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COMPARING GREAT APES’ AND CHILDREN’S ABILITY TO REASON BY ANALOGY

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i. List of scientific articles for the cumulative dissertation

1.) Hribar, A., Haun, D., & Call, J. (2011). Great apes' strategies to map spatial relations. *Animal Cognition, 14*(4), 511-523. Doi: 10.1007/s10071-011-0385-6

2.) Hribar, A., & Call, J. (2011). Great apes use landmark cues over spatial relations to find hidden food. *Animal Cognition*, 14(5), 623-635. Doi: 10.1007/s10071-011-0397-2

3.) Hribar, A., Haun, D., & Call, J. (sub.). Children's reasoning about spatial relational similarity: the effect of alignment. *Journal of Experimental Child Psychology*.

1. Introduction

Analogical reasoning, reasoning about relational similarity, is often considered to be one of the hallmarks of human cognition. Rattermann and Gentner (1998a, pg.275) defined it as “the mapping of knowledge from one domain (the base) to another domain (the target) in which the systems that holds among the base objects also holds among the target objects”. As such, analogical reasoning provides a foundation for inductive inference, problem-solving, categorization and decision-making, and it is a powerful tool for learning about and explaining the world (Gentner, 2003a; Holyoak, Gentner, & Kokinov, 2001; Leech, Mareschal, & Cooper, 2008).

As analogical reasoning plays such an important role in many human cognitive abilities, it has been suggested that this ability is the “thing that makes us smart” (Gentner, 2003b). However, although analogical reasoning has been studied extensively in humans (e.g., Cho, Holyoak, & Cannon, 2007; Gentner, 1977; Gentner & Gunn, 2001; Goswami, 1995; Goswami & Pauen, 2005; Holyoak, Junn, & Billman, 1984; Kroger, Holyoak, & Hummel, 2004; Loewenstein & Gentner, 2001, 2005; Paik & Mix, 2006; Pauen, 1996), we know very little about this cognitive ability in our phylogenetically closest living relatives, the other great apes.

While some researchers have argued that the ability to reason by analogy represents the “discontinuity between human and nonhuman minds” (Penn, Holyoak, & Povinelli, 2008), others have proposed that if great apes are provided with a symbol system that enables them to encode and manipulate relations, then they are capable of reasoning by analogy (Gillan, Premack, & Woodruff, 1981; Premack, 1983; Thompson & Oden, 1995, 2000; Thompson, Oden, & Boysen, 1997). A third view, however, is that language - or any other symbol system - is not a prerequisite for an animal to be capable of analogical reasoning (Fagot & Parron, 2010; Fagot, Wasserman, & Young, 2001; Haun & Call, 2009; Kennedy & Fragaszy, 2008).

There are now many studies that suggest that nonhuman primates can reason by analogy. Interestingly, however, most of these studies have used the same kind of task; namely, the relational match-to-sample (RMTS) task (Dépy, Fagot, & Vauclair, 1999; Fagot & Parron, 2010; Fagot, et al., 2001; Flemming, Beran, Thompson, Kleider, & Washburn, 2008; Flemming, Beran, & Washburn, 2007; Thompson, et al., 1997).

With respect to children though, their reasoning by analogy is affected by numerous factors: for example, the surface similarity between the known and novel problems (Chen, 1996; Chen, Sanchez, & Campbell, 1997; Holyoak, et al., 1984; Paik & Mix, 2006); the relational complexity of the problem (Halford, Wilson, & Phillips, 1998; Kroger, et al., 2004; Richland, Morrison, & Holyoak, 2006); knowledge about the relations (Goswami, 1991; Goswami & Brown, 1990); the amount of training and instruction given (DeLoache, de Mendoza, & Anderson, 1999; Kotovsky & Gentner, 1996; Loewenstein & Gentner, 2005); and, the presence of an interfering item (Chen, 2007; Rattermann & Gentner, 1998b; Richland, et al., 2006).

It is apparent, therefore, that to fully investigate nonhuman primates' analogical abilities, we should present them with various tasks, employing different kinds of relations and the relational complexity. Moreover, very few individuals within each nonhuman great ape species have been investigated. This means that we do not have a clear sense of how general the ability to reason by analogy is within and between each species, especially since some discrepancies have already been observed between chimpanzees and bonobos, and orangutans and gorillas (see Haun & Call, 2009). Obtaining enough data from each species is critical in order to assess interspecies differences and to make solid inferences about the evolution of analogical reasoning. To date, only one study has directly compared great apes' performance on an analogical reasoning task with that of human children in a comparable manner (Haun & Call, 2009). Critically, most studies that have investigated analogical reasoning in children have provided children with extensive instructions, and some have even provided a straightforward cue indicating where to search for the reward (e.g., in the same place, under the same object) (e.g., Blades & Cooke, 1994; Goswami, 1995; Loewenstein & Gentner, 2005; Richland, et al., 2006; Vasilyeva & Bowers, 2010). If we want to evaluate the similarities and differences between human and nonhuman primates' reasoning about relational similarity, it is crucial that we present all species with formally equivalent tasks that are comparable in terms of their complexity, the amount of training provided, and in the instructions given.

This dissertation had two primary goals: 1) to investigate "language naïve" apes' flexibility in analogical reasoning. More specifically, for that purpose, I used a novel paradigm – a relational mapping task, which does not require any prior training.

This enabled me to examine apes' spontaneous reasoning about relations; 2) to compare great ape's analogical reasoning with that of human children. To be able to do that, I presented children with almost identical mapping task and I did not provide them with any kind of scaffolding – i.e., training trails and verbal instructions.

2. Analogical reasoning

Analogical reasoning refers to reasoning about the relational similarity between two problems. More specifically, analogical mapping consists of the alignment of representational structures of a base and a target problem, and it requires the recognition of relational similarity between these two structures. Such analogical mapping allows for inferences to be made from one problem to another. Figure 1 depicts a very simple example of analogy: item A is bigger than item A', and item B is bigger than item B'. Therefore, the relation that holds between the A and A' also holds between B and B', meaning that item A maps directly onto item B, and item A' maps directly onto item B'.

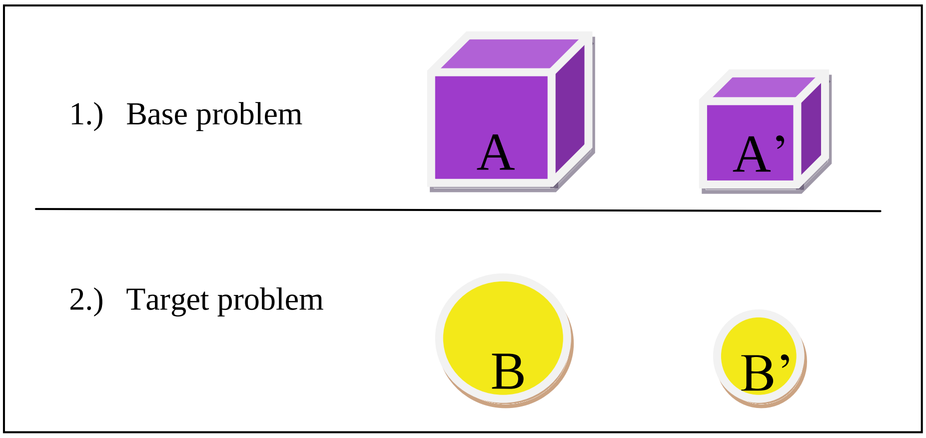

Figure 1. An example of a simple analogy. The relation that holds between A and A' also holds between B and B'.

2.1. What is a relation?

In order to be able to reason by analogy, an individual first needs to be able to detect and reason about relations. A relation could be described as the connection between two entities, and one’s representation of a relation is generally considered to consist of two parts: a predicate and the arguments (Halford, 1999). Relations can be defined either as first-order or higher-order relations. First-order relations have objects as arguments, whereas higher-order relations have relations as arguments (Halford, 1999). When a relation includes two arguments and a predicate, then it is called a binary relation. Extending this further, a ternary relation includes three arguments, a quaternary relation four, and so on. An example of a binary relation would be a relation such as BIGGER-THAN (e.g., a *chimpanzee* is BIGGER-THAN a *capuchin monkey*), where *chimpanzee* and *capuchin monkey* are the arguments, and BIGGER-THAN is the predicate. In addition, *chimpanzee* and *capuchin monkey* are both bound to their relational role; *chimpanzee* refers to the bigger entity and *capuchin monkey* the smaller one. As can be seen then, with regard to analogical mapping, the first step is to recognize the relation, and the second step is to specify the bindings of the relational roles to their arguments (Doumas, Hummel, & Sandhofer, 2008; Hummel & Holyoak, 2003). Human infants can detect violations of specific relations, such as support, occlusion or identity from an early age (Baillargeon, 2004; Tyrrell, Stauffer, & Snowman, 1991; Tyrrell, Zingaro, & Minard, 1993). However, their ability to reason about relations and relational similarity develops gradually over the first few years of life.

2.2. Development of analogical reasoning in humans

Analogical reasoning appears to be a higher-order cognitive ability that only develops fully late in childhood. To illustrate this, I will focus on the development of the identity relation: Infants at 7 months of age can already discriminate between identity/ nonidentity relations (Tyrrell, et al., 1991; Tyrrell, et al., 1993). At the age of 2.5 years old, children are able to select two identical objects (e.g., two green cups) out of a set of three objects, if they have seen two experimenters before them also pick two identical objects (e.g., two red cars and two white daisies) (Smith, 1984). At the age of 6 years old, children begin to pass a task in which they have to match identity/non-identity relations, but only when there are no perceptual distractors present. It is not until the age of 8 years old when children are able to ignore other perceptual distractors and attend fully to the relational commonalities present in the matching task (Christie & Gentner, 2007; Thibaut, French, & Vezneva, 2008). Despite this, some researchers have argued that one-year-old infants already have a “rudimentary ability” to solve problems by analogy (Chen, et al., 1997). For infants at this age, however, their ability to transfer a solution from a base problem to an analog target problem relies heavily on the shared perceptual similarity between the base and target problems. With age, children become increasingly more efficient in solving analogous problems that share structural similarity, but almost no featural similarity (Holyoak, et al., 1984).

Several factors have been proposed that may affect the development of analogical reasoning in children. Piaget and colleagues (Piaget, Montangero and Billeter 1977, as described in Goswami, 2001) presented children with item analogy tasks, in which a child was first presented with one pair of items, A:A’ and one item B taken from a second pair of items. These children were required to complete the analogy by selecting the item B’ from a number of alternatives presented to them. The correct item B’ held the same relation to item B as item A’ held to item A. For example, a child would see two pictures of the first item pair depicting a steering wheel and a car, and a picture of one item from the second item pair depicting a handlebar. To correctly complete the analogy, children need to select the picture of the bicycle from the possible alternatives presented to them. Piaget found that children were able to solve these kinds of analogical problems at around eleven to twelve years of age. Later, however, Goswami and Brown (1989, 1990) showed that 3- and 4-year-old children could also solve such item analogy tasks. These authors employed relations that were highly familiar to younger children (i.e., simple causal relations such as melting, wetting and cutting, and thematic relations such as “a bird lives in a nest”). Given such evidence, Goswami (1991, 2001) has argued that infants are capable of analogical reasoning as long as they understand the relations needed to solve the analogy task. With increasing age, children gain more knowledge about relations and so their performance on analogical reasoning tasks also increases.

