it. Failing to take this information into account would have prevented them from solving the task. In Experiment 1, therefore, we sought confirmation that apes had successfully encoded the initial hiding information by letting them choose both from the Hiding and Search arrays.

Methods

Subjects

Five bonobos (*Pan paniscus*), three males and two females, aged between 11 and 26 years, housed at the Wolfgang Köhler Primate Research Center, Zoo Leipzig, Germany participated in this study. Their exact ages at the time of the

study and their rearing histories are shown in Table 1. The bonobos live in a group with their conspecifics with access to spacious indoor and outdoor areas. They are fed a variety of fruits, vegetables, and cereals several times per day. They are never food deprived and water is available ad libitum. Subjects were tested individually in their sleeping rooms. All subjects had previously participated in a study that involved recognizing spatial relational similarity (Haun and Call 2009).

Materials

We used two arrays of three identical round blue cups ($d = 8$ cm) placed next to each other to form a straight line. Each array was placed on a blue tray ($32 \text{ cm} \times 13 \text{ cm}$). The two trays rested side by side on a table ($80 \times 35 \text{ cm}$), separated by a distance of 5 cm and a 5-cm-high gray plastic divider. The distance between the cups on each tray was ca. 3.5 cm.

Procedure

One of the arrays was designated as the Search array and the other as the Hiding array. At the beginning of each trial, an occluder was raised and a grape was hidden underneath one of the cups in the Search array. The occluder was then removed and one of the cups in the Hiding array was baited in full view of the ape. After baiting was completed, we allowed subjects to choose twice, once from the Search

Table 1 Details of the apes tested in this study, the experiments in which each subject participated and the starting condition in Haun and Call's study (2009)

Name	Age (years)	Sex	Rearing history	Experiment participation	Start condition in H&C's study
<i>Chimpanzees</i>					
Jahaga	15	Female	Mother	P, 2, 3	Relational ^a
Fifi	15	Female	Mother	P, 2, 3	Relational ^a
Trudi	15	Female	Mother	P, 2, 3	Relational ^a
Alex	7	Male	Nursery	2, 3	Relational
Annett	9	Female	Nursery	2, 3	Causal
Alexandra	9	Female	Nursery	2, 3	Relational
<i>Bonobos</i>					
Joey	26	Male	Nursery	1, 2, 3	Relational
Limbuko	13	Male	Nursery	1, 2, 3	Causal
Kuno	12	Male	Nursery	1, 2, 3	Causal
Ulindi	15	Female	Mother	1, 2, 3	Causal
Yasa	11	Female	Mother	1, 2, 3	Relational
<i>Orangutans</i>					
Bimbo	28	Male	Nursery	2, 3	Causal
Dunja	35	Female	Nursery	2, 3	
Pini	20	Female	Mother	2, 3	Causal
Dokana	19	Female	Mother	2, 3	Relational
Padana	11	Female	Mother	2, 3	Relational

P pilot study

^a These three subjects were presented only with the relational task

array and once from the Hiding array. Three subjects chose first from the Search array and then from the Hiding array (Search first group); two subjects chose first from the Hiding array and then from the Search array (Retrieve first group). We counterbalanced the order of the selected arrays to investigate whether choosing first from the Hiding array, where the apes knew where the reward is, might increase the success of finding a reward in the Search array. We had two reasons to expect this: first, the apes would not be distracted by the “known” reward in the Hiding array when they chose from the Search array. Second, the apes might persevere in choosing the same cup in the Search array as they had just chosen in the Hiding array.

We tested two relation conditions: *Relative condition*: The baited cups in the two arrays had the same relative position within the array. Thus, if the baited cup in the Hiding array was left, middle or right, then the baited cup in Search array was left, middle or right, respectively. *Arbitrary condition* (control): The baited cups in the two arrays had different (but consistent) relative positions within the array. In particular, if the baited cup in the Hiding array was left, middle or right, then the baited cup in Search array was right, left or middle, respectively. Although these three pairs of positions were arbitrary, they remained the same throughout testing. Consequently, apes could potentially learn these contingencies over time.

Two bonobos were in a relative condition and three were in an arbitrary condition (see Table 2). Fifteen 12-trial sessions were conducted with each subject.