Gentner and Rattermann (1991) have argued that children undergo a *“relational shift”*; that is, a shift from attending primarily to surface or featural similarity when comparing two objects or situations, to attending to the relational similarity. It is readily apparent that children notice the physical similarity between objects before they notice the relational similarity between them (Kotovsky & Gentner, 1996). Kotovsky and Gentner (1996) have proposed a progressive alignment mechanism, where perceiving object similarity improves children's perception of relational similarity. As a result of this, when young children are presented with two structures that contain a physically identical item, but this item plays a different relational role in each structure (items are cross-mapped), they prefer to map across structures on the basis of object match rather than relational match (Loewenstein & Gentner, 2005; Paik & Mix, 2006; Rattermann & Gentner, 1998a). For example, if one structure depicts a tow-truck pulling a car and the other structure depicts a car pulling a trailer, then the car stimuli are cross-mapped – both scenes contain a car, but in one scene the car is being pulled and in the other the car is doing the pulling, meaning that the car does not share the same relational role in both scenes (Markman & Gentner, 1990). Precisely when the relational shift occurs depends heavily on knowledge of the relevant relations. As such, the relational shift is domain specific (Kotovsky & Gentner, 1996). However, not only children, also adults tend to initially focus on surface features and overall similarity of the two situations, simply because they are easier to detect. As a consequence, this discovery of feature similarity leads to comparison, which in turn gives them an opportunity to detect relational commonalities between items (Christie & Gentner, 2010; Gentner, Loewenstein, & Thompson, 2003, 2004).

Halford (Halford, 1999; Halford, et al., 1998), however, has proposed a different explanation for developmental changes in analogical reasoning. He argues that children's ability to solve analogies is constricted by their working memory capacity. Working memory capacity limits the number of relations children (and adults) can process in parallel. The number of relations that need to be compared simultaneously represents the relational complexity of a problem, and the higher the relational complexity, the higher the memory processing load. He argued that children at the age of 2 years old can represent binary relations (i.e., a relation between two arguments), but that it is not until 5 years old that they are capable of reasoning about relations containing three arguments. Richland et al. (2006) have investigated how relational complexity and featural distractors affect 3 to 14 year old children. Specifically, they presented children with pairs of pictures that depicted simple relations between objects, such as kiss, chase and feed. One picture, for example, would show a dog chasing a cat, which in turn was chasing a mouse. A second picture would show a mother chasing a boy, who in turn is chasing a girl. If the second picture included a lying cat, for example, then this would represent a featural distractor. The authors varied relational complexity by presenting the children with pictures depicting either one or two relations. They found that while 3- to 7-year-olds were affected both by relational complexity and the presence of a distractor, 13- and 14-year-olds were affected only by relational complexity.

Language has also been proposed to be one of the key driving forces behind the development of analogical reasoning (Loewenstein & Gentner, 1998; Rattermann & Gentner, 1998a; Simms & Gentner, 2008). Gentner and Loewenstein (2002, pg. 101), for example, have suggested that “The acquisition of relational language influences the development of relational thought.” They propose that language represents a tool for extracting relations. However, they acknowledge that there are other ways to support relational thought apart from language – e.g., maps and diagrams (Loewenstein & Gentner, 2005). In contrast, some researchers have argued that relational language does not play a particularly important role in the development of analogical reasoning, and several studies have not found any direct correlation between relational language and relational reasoning (Chen, 2007; Mutafchieva & Kokinov, 2007; Richland, et al., 2006; Smith, 1984; Spetch & Parent, 2006). One obvious way to assess the importance of relational language is to study nonhuman animals and it is to this that I now turn my attention.

2.3. Analogical reasoning in nonhuman primates

A number of researchers have focused on whether nonhuman animals without language are capable of abstract thought. One of the most heavily studied abstract relations in animal research is that of “identity” (or sameness). Somewhat surprisingly, perhaps, many primates (e.g., Bovet & Vauclair, 2001; Fagot, et al., 2001; Flemming, et al., 2007; Katz, Wright, & Bachevalier, 2002; Oden, Thompson, & Premack, 1990; Premack, 1971; Wasserman, Fagot, & Young, 2001; E.A. Wasserman, M. E. Young, & J. Fagot, 2001; Wright & Katz, 2006), birds (Pepperberg, 1987; Wasserman, Hugart, &

Kirkpatrick-Steger, 1995; Wright & Katz, 2006), dolphins (Mercado, Killebrew, Pack, Mácha, & Herman, 2000; Nachtigall & Patterson, 1980) and honeybees (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001) were shown to detect relations. However, very few individuals have been found to be able to solve analogical reasoning tasks.

In a seminal study on whether nonhuman primates are capable of reasoning by analogy, one of the first subjects to be tested was a language-trained chimpanzee named Sarah (Premack, 1983). She was tested for her ability to engage in analogical reasoning when presented with item analogy problems (Gillan, et al., 1981; Oden, Thompson, & Premack, 2001) and with a relational match-to-sample task (Premack, 1983; Thompson, et al., 1997). For example, an item analogy problem was presented to her on a board in a 2 x 2 matrix, where the stimuli A and A' exemplified a certain relation and the stimuli B and B' exemplified the same relation, but with different items (similar to the example in Figure 1) (Gillan, et al., 1981). She either had to complete the analogy by choosing the B' item from a set of alternatives, or she was presented with a completed matrix and had to judge whether the two sides were the same or different with respect to the relations they presented. Moreover, the analogy problems presented could be 1) figural, in which the stimuli were geometric figures and the relations expressed were size, color and marking, or 2) conceptual, in which the stimuli were household object, and the relations connecting them were functional and spatial. Incredibly, Sarah was successful in all of these tasks. More recently, Oden, Thompson, and Premack (2001) presented Sarah with five items that were randomly placed in front of her. She arranged them spontaneously in a 2 x 2 matrix, but she did not always follow the A:A' :: B:B' pattern. The authors noted that her strategy appeared to be to match the two pairs in the number of within-pair featural differences. She ignored the actual physical nature of those differences, however. Oden et al. (2001) argued that Sarah's own strategy of numerically equating within-pair featural differences still involves analogical reasoning about relations between relations, proposing that Sarah could not only complete analogies, but also construct them. They further argued that Sarah's prior experience with symbols that represented the abstract relations of sameness and difference was critical for her to be able to explicitly express her reasoning in analogical reasoning tasks.

As noted above, the second task through which Sarah's analogical reasoning competence was tested was a relational match-to-sample (RMTS) task. The RMTS task has since become one of the most used paradigms to investigate nonhuman animals' reasoning about relations between relations (e.g., Cook & Wasserman, 2007; Fagot & Parron, 2010; Fagot, et al., 2001; Flemming, et al., 2008; Thompson, et al., 1997; Vonk, 2003).

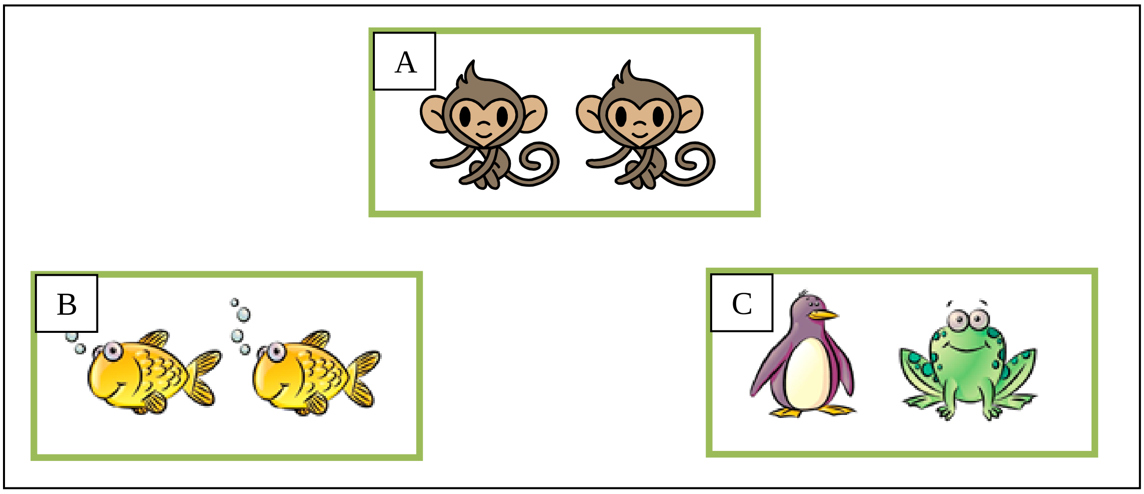

Figure 2. An example of a relational match-to-sample task. The sample A consists of two same items – therefore the relation it depicts is "identity". One of the alternatives (B) also consists of two items that are the same, whereas the second alternative (C) consists of two items that are different. Therefore, the alternative B matches the sample A in the "identity" relation.

In the RMTS task, an individual is required to match one of the alternative (choice) stimuli with a sample stimulus on a basis of a common relation. In Figure 2, stimulus A represents the sample and stimuli B and C the alternatives. Only one of the alternatives (stimulus B) matches the sample in the relation that the items within the array exhibit identity. In order to solve the RMTS task, the animal has to recognize the relational similarity between the sample and one of the alternatives. Importantly, the majority of those nonhumans that have been successful in solving the RTMS paradigm are those with a history of symbol training, especially in a symbol for "the same" (Premack, 1983; Thompson, et al., 1997). This fact, along with Sarah's remarkable achievements, have led some researchers to conclude that nonhuman animals need some kind of symbolic knowledge of relations to be able to reason by analogy

(Flemming, et al., 2008; Premack, 1983; Thompson & Oden, 2000; Thompson, et al., 1997). However, this view has been challenged by findings showing that several subjects with no history of language training, and of different primate and bird species, do appear to be capable of solving analogical reasoning tasks (Cook & Wasserman, 2007; Fagot & Parron, 2010; Fagot, et al., 2001; Haun & Call, 2009; Kennedy & Fragaszy, 2008; Vonk, 2003).

The RMTS paradigm has, however, been criticized by a number of authors who have argued that it does not actually test animals' ability to match relations (Penn, et al., 2008). Rather, it could be solved simply by matching the perceptual variability between array items (also called "entropy"). For any array of identical objects, the perceptual variability will be lower than for arrays of different items, assuming similar complexity of the individual objects. Hence, subjects only have to match pairs with either low or high perceptual variability to succeed in a RTMS task. This claim has been supported by observations that pigeons' and baboons' performance on an identity/non-identity discrimination task increases with a number of items in an array (Wasserman, et al., 2001; Wasserman, Young, & Fagot, 2001). In line of these findings, Fagot et al. (2001) have reported that baboons' performance on the RMTS task also increases when the difference between identity and non-identity arrays' entropy score is increased.