Scoring and data analysis

We videotaped all trials and scored them both live and from the videotapes. A second coder scored 20% of the trials to assess inter-observer reliability. Inter-observer reliabilities for the Search array (Cohen’s kappa = 0.74) and Hiding array (Cohen’s kappa = 0.82) were good. Our independent variables were relation condition (Relative and Arbitrary) and order of selection (Search first and Retrieve first), and the dependent measure was the percentage of correct trials (i.e., those trials on which apes chose the cup that led to a food reward). A Binomial test was used to determine whether subjects selected the baited cup above chance levels. We also investigated whether

subjects may have used the landmark strategy. For this analysis, we scored whether the apes selected the cups as follows: when the Right cup (that was located by the table’s edge) in the Hiding array was baited, the Left cup in the Search array counted as the correct choice; when the Middle cup was baited, also the Middle cup in the other array was correct; and finally, when the Left cup (in the middle of the table) in the Hiding array was baited, the Right cup (also in the middle of the table) in the Search array was considered correct based on the landmark strategy.

Results

Table 2 presents the percentage of correct trials for each subject as a function of relation condition and order of selection. All subjects found the reward at above chance levels in the Hiding array (Binomial test: $P < 0.001$ in all cases) both when it was searched first (99.5% of trials) and second (75.3% of trials). In contrast, subjects failed to find the reward at above chance levels in the Search array (Binomial test: $P > 0.05$ in all cases) regardless of whether they searched the Search array first (32.5% of trials) or second (32.5% of trials). The bonobos also did not choose cups after the landmark strategy at above chance levels, neither at the group level (Wilcoxon test: $z = 0.135$, $P = 1.00$, $N = 5$) nor at the individual level (all $P > 0.05$).

Discussion

Overall, the results from Experiment 1 do not provide any evidence that apes applied a relational mapping strategy in our task. Neither did they use the landmark strategy, which is not surprising given that the bonobos were never rewarded for it. Critically, their poor performance was not a product of them simply not paying attention to the Hiding array, or due to forgetting about where the reward was hidden in the Hiding array. Contrasting the data with previous reports (Haun and Call 2009), it seems that positioning the two arrays of cups next to each other made it too difficult for apes to recognize the relational commonalities between them. One possible explanation could be that apes did not know what they should do. The connection between the two arrays was established only through

Table 2 Individual performances in Experiment 1

Name	Relation condition	Group	Retrieve % correct	P	Search % correct	P
Limbuko	Relative	Retrieve first	99	<0.001	32	0.35
Joey	Relative	Search first	88	<0.001	34	0.46
Kuno	Arbitrary	Retrieve first	100	<0.001	33	0.52
Ulindi	Arbitrary	Search first	70	<0.001	32	0.41
Yasa	Arbitrary	Search first	68	<0.001	31	0.26

the experimenter, who hid the two grapes under the two cups in the same position. When children are presented with a searching task the experimenter explains them that they should search under the same cup or in the same position (e.g. Loewenstein and Gentner 2005). In addition, maybe one needs to recognize that one array represents (or provides information about) the other array (DeLoache 2004). However, in Haun and Call's study (2009) children and apes did not get any instructions where they should look for the reward. They had to figure out the rule "search under the cup in the same relative position" by themselves. However, children and apes performed better in the relational task, if they were first confronted with the causal task than if they started with the relational task and then went on to causal task. It seems that causal task provided some sort of scaffolding to the children and apes or helped them to recognize that the cups from the two sets were "connected" in some way. Similarly one capuchin monkey that was able to match size relations in a similar searching task was first provided with intensive training in matching to sample task and went through a series of steps before it was capable of solving an analogy task (Kennedy and Fragaszy 2008). Therefore, in Experiment 2 we tried to make the relational similarity between the two arrays more obvious for the apes.

Experiment 2: two rows

In Experiment 2, we sought to test whether arranging the two arrays one behind the other would allow apes to solve the spatial mapping task. That is, would this particular constellation of arrays allow apes to comprehend the similarity between the Hiding array and the Search array—in that they both have three cups (a left cup, a middle cup and a right cup)—and, as such, enable them to appreciate that the cups that share the same relationally equivalent location will always contain the food reward? Moreover, this information may help apes realize that the same is true when the two arrays are positioned side by side, in a straight line. Critically, then, in Experiment 2 apes were able to observe the transition of the two arrays from being positioned one behind the other to being positioned next to each other, forming a straight line. In addition, the Arbitrary condition from the Exp 1 was dropped and the apes could choose only from the Search array.