More recently, mapping tasks have been administered to investigate analogical reasoning in primates. In these tasks, individuals are unable to rely on perceptual similarities between objects to solve the task. In a mapping task, an individual is required to find a reward in her set of cups after observing another reward being hidden amongst an experimenter's set. To be successful, an individual has to choose the cup in her set that holds the same spatial relation as the baited cup in the experimenter's set. More precisely, they needed to go through several steps. As a first step, apes had to recognize the relations between the cups within each array. Secondly, they needed to recognize that these relations were the same in both arrays. Then they had to define the relation the baited cup held within the array (e.g., it was left of the middle and the right cup). And finally, apes needed to find a cup in the other array, which held the same relation. In one such study, capuchin monkeys had to map the cups from two sets based on their common size relations (Kennedy & Fragaszy, 2008). One capuchin monkey was successful in this mapping task, even when a distracter cup was present and the two sets of cups differed in color, shape and size. Here, the distracter was a cup that was of identical size in both sets, but it did not have the same size relation within each set. Importantly, this capuchin went through intensive training in matching objects of the same absolute size before it was capable of matching objects of different absolute, but of the same relative size. In another study along the same lines, Haun and Call (2009) tested human children, chimpanzees, bonobos, orangutans and gorillas on two types of relational reasoning: causal and spatial relational reasoning. Apes and children were tested with the same apparatus and with a similar amount of training and instructions. Two arrays with three possible hiding containers were placed horizontally, one behind the other, on an inclined table. In the causal reasoning condition, the cups in the two arrays were connected with tubes, whereas in the spatial relational condition they were not. The two arrays differed in length, but they were aligned flush left or flush right. As a result, the corresponding pairs of cups in the spatial relational condition could be connected by three different combinations of strategies: gravity (the corresponding cups were in the line of gravity), proximity (the corresponding cups were the closest cups), and same relative position (the corresponding cups held the same relation within the arrays). The aligned pair could be solved by all three strategies; the middle cup could be solved by using the proximity and relative position strategy; and the third cup could be solved only by matching the relative position of the cups. The study revealed that when subjects needed to reason about causal connectedness of the cups, all five great ape species were successful, whereas when reasoning about spatial relational similarity, only children of 4 years of age and older, chimpanzees and bonobos, but not gorillas and orangutans, were successful. However, children and apes performed above chance on the spatial relational task only if they were first confronted with the causal task. It appears, therefore, that causal task provided scaffolding for the subsequent relational task.

3. Parallels in human and nonhuman primates' analogical reasoning

Based on the above overview of the literature, we can draw some parallels between apes' and children's analogical reasoning. For children and apes, the ability to detect relations precedes the ability to reason about relational similarity (Oden, et al., 1990; Tyrrell, et al., 1991). Language (or a symbolic system) appears to facilitate relational thought in both young children and apes, but not in monkeys (Flemming, et al., 2007; Loewenstein & Gentner, 1998, 2005; Thompson & Oden, 1995). Young children perform much better on relational tasks when they are tested with relations that they understand (Goswami & Brown, 1989). Similarly, all nonhuman animals that have passed analogical reasoning tasks have had some prior training or experience with the tested relations (e.g., Fagot, et al., 2001; Kennedy & Fragaszy, 2008; Thompson, et al., 1997). Moreover, it appears that progression from easier examples to more difficult ones helps children and primates to solve the difficult examples (Haun & Call, 2009; Kennedy & Fragaszy, 2008; Loewenstein & Gentner, 2001). In addition, young children and primates (and pigeons) rely heavily on perceptual similarity when solving analogical reasoning tasks (Fagot, et al., 2001; Paik & Mix, 2006). Haun and Call's (2009) study has shown more specific similarities between chimpanzees', bonobos' and 4-year-old children's performance in spatial relational reasoning tasks.

Therefore, in the studies that I describe in the following sections, I used a relational domain known to children and apes – that of the spatial domain. Apes and children have shown comparative spatial cognitive abilities in tasks such as spatial memory, object permanence, rotation and transposition (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007), as well as in a task demanding an ability to reason about relational similarity of spatial arrays (Haun & Call, 2009). In addition, in Studies 1 and 3, mapping tasks varied in overall similarity and difficulty.

4. Summary of studies

As highlighted above, most of the studies to date that have assessed analogical reasoning in nonhuman animals have used a single paradigm – the relational match-to-sample task (RMTS) - and have focused on the relation of identity/non-identity. All of these RMTS studies have also required that animals have some sort of previous experience with either the MTS procedure, or with discrimination of identity/non-identity relations (Fagot, et al., 2001; Thompson, et al., 1997; Vonk, 2003). It is noteworthy, therefore, that the RMTS task has received criticism with regard to whether it really does assess relational reasoning, or whether successful animals solve it using perceptual cues alone (Penn, et al., 2008). Therefore, the aim of the first study outlined below was to investigate great apes' ability to reason by analogy by employing a spatial mapping task that did not require prior training, and where animals could not rely on the perceptual similarities to solve it. The results of the first study showed that great apes have some rudimentary ability to engage in analogical reasoning. However, the results also suggested that the apes might have employed a different approach and encoded different type of spatial relations than I expected them to. More specifically, the apes appeared to encode the baited cup in relation to a nearby landmark, rather than in relation to the other cups present in the array. The second study presented here extended the findings of Study 1 by investigating in more detail how apes encode the location of a hidden reward. I tested whether apes encoded the location of a hidden reward in relation to 1) the other cups present 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. Since most studies on analogical reasoning in children have provided them with detailed instructions about where to search for a hidden reward, in the third study presented here, I investigated whether 4- and 5-year-olds - that have previously been shown to be capable of mapping spatial relations (Loewenstein & Gentner, 2005) - would spontaneously engage in relational mapping, without any explicit instruction to do so. In addition, I was interested to see whether children, like apes, would show a constellation-dependent pattern of performance, and a preference for mapping between item arrays using landmark cues (i.e., the landmark strategy).

4.1. Study 1: Great apes' strategies to map spatial relations (Hribar, et al., 2011)

Study 1 investigated bonobos', chimpanzees' and orangutans' ability to reason about spatial relational similarity. Three spatial mapping tasks were employed in which apes were required to find a hidden food reward in an array of three identical-looking cups, after observing an experimenter hide a food reward in a different array of three cups. To be successful, apes needed to infer the reward's position in their array of cups based on the position of the reward in the experimenter's array. A similar spatial mapping task has already been used to good effect with great apes (Haun & Call, 2009). Haun and Call (2009) tested apes on two types of relational reasoning – causal and spatial relational reasoning. They found that all great ape species were successful in a task that required reasoning about causal relations, but that only chimpanzees and bonobos, and not orangutans and gorillas, were successful in a task that required reasoning about spatial relations. However, the corresponding pairs of cups in the spatial relational condition could be connected by three different strategies: gravity, proximity and a relational strategy. This means that apes had to pay attention to the relational strategy and ignore the other two. Moreover, the authors found an order effect for the relational task, finding that those subjects that started with this task performed worse than those that were presented with it after the causal task.

In the first experiment of the present study, two 3-cup arrays (designated the Hiding and Search arrays) were placed next to each other, thereby eliminating the possibility of apes using gravity or proximity search strategies. Specifically, apes in the experimental condition saw the experimenter hide a food reward underneath a cup in the Hiding array (baited cup) and had to select the cup from the Search array that was located in the same relative position (left, middle or right) as the baited cup. For the control condition, the baited cups in the two arrays had different (but consistent) relative positions within the array. Consequently, apes had to learn these arbitrary pairings in order to be successful. In both conditions, apes could choose twice, once from the Search array and once from the Hiding array. This allowed verification that apes had paid attention to the baiting of the Hiding array, and that they did not forget where the food was hidden.

Subjects from both groups found the food reward at above chance levels in the Hiding array, but not in the Search array. Their poor performance on the Search array could not, therefore, be attributed to them ignoring the baiting event, or forgetting the location of the reward in the Hiding array. The results from this first experiment provided no evidence that apes applied a relational mapping strategy to find the hidden reward, which is not consistent with the data from Haun and Call's study (2009). However, the apes in Haun and Call's study performed better in their spatial relational task following experience with a causal relational task. It seems, then, that the causal task helped them to recognize the relational similarity between the arrays by, perhaps, providing necessary scaffolding. In addition, the arrays were positioned one behind the other, which might have further facilitated relational mapping.

In the second experiment of Study 1, therefore, I assessed whether arranging the two arrays one behind the other would help apes to notice the relational similarity between the arrays. Moreover, I was interested to see whether apes would continue to recognize that the same relations still hold between the cups when the two arrays are moved next to each other. Specifically, they were able to observe the transition of the two arrays from being positioned one behind the other to being positioned next to each other. Thus, in Experiment 2, there were three conditions: the *Two rows* condition, *Transition* condition and *One line* condition. At the start of each trial in all three conditions, the two arrays were positioned one behind the other, in perfect alignment. First, the Search array (the array closest to the ape) was baited behind an occluder. Following baiting, the procedure differed between the three conditions. In the Two rows condition, the two arrays stayed in two rows throughout the whole trial (i.e., baiting of the Hiding array and allowing apes to choose a cup from the Search array). In the Transition condition, the two arrays stayed in two rows during baiting of one of the cups in the Hiding array, but before the ape was allowed to choose a cup in the Search array, the Hiding array was pushed forward next to the Search array (thereby forming a single line). Finally, in the One line condition, the Hiding array was first pushed forward next to the Search array, and then the Hiding array was baited and the ape allowed to choose.

As expected, the arrangement of the arrays had an effect on apes' success. Apes' performance was best in the Two rows condition, then in the Transition condition, and worst in the One line condition. As the apes passed the Two rows and Transition conditions, it is clear that they transferred information from the Hiding array to infer the reward's position in the Search array. One plausible strategy that apes may have used was to simply pick the cup in the Search array that was closest to the reward that they had just seen being hidden (i.e., a proximity bias). This strategy would, of course, be unsuccessful in the One line condition. Apes' success also varied depending on the position of the baited cup, being significantly lower when the middle cup was baited than when either the left or the right cups were baited.

Furthermore, I noticed that some individuals in the One line condition might have used a 'mirror' strategy. In particular, they tended to choose the cup closest to the table edge (the Left cup) in the Search array when the cup closest to the other table edge (the Right cup) was baited in the Hiding array. Similarly, they tended to choose the cup in the middle of the table (the Right cup in the Search array) when the cup in the middle of the table (the Left cup) was baited in the Hiding array. This strategy was termed a Landmark strategy, due to the assumption that apes were mapping the cups with respect to the relations they held to nearby landmarks (i.e., the table's visual boundaries). Indeed, when apes' choices in the One line condition were analyzed, it was found that they selected the cups that adhered to this landmark strategy more often than would be expected by chance.