Methods

Subjects

Six chimpanzees (*Pan troglodytes*), five bonobos (*Pan paniscus*) and five orangutans (*Pongo pygmaeus*) housed at

the Wolfgang Köhler Primate Research Center, Zoo Leipzig, Germany participated in this study. There were 11 females and 5 males ranging from 7 to 35 years of age. Their ages at the time of the study and their rearing histories are shown in Table 1. All apes lived in social groups of various sizes, with access to big indoor and outdoor areas. They were fed several times a day and were not food or water deprived for testing. Each ape was tested individually in their sleeping room. Three of the chimpanzees participated in the pilot study and all of the bonobos participated in the Exp 1. In a way they could be considered experienced subjects, even though they all had failed the previous tasks. Moreover, all subjects had participated in a variety of cognitive tests, and all but one individual (orangutan Dunja) had previously participated in Haun and Call's (2009) study.

Materials

As for Experiment 1, we used two arrays of three identical plastic cups (8 cm × 8 cm) that were placed on two blue trays (30 cm × 14 cm) and situated on a testing table (80 cm × 35 cm). The cups were different in color, shape and size from those used in Experiments 1. The distance between the cups within each array was ca. 3.5 cm.

Procedure

Both trays, with their respective 3-cup arrays, were placed on the testing table with the Hiding array located approximately 5 cm behind the Search array (see Fig. 1). At the beginning of each trial, an occluder was raised so that apes could not observe the hiding of a food reward underneath one of the cups in the Search array. Following baiting, the occluder was removed and the three cups in the Search array were turned upside down, while the cups in the Hiding array were still lying on their sides. Then the following three conditions were administered:

1. *Two rows condition*: One of the cups in the Hiding array—a cup that had the same relative position within the array as the baited cup in the Searching array—was baited in full view of the ape and all three cups were then upturned. Subsequently, the tray with the Search array was pushed forward and the ape could make her choice.
2. *Transition condition*: The baiting of the Hiding array was identical to the previous condition, but before subjects were allowed to pick a cup from the Search array, the Hiding array was moved next to the Search array, forming a straight line. The Search array was then pushed forward (and the straight line that the arrays formed was broken) so that the subject could choose a cup.

3. *One line condition*: Initially, the Hiding array was moved next to the Search array, forming a straight line. Following this, one cup from the Hiding array was baited in full view of the ape, and then the Search array was pushed forward.

After the subject made her choice, the experimenter lifted the chosen cup. If it was the correct one, the ape was immediately given the grape hidden underneath it. If she was wrong, the experimenter lifted the correct cup and took away the grape before the next trial was administered. Apes occasionally pointed to the cups in the Hiding array; when this happened, they were ignored and encouraged to choose a cup from the Search array by moving it back and forward again. One session consisted of 18 trials (6 trials per condition). The order of trials (conditions), as well as the position of the food reward, was semi-randomized, allowing for the constraint that the same condition and position of the food reward could only occur twice in a row. Each subject received 15 sessions (creating a total of 90 trials per condition).

Data scoring and analysis

We videotaped all trials and scored them both live and from the videotapes. A second coder scored 20% of the trials to assess inter-observer reliability. Inter-observer reliability was excellent (Cohen's kappa = 0.97). The same scoring procedure as in Experiment 1 was used. That is, we analyzed the percentage of correct choices made in the Search array, split as a function of species and condition. We also investigated whether subjects may have used the landmark strategy.

Additionally, in the Transition condition, apes sometimes pointed to a cup in the Hiding array after they were moved forward and next to the Search array. Given this, we also analyzed how often apes pointed correctly to the baited cup in the Hiding array, and whether this behavior varied depending on the position of the baited cup. Since they were never rewarded for pointing to the Hiding array, this behavior decreased across sessions; therefore, we only analyzed the first two sessions in this case.