In Experiment 3 of Study 1, to investigate whether apes preferred the proximity strategy over relational/landmark (both relational and landmark strategy led to the same outcome), I placed the arrays in two, misaligned rows (see Figure 3). Due to this misalignment, choosing the most proximate cup to the baited cup was not the most successful strategy. Indeed, such a strategy would work only one third of the time. The results showed that apes found the hidden food reward at above chance levels; however, their performance again varied depending on which cup was baited. Success rate was highest for the cup where both strategies (relational/landmark and proximity) could be used (H1). When the middle cup (H2) was baited, apes preferentially chose the closest cup to H2 in the Search array (S1), and when the third cup (H3) was baited, chimpanzees and bonobos tended to choose the cup that held the same relative position in the Search array - orangutans showed no such preference. In conclusion, the results of Experiment 3 could not be explained by proximity-based search strategy alone; neither could they be explained by relational/landmark strategy alone.

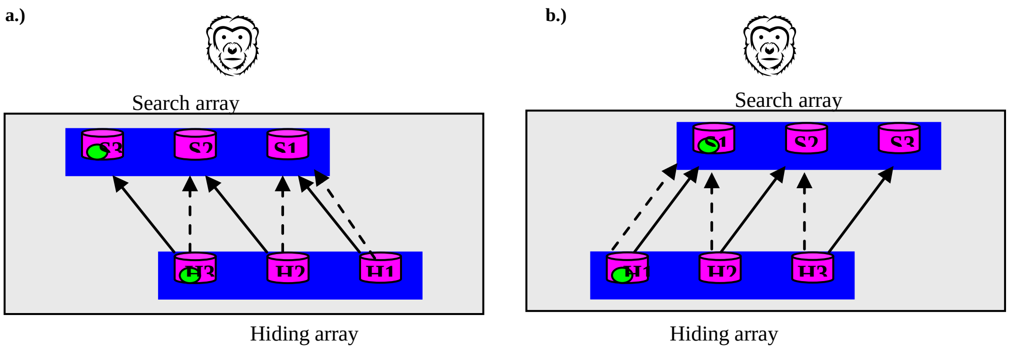

Figure 3. Position of the cups in **a.** Right side trials and **b.** Left side trials. The solid arrows show which cup in the Search array apes would choose when using the relational similarity between cups (spatial relation strategy). The dashed arrows show the cup that apes would choose if they just went for the closest cup (proximity strategy). When a reward is hidden under cup H1, apes may choose cup S1 using either of the two strategies to find the hidden reward. When food is hidden under cups H2 and H3, apes have to use a spatial relation strategy (cups S2 and S3 respectively) to find the hidden reward.

The three experiments of Study 1 provide no evidence that apes mapped the two arrays of cups on the basis of their relative positions within the arrays. However, they ruled out the possibility that apes' choices were based solely on a proximity strategy. Rather, it appears that apes applied a strategy where they mapped together the cups with respect to their relations to the table's boundaries. This strategy assumes that apes encoded the baited cup not in a relation to the other cups in the array, but with respect to a landmark in the surrounding environment. This means that instead of using an intrinsic frame of reference - encoding relations that hold within the array - they used an allocentric frame of reference – encoding relations that hold between an individual cup and one's surroundings (Levinson, 2003). In addition, their performance was dependent on the position of the baited cup: they performed worst when the middle cup was baited, which could be explained by the absence of a differential landmark cue next to it. Extending the work of Study 1, and to follow-up on some of the assumptions made, Study 2 directly assessed whether apes primarily encode the location of a hidden reward in relation to the table's boundaries.

4.2. Study 2: Great apes use landmark cues over spatial relations to find hidden food (Hribar & Call, 2011)

Study 1 showed that apes did not recognize the relational similarity between two linear arrays of three identical cups when they were placed side by side, in one line. It was proposed that the reason they failed in the task, therefore, was because they employed a different encoding strategy. Specifically, rather than encoding the cups as the left-most, middle and right-most cups, I proposed that they encoded them as 'the cups situated nearest the table's edge', and 'the cups in the middle of the table'.

We know from previous studies that primates can successfully find a reward that they have seen placed underneath one of several identical, linearly arrayed opaque containers (Albiach-Serrano, Call, & Barth, 2010; Barth & Call, 2006; Call, 2001; de Blois & Novak, 1994; de Blois, Novak, & Bond, 1998; Deppe, Wright, & Szelistowski, 2009; Fedor, Skollár, Szerencsy, & Ujhelyi, 2008; Hoffman & Beran, 2006; Mendes & Huber, 2004). However, these studies did not investigate the specific cues that primates may use to encode the reward's location. Hoffman and Beran (2006) investigated whether chimpanzees used allocentric or egocentric cues when searching for food hidden underneath a linear array of 3 or 4 containers. Chimpanzees performed worse when they had to walk around an array than when they stayed still, suggesting that they primarily use allocentric cues to locate hidden food. Moreover, they found that when chimpanzees had to walk around the array, they performed worse on the middle cup(s) than when either of the two outer containers was baited. These authors suggested that this could be due to the salient features that surrounded the outer containers. Therefore, the aim of Study 2 was to investigate whether apes encoded the baited cup with respect to its relative position within the array, or with respect to its relation to the table's edge.

Three experiments were conducted in which apes could observe the hiding of a food reward in an array of three identical cups, which rested on a platform and formed a straight line. After the food reward had been hidden, I walked to another panel where I offered the subject a piece of low value food (e.g., carrot). After 30sec, I returned to the array and pushed the platform on which the array rested forward so that the subject could point through the mesh to their chosen cup. Over the three experiments, the position of the cups on the table and the distance between the cups was varied. Specifically, in the first experiment the array was placed on the left half of the table, such that the Left cup rested near the table’s edge, whereas the Right cup rested near the middle of table. Apes’ retrieval accuracy was significantly higher when the reward was hidden underneath the Left and the Right cups compared to the Middle cup. In Experiment 2, a further condition was added in which the array was placed over the whole table, such that both outer cups rested next to the table’s edges and the Middle cup rested in the middle of the table. As such, if apes encode the baited cup with respect to its relation to a nearby landmark, and they treated the edges and the middle of the table as landmarks, then their performance on the Middle cup should not differ from their performance on the Left and Right cups. On the other hand, if apes encoded the baited cup by its relative position within the array, then the performance on the Middle cup should still be lower than on the other two cups. Apes’ retrieval accuracy improved significantly when the array was placed over the whole table and the Middle cup occupied a position in the middle of the table. Therefore, the results support the landmark account of encoding. Moreover, apes’ performance on the Right cup, which also now rested at one of the table’s edges, improved. This supports the suggestion that, for apes the edges of the table might be more salient landmark than the middle of the table.

In the third experiment, the effects of the distance to the landmarks (i.e., table’s edge and the middle of the table) and the distance between the cups were investigated. Apes were presented with four conditions, in which I varied the positioning of the cups on the table (either on one half of the table or over the whole table) and the distance between the cups: 1) Full table-Near condition, 2) Full table-Far condition, 3) Half table-Near condition, and 4) Half table-Far condition (Figure 4).

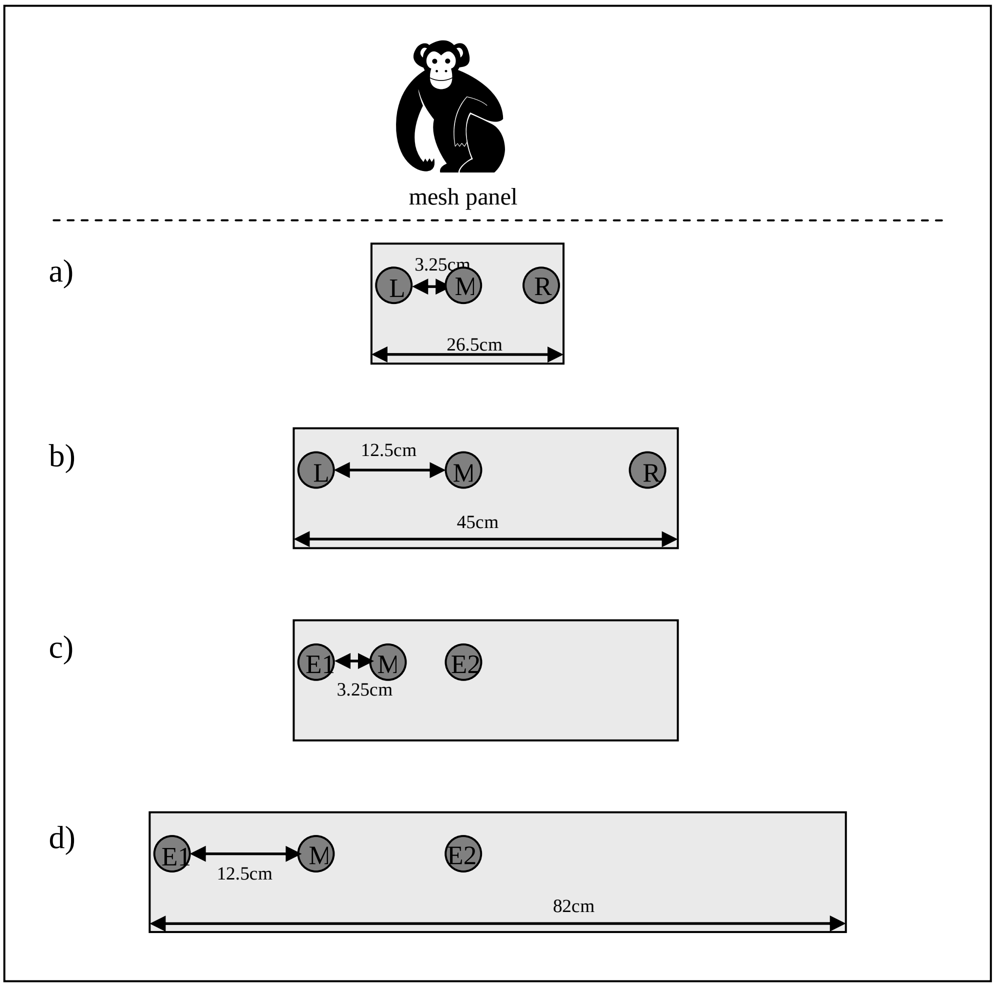

Figure 4. The positioning of the cups in the four conditions of Experiment 3: **a.** Full table Near, **b.** Full table Far, **c.** Half table Near, **d.** Half table Far. L - Left cup, M - Middle cup, R - Right cup, E1 - Edge1 cup, E2 - Edge2 cup.

Apes retrieval accuracy was found to be at above chance levels for all four conditions. However, they were more successful in the conditions where the cups were further apart (Far conditions) than when they were closer together (Near conditions). Hence, the distance between the cups markedly affected apes' recall. Moreover, apes' success was highest when the reward was hidden underneath an outer cup that was placed directly at a table's edge and lowest when the Middle cup hid the reward (no matter its location on the table). This finding suggests that apes primarily used the table's edges as a landmark. Previous studies have shown that the edges of a platform or a boundary has an influence on the spatial recall of nonhuman animals and humans (Bullens et al., 2010; Cheng & Sherry, 1992; Huttenlocher, Newcombe, & Sandberg, 1994; Kubo-Kawai & Kawai, 2007). In addition, apes' poor performance on the Middle cup can be explained by the requirement that one needs two relations to encode such. Primates readily use landmark cues to search for hidden food (Deipolyi, Santos, & Hauser, 2001; Dolins, 2009; MacDonald, Spetch, Kelly, & Cheng, 2004; Menzel, 1996; Potì, 2000; Potì, Bartolommei, & Saporiti, 2005; Potì et al., 2010; Sutton, Olthof, & Roberts, 2000); however, to use two landmarks cues relationally is far more cognitively demanding for primates (MacDonald, et al., 2004; Marsh, Spetch, & MacDonald, in press; Potì, et al., 2005; Potì, et al., 2010; Sutton, et al., 2000).

In summary, the results of present three experiments show that apes' retrieval accuracy was affected by two main factors: the distance between the cups and the position of the cups in relation to the table's edges. The larger the distance between the cups, the better performance became, and apes' performance was higher for the outer cups than for the middle cup, especially if the outer cups were placed at the table's edges.

4.3. Study 3: Children's reasoning about spatial relational similarity: the effect of alignment (Hribar, et al., sub.)

Study 1 showed that apes' mapping ability was affected by the constellation of the arrays, and Study 2 confirmed that apes' choice behavior was driven primarily with respect to landmark cues. In Study 3, I shifted my focus to children to assess how generalizable the previous results were across species. Specifically, 4- and 5-year-old children were presented with a similar spatial mapping task as used with the great apes in Study 1. However, the procedure was modified in three ways: First, one group of children was rewarded with respect to an aligned mapping strategy between the Hiding and Search arrays (Left-Left, Middle-Middle and Right-Right cups), while a second group was rewarded with respect to a landmark mapping strategy. The Two rows condition could not differentiate between the two mapping strategies, as they would both result in choosing of the same cups, due to the fact that the Left cups from both the Hiding and Search arrays were also the cups situated at the edges of the table in both arrays, for example. The One line condition, on the other hand, could differentiate between the two mapping strategies - the Right cup from the Hiding array would map onto the Right cup from the Search array when children were rewarded for the aligned mapping, but when they were rewarded for the landmark mapping, the Right cup in the Hiding array would map onto the Left cup in the Search array, since they were both located at the table's edges. When the landmark mapping strategy was rewarded, however, the Transition condition would lose its purpose of showing that the corresponding cups in the Two rows condition were the same as in the One line condition. Therefore, the second modification was to omit the Transition condition altogether. Finally, I blocked the two conditions and presented them sequentially. Half of the children started with the Two rows condition and the other half started with the One line condition. This modification allowed me to test for a transfer effect from an easier task to a more difficult task. Critically, in order to be able to make the comparison between children and apes valid, I gave children only minimal verbal instructions. Specifically, they were told only that I will hide some pictures and that they will need to search for them.

4- and 5-year-old children spontaneously engaged in relational mapping, even though they were not explicitly told to do so. They found the hidden picture more often in the Two rows condition than in the One line condition. Therefore, it was easier for children to recognize relational similarity when the arrays were aligned one behind the other than when they were placed next to each other. One reason for this might be a higher level of similarity between the arrays in the Two rows condition than in the One line condition. When humans compare two spatial scenes (A and B), for example, they rate those scenes where B can be changed into A through relatively few changes to be more similar than where many changes are required to change B into A (Bruns & Egenhofer, 1997). Overall, therefore, it is clear that similarity plays an important role in aligning and mapping between scenes (Chen, 1996; Chen, et al., 1997; Holyoak, et al., 1984; Paik & Mix, 2006). In addition, the perfect alignment of the two arrays in the Two rows condition might have also increased children's mapping success, as children could further rely on egocentric cues to solve the task (Blades & Cooke, 1994; Paik & Mix, 2008; Vasilyeva & Bowers, 2006). Contrary to results from other studies, which reported that children performed better on a more difficult task following experience with a simpler task, the experience of successfully mapping relations in the Two rows condition did not increase children’s success in the One line condition. If children indeed used egocentric cues instead of relative position in the Two rows condition, then these cues were no longer helpful when children were presented with the One line condition. The most interesting finding was that those children rewarded for the landmark mapping strategy performed better than those children rewarded for the aligned mapping strategy - indeed, some children that were rewarded for the aligned mapping strategy actually came to engage in the landmark mapping strategy. It appears, therefore, that just like great apes (see Study 1), children at the age of 4 and 5 years old prefer to employ a landmark strategy over an aligned strategy when engaged in a spatial mapping task. These results, then, assume that children also encoded the location of the hidden reward in relation to nearby landmarks, rather than in relation to the other cups within the array.

It is also possible, however, that the children encoded the location of the hidden reward in relation to their body position, mapping together those cups that were furthest away from them, those that were half way away from them, and those that were closest to them. Unfortunately, Study 3 was not able to discriminate between these possible encoding and mapping strategies. However, Nardini et al. (2006) investigated which cues children use when searching for a hidden toy in an array of 12 identical cups. The array was placed on a rotating platform together with a number of distinctive landmark cues. The cues employed by children to find the hidden toy, therefore, could be related to their own body (egocentric frame of reference), to the room (allocentric frame of reference), or to the array’s configuration and nearby landmarks (intrinsic frame of reference). They found that while 3- and 4-year-olds used body and room cues to find the hidden toy, 5- and 6-year-olds also used cues present within the array itself and within the array’s immediate surroundings (i.e., the landmarks, the platform’s edges). Therefore, it is highly possible that the children in Study 3 preferred to encode the baited cup of the Hiding array with respect to the table’s edges, mapping this relation to a cup in the Search array.

5. Conclusions

Several studies have shown that a variety of nonhuman animals can reason about relations (e.g., baboons, Bovet & Vauclair, 2001; bees, Giurfa, et al., 2001; Californian sea lions, Kastak & Schusterman, 1994; rhesus monkeys, Katz, et al., 2002; bottlenose dolphins, Nachtigall & Patterson, 1980; chimpanzees, Oden, et al., 1990; an African gray parrot, Pepperberg, 1987; gorillas and orangutans, Vonk, 2003; pigeons, Wasserman, et al., 1995; capuchin monkeys, Wright & Katz, 2006). However, few studies have been able to demonstrate that nonhuman animals can also reason about relations between relations (pigeons, Cook & Wasserman, 2007; baboons, Fagot & Parron, 2010; capuchin monkeys, Kennedy & Fragaszy, 2008; great apes, Premack, 1983; Thompson, et al., 1997; Vonk, 2003). It has been postulated that to do such, an animal needs to possess some sort of symbolic system that is capable of representing the abstract relations available (Premack, 1983). More recently, however, this view has been challenged by a number of studies that have demonstrated that nonhuman animals, with no knowledge of relational symbols, can solve tasks that require analogical reasoning (e.g., Kennedy & Fragaszy, 2008). Moreover, traditional paradigm to investigate analogical reasoning in animals was the RMTS task; I employed a more recent paradigm – a mapping task. The first study presented in this dissertation provides additional support for the view that "relational language" is not a prerequisite for relational thought. Critically, apes in Study 1 were not trained to pay attention to specific parts of the task; instead, I investigated their spontaneous responses. Importantly, apes were able to transfer information about a reward's position in one array to a second array, but their ability to do so depended heavily on the constellation of the arrays and the relative position of the baited cup. I proposed that the reason for this was that apes did not encode the relative location of the baited cup in the array, but rather its location in relation to the nearest landmark (e.g., a table edge). Subsequently, therefore, they searched under the cup in the Search array that held the same relation to that landmark. Study 2 confirmed this assumption that apes encoded the location of the baited cup in terms of its relationship to a nearby landmark and not with respect to the other cups in the array: Apes' performance was highest for the cup closest to the table edge and lowest for the middle cup. In addition, reducing the distance between the cups substantially reduced apes’ retrieval accuracy. Finally, in Study 3, I presented children with a mapping task, which was very similar to the one from Study 1. Furthermore, children were not provided with any verbal instruction, thus I was able to compare children’s and apes’ performance into more detail. Study 3 has provided very similar results to Study 1: children’s mapping performance was higher, when the two arrays were aligned one behind the other, than when they were lying next to each other, extending the earlier findings from apes that the alignment and as such the overall similarity of the arrays promoted relational mapping. A second important finding was that children, like apes, did not appear to encode and map the relative position of the baited cup across the two arrays. And therefore it is likely that children employed the same mapping strategy as apes - the landmark mapping; however, other possible strategies cannot, as yet, be ruled out.

In conclusion, the present dissertation provides additional support for the view that nonhuman primates, without any symbolic knowledge, have the capacity to perform the cognitively complex skill of aligning and transferring relations when engaged in an analogy task. Moreover, the work presented here highlights the intriguing parallels that are present when comparing apes’ and children’s reasoning about spatial relational similarity.

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7. Appendix: Original articles

1.) Hribar, A., Haun, D., & Call, J. (2011). Great apes' strategies to map spatial relations. *Animal Cognition, 14*(4), 511-523. Doi: 10.1007/s10071-011-0385-6

2.) Hribar, A., & Call, J. (2011). Great apes use landmark cues over spatial relations to find hidden food. *Animal Cognition*, 14(5), 623-635. Doi: 10.1007/s10071-011-0397-2

3.) Hribar, A., Haun, D., & Call, J. (sub.). Children's reasoning about spatial relational similarity: the effect of alignment. *Journal of Experimental Child Psychology*.

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ORIGINAL PAPER

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.

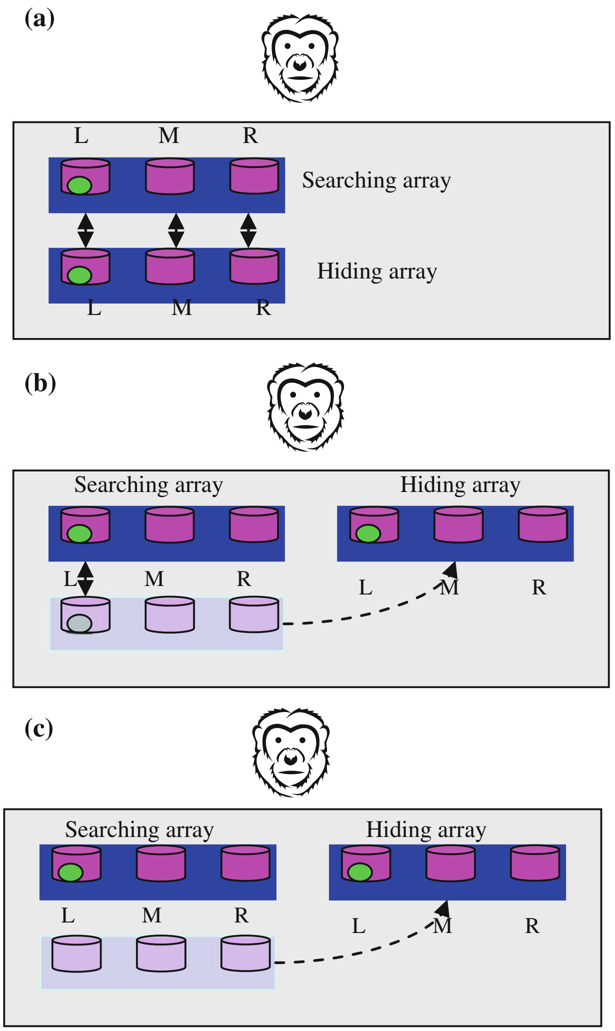

Fig. 1 Position of the two arrays for **a** Two rows, **b** Transition and **c** One line conditions in Experiment 2

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 cm × 13 cm). The two trays rested side by side on a table (80 × 35 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
Chimpanzees					
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
Bonobos					
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
Orangutans					
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 perseverate 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: $\chi^2 = 2.363$, $P > 0.05$, $df = 2$ $N = 16$; 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: $r = 0.551$, $P = 0.03$).