Results

Success

Figure 2 presents the percentage of correct trials as a function of condition and species. As there were no significant differences in performance between species in any of the three conditions (Kruskal–Wallis test: Two rows condition: $\chi^2 = 3.897, P > 0.05, df = 2, N = 16$; Transition condition:

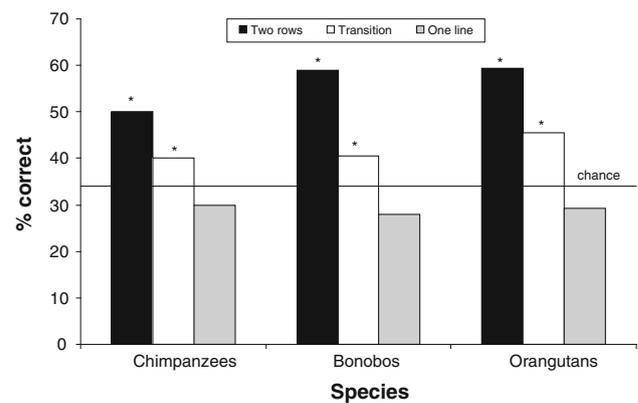


Fig. 2 Experiment 2. Species' mean percent correct for the three conditions. All three species performed at above chance level on conditions Two rows and Transition

$\chi^2 = 2.363, P > 0.05, df = 2, N = 16$; One line condition: $\chi^2 = 0.495, P > 0.05, df = 2, N = 16$), we collapsed the data across species for further analyses. Collapsing the data in this way revealed that apes chose the cup in the Search array that was in the same relative position to the baited cup in the Hiding array significantly above chance in the Two rows condition (Wilcoxon test: $z = 3.521, P = 0.001, N = 16$) and the Transition condition (Wilcoxon test: $z = 3.260, P = 0.001, N = 16$). In contrast, subjects' performance was significantly below chance levels in the One line condition ($z = 2.434, P = 0.015, N = 16$). Interestingly, we found no evidence that subjects' performance changed across sessions for any species in any of the conditions except for the orangutans, who improved their performance in the Transition condition as testing progressed (Spearman: $r = 0.551, P = 0.03$).

Overall, we found a significant difference between conditions (Friedman test: $\chi^2 = 28.5, P < 0.001, df = 2, N = 16$). Post hoc tests revealed that apes performed better in the Two rows condition than in both the Transition and One line conditions (Wilcoxon test: $z = 3.362, P = 0.001, N = 16$, and, $z = 3.519, P < 0.001, N = 16$, respectively). Apes also performed better in the Transition condition than in the One line condition (Wilcoxon test: $z = 3.518, P < 0.001, N = 16$).

Individual analyses revealed that all apes, except one chimpanzee (Jahaga, 42%, $P = 0.057$), selected the baited cup in the Search array at above chance levels in the Two rows condition (Binomial test: all $P < 0.02$). Similarly, three chimpanzees—Jahaga, Alexandra, Annett (Binomial test, $P < 0.031$), one bonobo—Yasa ($P < 0.001$) and three orangutans—Padana, Dunja, Bimbo ($P < 0.003$) selected the baited cup in the Search array at above chance levels in the Transition condition. In contrast, none of the apes were above chance at picking the baited cup in the Search array

in the One line condition; in fact, two chimpanzees and one bonobo chose the correct (baited) cup at significantly below chance levels (Binomial test: $P < 0.02$).

Analysis of whether apes' success varied depending on the position of the cup that was baited revealed that there was a significant difference in apes' performance on the three cups (left, middle or right cup) in all conditions (Friedman test: Two rows condition: $\chi^2 = 11.65$, $P = 0.003$, $df = 2$, $N = 16$; Transition condition: $\chi^2 = 11.65$, $P = 0.003$, $df = 2$, $N = 16$; One line condition: $\chi^2 = 10.38$, $P = 0.006$, $df = 2$, $N = 16$). Specifically, apes' performance when the middle cup was baited was significantly lower than when either the left or right cup was baited in the Two rows condition (Wilcoxon test: left-middle cup, $z = 2.692$, $P = 0.007$, $N = 16$; right-middle cup, $z = 2.975$, $P = 0.003$, $N = 16$) and the Transition condition (Wilcoxon test: left-middle cup, $z = 2.225$, $P = 0.026$, $N = 16$; right-middle cup, $z = 3.032$, $P = 0.002$, $N = 16$). Apes' performance when the middle cup was baited was also significantly lower than when the right cup was baited in the One line condition (Wilcoxon test: $z = 2.388$, $P = 0.017$, $N = 16$).

In the first two sessions of the Transition condition, chimpanzees pointed to the Hiding cup that contained the food reward in 85% of cases, bonobos in 93% of cases, and orangutans in 65% of cases, irrespective of the position of the baited cup (Friedman test: $\chi^2 = 2.923$, $P = 0.407$, $df = 2$, $N = 10$). As such, the differences found between apes' correct choice behavior to the middle cup and the other two cups in the Search array cannot be explained simply as a product of apes ignoring the middle cup during baiting of the Hiding array: apes could remember which cup the reward had been hidden underneath in the Hiding array, and they could successfully point to it (even when the middle cup was baited).

Landmark strategy?

In the Two rows and the Transition condition the landmark strategy would lead subjects to chose the same cups as the relational strategy. However, in the One line condition the two strategies would lead to different cups. Therefore, we only analyzed the choices for the One line condition. Indeed, in the One line condition, apes preferred to choose the cup in the Search array that occupied the similar position on the table as the baited cup in the Hiding array (Wilcoxon test: $z = 3.054$, $P = 0.002$, $N = 16$). Individual analyses revealed that two chimpanzees—Alex, Alexandra (Binomial test, $P < 0.02$), one bonobo—Ulindi ($P = 0.019$) and one orangutan—Pini ($P = 0.011$) selected the cup in the Search array after the landmark strategy at above chance levels in the One line condition.

Discussion

As expected, the positioning of the two arrays had a strong influence on ape's performance. Their success was highest in the Two rows condition and lowest in the One line condition.

Although we cannot know for sure what the apes understood about the goal of the task, passing the Two rows condition indicated that the apes did use some kind of information from the Hiding array to infer reward's position in the Search array. However, it appeared they did so only in the Two rows and Transition condition and not in the One line condition. One possible explanation for these results could be that apes did not spontaneously recognize the stability of spatial relations between the two arrays when they were moved. A second possible explanation, however, is that apes did not recognize the relational similarity between the two arrays, no matter what the constellation of the arrays was. Rather, perhaps apes simply employed a strategy in which they picked the closest cup to the reward (proximity strategy). In order to employ such a proximity strategy, an ape would only need to be able to compare the distances between the baited cup in the Hiding array and the three cups offered in the Search array, and then choose the cup that was the shortest distance from the baited cup. In the Two rows condition, the closest cup was the cup that was directly in front of the baited cup. In the One line condition, the closest cup was always the same cup, the right cup, irrespective of the position of the baited cup in the Hiding array. In the Transition condition, however, apes would need to remember which cup was in front of the baited cup before the Hiding array was moved and ignore the real position of the reward when making their choice.

A detailed analysis of apes' choices revealed that even though the above proximity-based explanation can explain some of the results it can not explain all of them. In the first two conditions, apes only reliably chose the most proximate cup when the baited cup was on the left- or right-hand side of the Hiding array, but not when it was in the middle of the array. Moreover, in the One line condition, apes did not preferentially choose the most proximate cup; however, neither were their choices entirely random. Rather, it appears that, in this condition, they were employing the "landmark" strategy. Thus, when the cup at the edge was baited in the Hiding array (R cup), apes tended to choose the cup at the edge (L cup) in the Search array, for example.

Given that the three "pilot" chimpanzees and the bonobos did not perform any better than the rest of the subjects, we have no reason to believe that their experience modified the way they tackled the task of Experiment 2.

Although we do not fully dismiss the "proximity" explanation of the results (we test it in Experiment 3), the

above analysis suggests that apes were mapping the cups of the Hiding array to the cups of the Search array, but they were employing a different strategy than we expected them to in this mapping—the landmark strategy. The possible explanations for why apes employed a different strategy to the one we expected will be discussed in the General Discussion.

Experiment 3: misaligned rows

To investigate apes' bias to engage in a proximity-based mapping strategy, in Experiment 3, the two arrays were positioned in two rows, but were misaligned, such that the center cup in the Hiding array was positioned behind the right or the left cup in the Search array. With this constellation, we sought to examine directly whether apes would preferentially engage in a proximity-based strategy or a relationally based strategy.

Methods

Subjects

Subjects were the same as those in Experiment 2.

Materials

The same testing table, blue trays, food reward and six cups used in Experiment 2 were used here. The distance between the cups within each array was 8 cm.