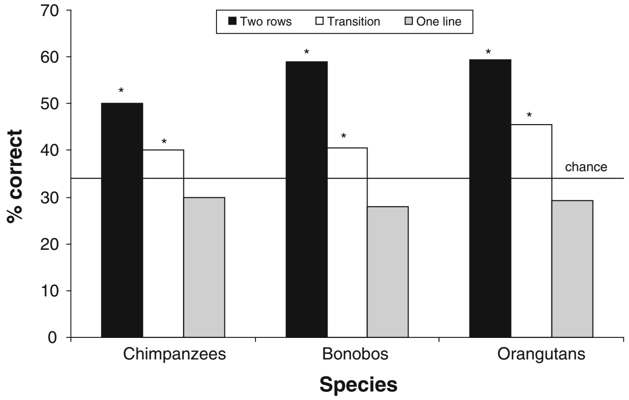

Fig. 2 Experiment 2. Species' mean percent correct for the three conditions. All three species performed at above chance level on conditions Two rows and Transition

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 then 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,

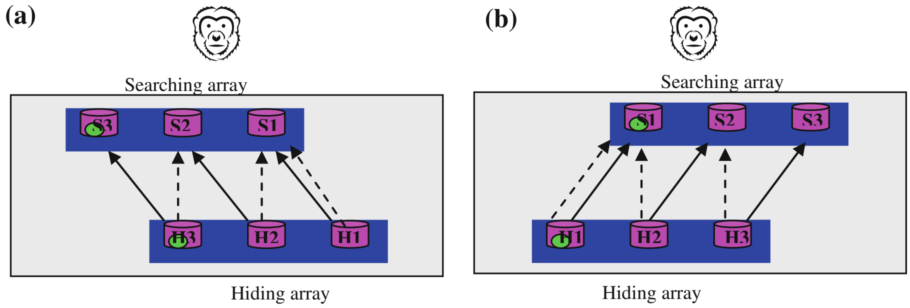

Fig. 3 Position of the cups in **a** Right side trials and **b** Left side trials. The solid arrows show, which cup in the searching array apes would choose, when using the relational similarity between cups (spatial relation strategy). The dashed arrows show the cup that apes would choose, if they just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

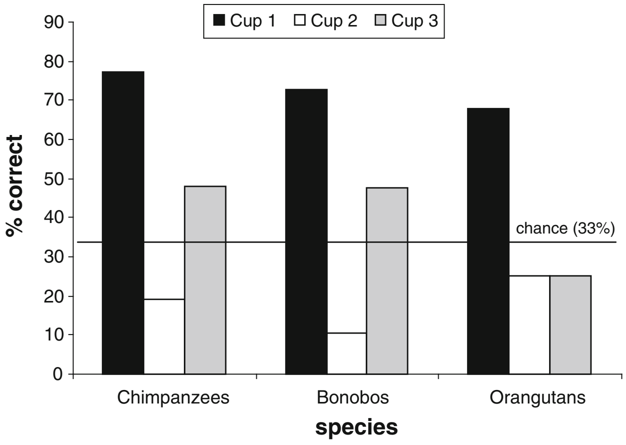

Fig. 4 Experiment 3. Species' mean percent correct for each individual cup (cup 1, cup 2, and cup 3)

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 nonhuman 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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ORIGINAL PAPER

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

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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, 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; Potì 2000; Potì 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 m^2, bonobos: 2,620 m^2, orangutans: 1,999 m^2). 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. 2010) and spatial mapping (Haun and Call 2009; Hribar et al. 2011).

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

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 × 14 cm). This array always rested on the left half of a sliding table (80 × 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 × 50 cm) through which apes could observe and

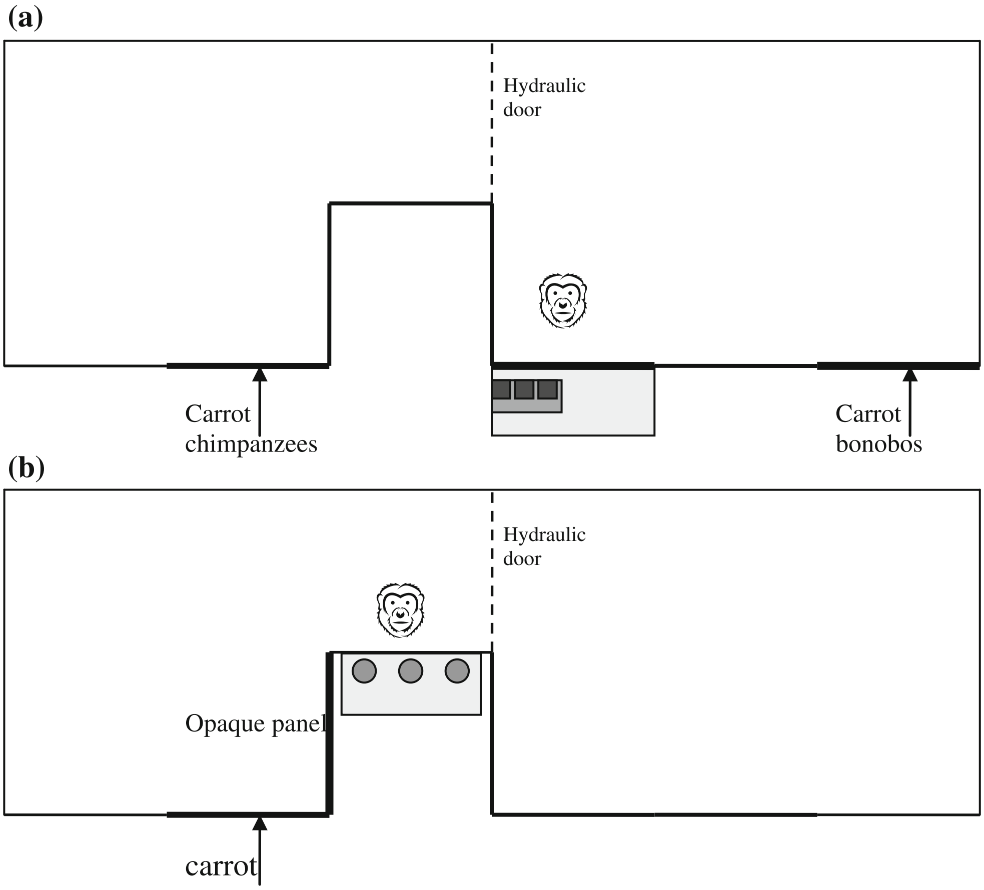


Fig. 1 Experimental setup for **a** Experiments 1 and 2. Depicted is a testing room with a setup for the bonobos and chimpanzees (with one difference—the bonobos had to walk to the *right panel* and the chimpanzees to the *left panel* to get carrot). For the orangutans, a room and a setup were an exact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

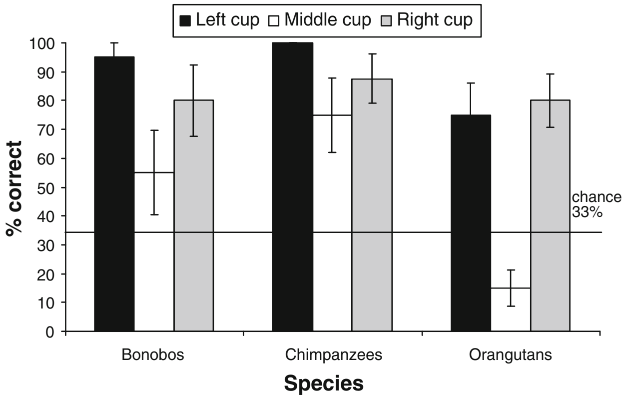


Fig. 2 Experiment 1: apes' percentage correct for each cup as a function of species. *Bars* represent *standard error*

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

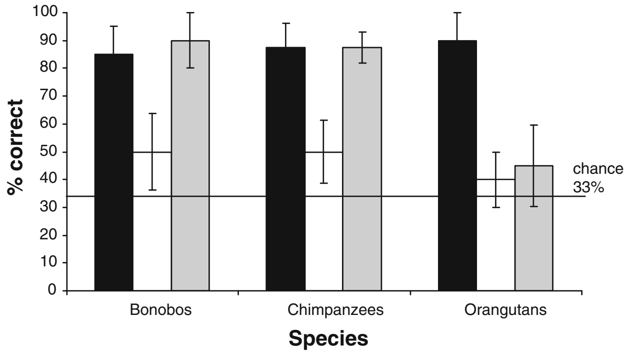
Scoring was done in the same way as in the previous experiment. Inter-observer agreement was 100% (Cohen's kappa = 1). Preliminary analyses showed no sex differences in performance on any of the cups, and as such, we did not include this variable in the subsequent analyses. To investigate the effect of the baited cups' position in the two conditions, we conducted a 3 (Cups) × 2 (Condition) × 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 × Condition ($F_{2,\ 26} = 7.344$, $P = 0.003$) and Cups × Condition × 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 significant performance difference between the chimpanzees and the bonobos ($P > 0.05$).

(a) **Half table condition**



(b) **Full table condition**

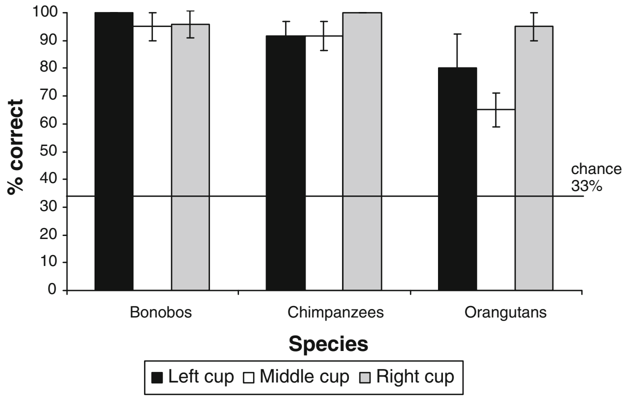


Fig. 3 Experiment 2: percentage of correct responses for each cup as a function of species in **a** Half table condition, **b** Full table condition. *Bars* represent *standard error*

Because the key variable of interest was Condition, we investigated the pattern of the three-way interaction by conducting a mixed 3 (Cups) × 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 × 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 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.