Procedure

The two arrays of cups were positioned one behind the other, but misaligned, such that the center cup in the Hiding array was aligned with either the right or left cup in the

Search array (see Fig. 3). The distance between the blue trays (upon which the arrays of cups sat) was 15 cm. The general procedure was the same as in the Two rows condition of Experiment 2. That is, apes did not see the hiding of the food reward in the Search array, but they did watch a grape being hidden underneath one of the cups in the Hiding array. Subsequently, the Search array was pushed forward, and the subject could make her choice. Two 12-trial sessions were conducted. Within each session, the Hiding array was misaligned to the left in half of the trials and to the right in the other half of the trials. The trials were semi-random, with the constraint that there could be a maximum of two consecutive trials in which the Hiding array was misaligned to the same side of the Search array.

Data scoring and analysis

We videotaped all trials and scored them both live and from the videotapes. A second coder scored 20% of the trials to assess inter-observer reliability. Inter-observer reliability was perfect (Cohen's kappa = 1). The same scoring procedure used in the previous experiments was employed. We analyzed both correct choices and choices irrespective of success, as a function of species and cup position. We investigated whether the apes chose the cups following the proximity strategy. We made no extra analysis for the landmark strategy because both relational and landmark strategy led to the same outcome.

Results

Success

Overall, we found no differences in performance between species (Kruskal–Wallis test: $\chi^2 = 2.107$, $P = 0.366$, $df = 2$, $N = 16$). They performed at above chance levels (Wilcoxon test: $z = 3.267$, $P < 0.001$, $N = 16$), however,

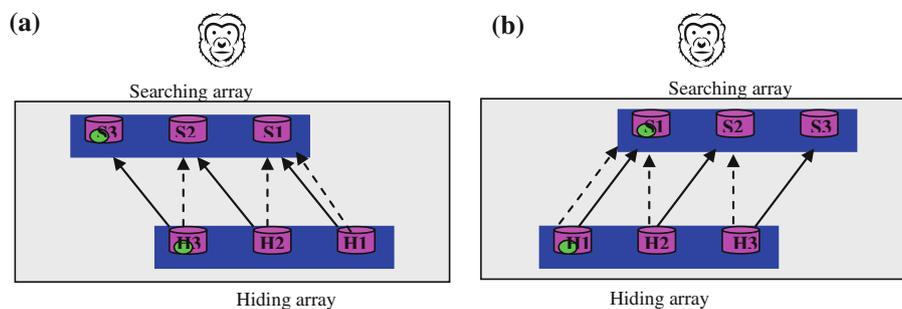


Fig. 3 Position of the cups in **a** Right side trials and **b** Left side trials. The solid arrows show, which cup in the searching array apes would choose, when using the relational similarity between cups (spatial relation strategy). The dashed arrows show the cup that apes would choose, if they just went for the closest cup (proximity strategy).

When reward is hidden under cup H1, apes will choose cup S1 using either of the two strategies. When food is hidden under cups H2 and H3, apes have to use spatial relation strategy (cups S2 and S3, respectively) to find a hidden reward

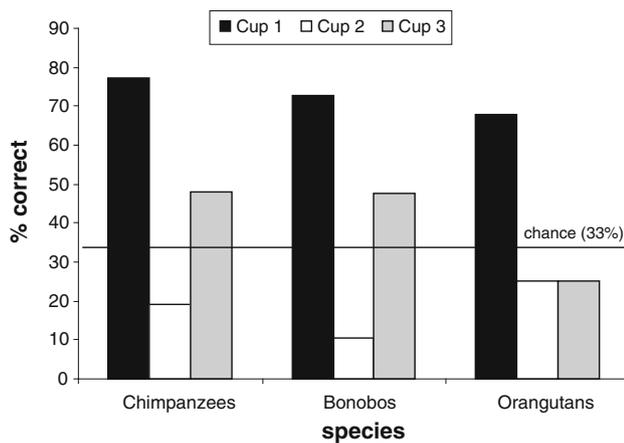


Fig. 4 Experiment 3. Species' mean percent correct for each individual cup (cup 1, cup 2, and cup 3)

the performance of the apes varied substantially depending on which cup hid the food reward (Friedman test: $\chi^2 = 20.258$, $P < 0.001$, $df = 2$, $N = 16$, Fig. 4). Apes performed at above chance level (chance = 33%) when cup H1 was baited (Wilcoxon test: $z = 3.482$, $P < 0.001$, $N = 16$) and at below chance level when cup H2 was baited (Wilcoxon test: $z = 3.085$, $P = 0.002$, $N = 16$). When cup H3 was baited their choices were random. More specifically, we found no species differences in performance when cups H1 (Kruskal–Wallis test: $\chi^2 = 1.029$, $P > 0.5$, $df = 2$, $N = 16$) and H2 (Kruskal–Wallis test: $\chi^2 = 2.414$, $P > 0.3$, $df = 2$, $N = 16$) hid the food reward. In contrast, chimpanzees and bonobos performed better (both 48%) than orangutans (25%), though not significantly, when cup H3 hid the food reward (Mann–Whitney test: $z = 1.547$, $P = 0.07$, $N = 16$).

Proximity strategy?

When a food reward was hidden under the H1 cup, both proximity and relational strategy led to the same cup—S1. When the middle cup (H2) was baited, apes chose the closest cup (S1) at above chance levels (Wilcoxon test: $z = 3.337$, $P < 0.001$, $N = 16$). However, they chose cup S1 more often when cup H1 was baited (Wilcoxon test, $z = 2.192$, $P = 0.028$, $N = 16$). Finally, when the reward was hidden under the H3 cup, apes did not choose the closest cup at above chance levels (Wilcoxon test: $z = 1.297$, $P = 0.211$, $N = 16$).

Discussion

The results of Experiment 3 provide no straightforward answer regarding the strategy apes used in our choice tasks. Similarly as in Experiment 2, some of the results of Experiment 3 could be explained by proximity strategy, but

not all—when cup H3 was baited, the chimpanzees and bonobos tended to choose in the Search array a cup with the same relative position.

In cases where both proximity and relational strategies were successful (cup H1), apes consistently chose the correct cup (cup S1). When these two strategies led to a different cup choice, however, apes' choices were not consistent with only one strategy. When a food reward was hidden under the middle cup (H2), apes mainly chose the closest cup (S1); however, they chose S1 in this situation less often than when cup H1 was baited. When apes had seen a food reward being hidden under cup H3, chimpanzees and bonobos, unlike orangutans, seemed to mainly follow a relational strategy.

General discussion

Over Experiments 1, 2 and 3, we presented apes with three different spatial mapping tasks in which they were required to find a food reward in one array of cups after witnessing the experimenter hiding a food reward in a different array of cups. The two arrays of cups were either positioned one behind the other (in two rows), or next to each other (in one line). In Experiment 1, where the two arrays were always positioned in one line, apes' success in finding the food reward was at chance. In Experiment 2, the positions of the two arrays varied between being in two rows and being in one line. When they were in one line, apes' success was again at chance; however, when the arrays were in two rows, apes found the reward at above chance levels. In Experiment 3, the two arrays were positioned in two rows, but misaligned. Apes' performance was again above chance, but lower than when the two arrays were aligned one behind the other. Overall, then, it appears that the major variable affecting apes' success was the constellation of the two arrays.

As was proposed earlier, one possible explanation for this constellation dependent performance is that apes employed a strategy in which they simply chose the cup that was closest to the reward they saw hidden in the Hiding array—the *proximity strategy*. Numerous studies have reported that apes' choices are often biased by proximity to a reward and that apes regularly experience difficulty inhibiting this proximity-based response bias (Barth and Call 2006; de Blois et al. 1998; Call 2001). However, proximity fails to explain the results perfectly.

The second possible strategy might be the *relational strategy*—choosing the cup in the Search array that held the same relative position as the baited cup in the Hiding array. To be capable of comparing the arrays relationally, correctly mapping left cup in the Hiding array to left cup in the Search array, for example, apes would need to encode

each array of cups as one unit, comprised of three items that hold special relations to one another, but the units as a whole are contained within a bigger spatial framework, relative to a subject; hence, to engage in relational mapping, apes must use an egocentric frame of reference. However, assuming that apes predominantly used a relational strategy in our tasks also does not fit perfectly with the present results. It does not explain, for example, why apes in the One line condition of Experiment 2 preferentially chose the cup in the Search array that held the same relation to the table edge as the baited cup in the Hiding array. Neither can the relational strategy explain the low performance of apes on matching the middle cups in all constellations of Experiments 2 and 3. In light of the above, we provide an alternative account of apes' choice behavior in our Experiments that we feel provides a better explanation for the observed pattern of results.