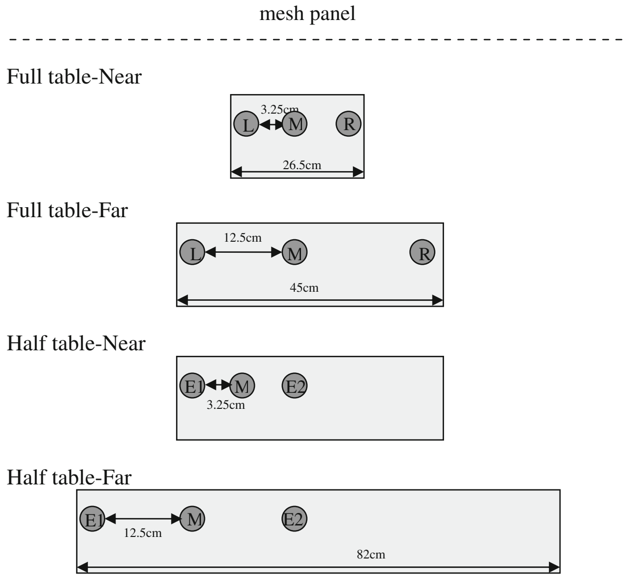


Fig. 4 The positioning of the cups for the four conditions. *L* Left cup, *M* Middle cup, *R* Right cup, *E1* Edge1 cup, *E2* Edge2 cup

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

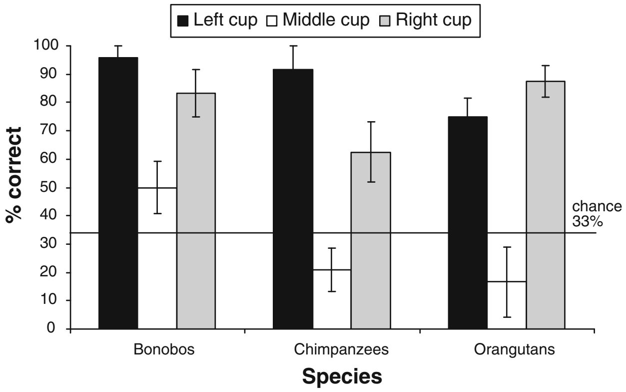
Edge cups—one at the edge and the other in the middle of the table—we analyzed the Half and Full table conditions separately. Therefore, a mixed 2 (Distance) × 3 (Cups) × 3 (Species) analysis of variance (ANOVA), with Distance and Cups as within-subjects variables, and Species as a between-subjects variable, 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, $F_{1.223,18.338} = 41.948$, $P < 0.001$), 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 *Ps* < 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 showed that, in both conditions, apes' success was higher on the Left and Right cups than on the Middle cup (all *Ps* < 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).

(a) **Full table Near condition**



(b) **Full table Far condition**

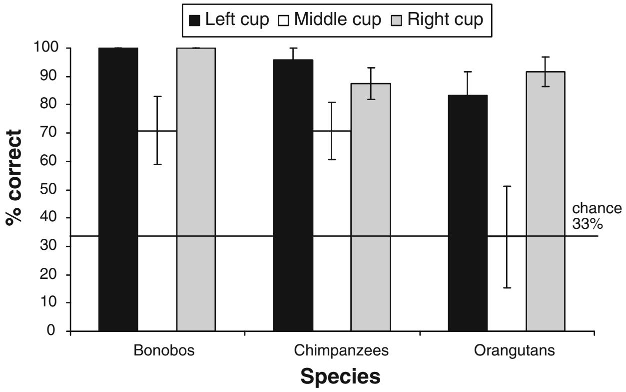
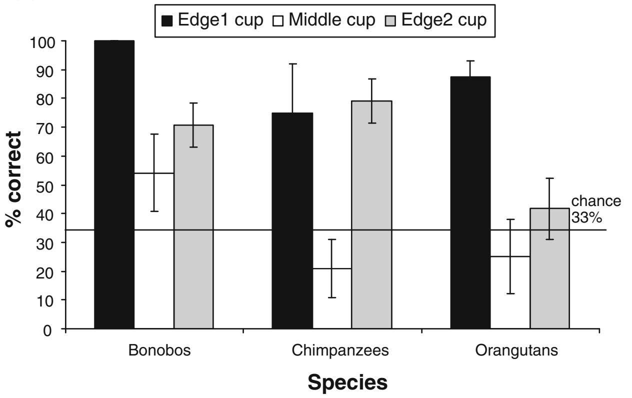


Fig. 5 Experiment 3: percentage of correct responses for each cup as a function of species in **a** Full table Near condition, **b** Full table Far condition. *Bars* represent *standard error*

(a) **Half table Near condition**



(b) **Half table Far condition**

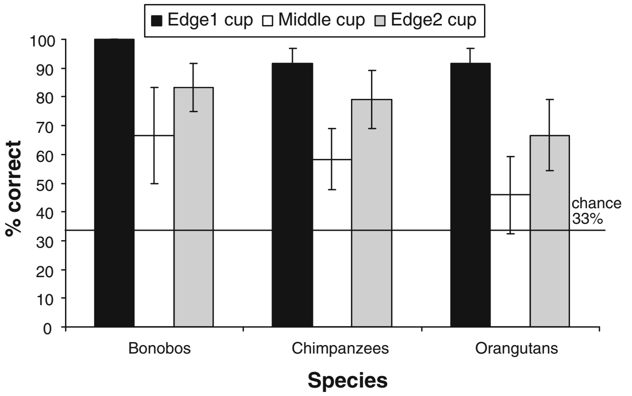


Fig. 6 Experiment 3: percentage of correct responses for each cup as a function of species in **a** Half table Near condition, **b** Half table Far condition. *Bars* represent *standard error*

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 und 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 tasks 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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Children’s reasoning about spatial relational similarity: the effect of alignment

Hribar Alenka, Haun Daniel, Call Josep

ABSTRACT

We investigated 4- to 5-year-old children’s dependence on the alignment of the base and target arrays in a spatial mapping task. Children were required to find a reward in an array of three identical cups after observing the reward being hidden in another array of three cups. The arrays were either aligned one behind the other in two rows, or placed side by side forming one line. Moreover, children were rewarded for two different mapping strategies: Half of the children had to choose a cup that held the same relative position as the baited cup in the other array - they had to map Left-Left, Middle-Middle and Right-Right cups together (Aligned group). The other half needed to map together the cups, which held the same relation to the table’s special features – the cups at the edges, the middle cups, and the cups in the middle of the table (Landmark group). Results showed that children’s success was constellation dependent: performance was higher when the arrays were aligned one behind the other in two rows than when they were placed side by side. Furthermore, children showed a preference for landmark- over aligned-based mapping.

Keywords analogy, spatial relations, relational reasoning, landmark use, similarity

INTRODUCTION

One of humans' most powerful cognitive tools for mental organization is reasoning by analogy - the perception and use of like relational patterns across contexts. This ability has been argued to be one, or even *the* driving force behind humans' mental prowess (Gentner, 2003). An analogy reveals common structure between two situations and, based on these similarities, suggests further inference.

Theories of analogy have divided the phenomenon into several individual processes: retrieval, mapping, evaluation, abstraction and re-representation (Gentner & Colhoun, 2010). Arguably the most crucial one amongst them is *mapping*. Mapping describes the alignment of the representational structure of two situations in order to deduct similarities between them, which will in consequence allow for inferences from the base to the target situation (Gentner & Rattermann, 1991). The ontogeny of mapping abilities is characterized by the so-called "relational shift" (Gentner & Rattermann, 1991). Early in ontogeny, children judging similarity of two scenes attend solely to overall similarity or to object-level commonalities; later they shift their attention to relational similarity. Only after the age of 3-4 onwards do they start to appreciate relational similarities; although at that age they still find it hard to inhibit reacting on the basis of object similarity when it is pitted against relational similarity (Markman & Gentner, 1990; Paik & Mix, 2006, 2008; Rattermann & Gentner, 1998). In addition, a progression from an easier to more difficult problem increases their performance on the difficult problem (Kotovsky & Gentner, 1996).

One of the domains in which this developmental pattern of relational mapping becomes apparent in young children is the spatial domain. In most spatial mapping tasks, children are required to find a hidden object in a target array of hiding places after they have observed an experimenter hide the same object in a different array. In order to be able to infer the location of a hidden object in the target constellation based on knowing the position of a similar object in the base constellation, they have to recognize similarities in spatial organization between the two arrays (e.g., Loewenstein & Gentner, 2005). Children's ability to map spatial relations rests heavily on object matches – they perform better when the two arrays contain highly similar objects (DeLoache, de Mendoza, & Anderson, 1999; DeLoache, Kolstad, & Anderson, 1991). Children have even been reported to correctly interpret element-to-element correspondences before they could fully appreciate spatial relational correspondences (Blades & Cooke, 1994). Blades and Brooke (1994) tested children's mapping ability between two model rooms, which had two unique and two identical hiding places. To differentiate between the identical hiding places, children had to take spatial relationships into account – something that 5-year-olds, and not 3- and 4-year-olds, were able to do; however, 4-year-olds succeeded when the two model rooms were spatially aligned. Moreover, if children are first required to map between two spatial arrays with high object-similarity, they subsequently perform better on an array with low object-similarity, than if they do not get experience with the highly similar array (Loewenstein & Gentner, 2001).

Recently, the ability to map spatial relations has been investigated in our closest living phylogenetic relatives, the other great apes (Haun & Call, 2009; Hribar, Haun, & Call, 2011). In a spatial mapping task, apes were required to map the left, middle, and right cups of the base array to the left, middle, and right cups of the target array. It appears that after the relational shift, children generally outperform the other great apes on spatial mapping tasks (Haun & Call, 2009). Crucially, Hribar et al.(2011) varied the constellation of the two arrays - i.e., aligned one behind another, misaligned, and next to each other forming one line - and found that non-human great apes' performance was highly dependent on the relative positioning of the base and target arrays – they performed best when the two arrays were aligned one behind another and worst when the arrays were in one line. This indicated a degree of inflexibility in their mapping abilities (Hribar, et al., 2011). Moreover, authors reported that apes did not map together the cups that held the same relative position within the arrays – i.e., the left, middle, and right cups; instead, they appeared to encode the baited cup in the base array in a relation to a nearby special feature or a landmark (i.e., table's edge) and then they chose a cup from the target array that was also near that same landmark. These results indicated that apes' low performance on the one line constellation was due to apes' different spatial encoding strategy. Hribar and Call (2011) later demonstrated that indeed, when apes are presented with a linear array of identical-looking cups placed on a platform, they encode the baited cup by its relation to the table's edge and not by its relation to other cups.