In this alternative account, rather than viewing the individual cups as part of one unit (an array), apes are assumed to treat them as individual units within a larger spatial framework. Within this framework, cups are put in relations to some elements that are external to the target array and to the subject itself, that is, an allocentric, rather than an egocentric, frame of reference is employed (for a similar account described with children, see Huttenlocher and Presson 1979). Nonhuman primates, and other animals, readily use landmarks when searching for hidden food (Deipolyi et al. 2001; Dolins 2009; MacDonald et al. 2004; Menzel 1996; Potì et al. 2005, 2010; Sutton et al. 2000). There are even some indications from spatial memory studies that primates remember the location of a baited container better when it is located in a salient location, such as at the edge of a platform or tray, as opposed to when it is located somewhere else on the platform (Hoffman and Beran 2006; Kubo-Kawai and Kawai 2007). Moreover, human's spatial recall is influenced by visible boundaries, symmetry axes (Huttenlocher et al. 1994; Spencer et al. 2001), explicit visual landmarks (Diedrichsen et al. 2004), and by one's long-term memory of the target locations (Spencer and Hund 2003).

Given the above, we believe that in Experiments 2 and 3 when apes saw the experimenter hide a food reward underneath one of the cups in the Hiding array, they encoded that cup's position in relation to the nearest landmark. Subsequently, they would search under the cup in the Search array that was nearest the same landmark—the *landmark strategy*. Although we cannot be sure for certain, we favor the edge of the table (as opposed to the edge of the array) as the most plausible landmark for the following reason. When the arrays were in two rows in Experiments 3, one of the exterior cups was located at the edge of the table, while the other exterior cup was located in the middle of the table. Subjects performed better with

the cups near the edge of the table than the cups in the center of the platform (see Fig. 4). However, future studies are needed to confirm this finding.

The reduced performance of apes when the middle cup was the baited cup does not contradict this alternative account of encoding cups by landmarks. Following this alternative account, the middle cup, in comparison with the other two cups, was not positioned near a specific landmark (no matter the condition). Rather, it was situated next to the cup that was next to a landmark. Alternatively, it could also be said that the middle cup was situated between two cups, or between two landmarks. Either way, it was defined by two relations, in contrast to the left and right cups that were defined by only one relation. Relations between one object and a single landmark, such as “next to”, “above”, “below”, are understood by infants earlier than, for example, the relation “between”, where one object is put in relation to two landmarks (Quinn et al. 2003). For instance, children of 2 years of age are able to use one landmark to find a toy that is hidden in its vicinity (DeLoache and Brown 1983), while children of 4 years of age are able to find a toy hidden in the middle of two landmarks (Simms and Gentner 2008; Uttal et al. 2006). There has been some evidence that nonhuman primates can also learn to search in the middle of the landmark configuration, but their precision in searches is far from being perfect (Potì et al. 2010).

Children's performance on relational reasoning tasks is influenced by a multitude of factors: surface similarity between the base and target problem (Holyoak et al. 1984), children's knowledge about the relations tested (Goswami 1991; Goswami and Brown 1990), the number of relations needed to be mapped (Halford et al. 1998; Kroger et al. 2004; Richland et al. 2006), the type of instructions given (DeLoache et al. 1999; Loewenstein and Gentner 2005), and the presence of a distracter object in the target problem (Rattermann and Gentner 1998; Richland et al. 2006). Analogously, to investigate non-human primates' analogical abilities, ideally we should present them with different tests, varying along similar levels of relational complexity. Additionally, other dimensions such as size could also be explored. Size relations are probably a better choice because they are not ambiguous. A similar searching task with size relations has already been conducted with capuchin monkeys (Kennedy and Fragaszy 2008).

In summary, we expected that apes would spontaneously encode the cups by their relation to the other cups in an array and potentially map together left–left, middle–middle, and right–right cups. Instead they appeared to employ a different approach and encode them by their relation to the table edge and therefore mapped together the cups that shared the same relations to nearby landmarks.

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