Children's strategies to encode space, their relative reliance on certain cues over others, and their use of spatial frames of reference change throughout childhood (Haun, Call, Janzen, & Levinson, 2006; Haun, Rapold, Call, Janzen, & Levinson, 2006; Learmonth, Newcombe, & Huttenlocher, 2001; Nardini, Burgess, Breckenridge, & Atkinson, 2006; Newcombe & Huttenlocher, 2000). At 1.5-2 years of age children start using single landmarks to search for a hidden toy in their vicinity (DeLoache, 1986; DeLoache & Brown, 1983; Learmonth, et al., 2001; Newcombe, Huttenlocher, Drummey, & Wiley, 1998). At the age of 4-5 years, children can learn that a reward is hidden in the middle of two landmarks (Simms & Gentner, 2008; Spetch & Parent, 2006; Uttal, Sandstrom, & Newcombe, 2006), but fail when the location needs to be encoded in a relation to 4 landmarks (MacDonald, Spetch, Kelly, & Cheng, 2004). Four-year-olds are also successful in differentiating between two identical objects by their relation to a nearby landmark (being close or far), a platform's edge (next to it or in the middle of the platform) and in a relation to an platform edge's length (at the shorter edge or at the longer edge) (Vasilyeva, 2002). However, they fail when they need to encode a hiding container in a relation to two other containers in the array – one identical to the hiding array, and one unique, which could potentially be used as a landmark (Lee, Shusterman, & Spelke, 2006). Nardini et al. (2006) investigated how children aged between 3 and 6 encoded a location of a toy, which was hidden in an array of 12 identical cups, placed on a platform and surrounded on two edges of the platform by landmarks. By varying the consistency of the array's position in the respect with the child and the testing room, and by holding the toy's position constant in the respect of the array and bordering landmarks, they were able to explore which spatial frame of reference – egocentric (i.e., encode a location in a relation to their body), allocentric (i.e., encode a location in a relation to the environment) or intrinsic (i.e., encode a location in a relation to other objects in an array) - children used. Three- and four-year-olds were found to use egocentric and allocentric cues to retrieve hidden toys, whereas children at the age of 5 years and older additionally used cues intrinsic to the array and landmarks. However, the characteristics of these ontogenetic trajectories vary dependent on the cultural context (Haun, Rapold, et al., 2006).

The present study had three main objectives: First, we investigated how alignment of the arrays affects children's mapping performance. We presented children with two 3-cup arrays, which were either aligned one behind another in two rows, or were placed next to each other forming a line. Based on the previous studies that found that children and apes performed better on the mapping tasks when the two arrays were aligned, we expected that the children in our study will find the task easier when the two arrays were placed in two rows, than when they were in one line. In addition, we were interested to see whether those children who were first presented with the easier (i.e., two rows) constellation, would consequently perform better on the more difficult (i.e., one line) constellation than the children that were presented with the one line constellation first. Second, we investigated, which spatial relations children would find easier to map: relative position within the array (left-left, middle-middle and right-right cups) or relative position on the table (i.e., cup at the edge-cup at the edge, cup in the middle of the table-cup in the middle of the table). Finally, unlike most previous studies, we did not provide children with explicit instructions that they should compare the two arrays and search in the same place. This allowed us to investigate children's relational mapping while minimizing the effect of language and to more directly compare children's responses to previous studies with non-human great apes (Hribar, et al., 2011); in particular, to search for similarities and differences in flexibility and preferences in spatial mapping strategies, which might indicate homologies between species irrespective of a higher overall performance in humans.

METHOD

Participants

Twenty-four 4-year-old children (mean age = 48.2, SD = 1.7, range 45.7 - 51 months) and twenty-four 5-year-old children (mean age = 60.8, SD = 1.6, range 57.4 - 62.7 months) participated in this study. Half of the children in each age group were girls and the other half were boys. All children were recruited from local kindergartens. They were tested individually in a familiar room in their kindergarten. Children could stop participating at any time; one child stopped. The sample size reported above is the final number after exclusion.

Material

We used two arrays of three identical metal square cups (8.5cm x 8.5cm). Each array was placed on a yellow plastic tray (32cm x 12.5cm) resting on a wooden testing table (50cm x 80cm). In both conditions the distance between the trays as well as the distance between the cups within each array was 3.5 cm. We used small (3.5 x 3.5cm) cartoon animal pictures as rewards.

Procedure

After a short warm-up time in a group, a child was taken to a separate room in the kindergarten where the apparatus was set up. The child sat at the middle of the testing table opposite to the experimenter (E). E then showed her some animal pictures and explained her that they would play a game, where E would hide pictures underneath the cups and she could then search for them. If the child found a picture she could keep it. There was no specific mention that two pictures would be hidden – one underneath each array. There was also no mentioning that pictures would be under the same positioned cups in both arrays, nor that they would have to find a pattern or a rule of the "game". After this short introduction of the "game", the experiment started.

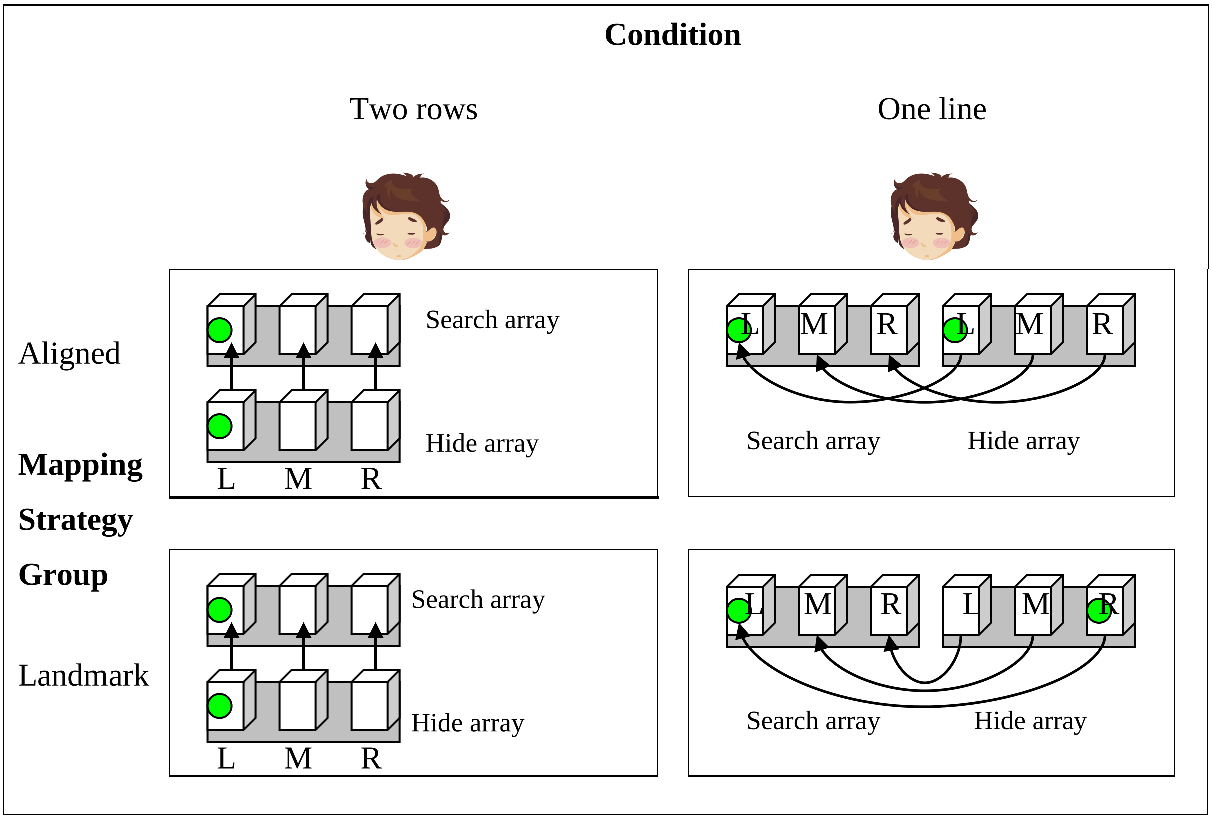

Fig. 1. Experimental set-up: positioning of the two arrays in the Two rows and One line conditions. The arrows indicate the corresponding cups.

There were two conditions. In the Two rows condition, both arrays were placed on the left half of the table, aligned one behind another, six centimeters from the left table's edge. In the One line condition, the arrays were placed side by side, each resting on the opposite halves of the table, the left array resting six centimeters from the left edge and the right array six centimeters from the right edge (see Figure 1). For both conditions the procedure was the same. One of the arrays was designated as a Search array and the other as a Hide array. In the Two rows condition, the Search array was the array closer to the child, and in the One line condition it was the left array (from E's view). At the beginning of each trial all six cups were empty and laying on their side, the opening facing the child. An occluder was put on the table between the child and the arrays, so that she could see that E was hiding one picture, but could not see underneath which cup. After E had hidden a picture underneath one of the cups in the Search array, all three cups in the Search array were upturned (closed) and the occluder was removed. The cups in the Hide array were still opened and the child could observe E first close two of the cups and then place a picture underneath the cup that remained open cup in the hide array and then close that cup as well. Finally, E pushed forward the tray with the Search array for one tray's width (ca. 12.5cm; note that in the One line condition this means that the two arrays were not forming a continuous line anymore) and asked the child where the picture was. If she indicated a cup in the Hide array, E pushed the Search tray back and forward again and said: "Yes, but where do you think the picture is here?" Children could either point to or lift the chosen cup. If the child was correct, she kept the picture and E opened all the remaining cups and removed the picture from the Hide array. If the child was wrong, E opened all the cups and took both pictures away without making any reference to the position of the pictures.

Each child received one block of 12 trials of each condition (24 trials total) in one session. There was a short (ca. 5-10min) break between the blocks. Half of the children started with the Two rows condition and the other half with the One line condition. Each position (left, middle, right) was bailed four times per condition, the order of the position being semi-randomized – the same position was not rewarded on more than two consecutive trials.

There were two different mapping strategies children could be rewarded for: Aligned and Landmark strategy. For the Aligned strategy, the two baited cups from the two arrays had the same relative position within the array. Thus, if the baited cup in the Hide array was left, middle or right, then the baited cup in the Search array was also left, middle or right, respectively. For the Landmark strategy, the two baited cups in the two arrays had the same relation to a landmark (i.e., table's special feature) next to them. Thus, in the Two rows condition, the cups that were in the same relative position also had the same landmark next to them (e.g., both the left cups were at the table's edge). In the One line condition however, if the baited cup in the Hide array was the cup in the middle of the table (the left cup), then the baited cup in the Search array was also the cup in the middle of the table (the right cup). Therefore, in the Two rows condition both strategies led to the same cup, whereas in the One line condition, except for the middle cup, they did not (see Figure 1). Half of the children were assigned to one strategy and the other half to the other strategy.

Scoring and data analysis

All sessions were videotaped and scoring was done live as well as subsequently from the videos. We scored which cup (Left, Middle, Right) the children chose and the dependent measure was the percentage of correct trials. A second coder scored 20% of the trials of each condition and strategy group to assess inter-observer reliability, which was perfect (Cohen's kappa = 1).

In the Two rows condition, both mapping strategies (Aligned and Landmark) led to the same cups (L-L, M-M, R-R). In the One line condition on the other hand, the two strategies led to different cups (except for the middle cup). Therefore, we decided to analyze the two conditions separately with the following factors: age (4 and 5 years), the rewarded mapping (Aligned and Landmark strategy), the order of condition administration (administered first or second), and the position of the baited cup (left, middle, right). We conducted a 2 (Age) × 2 (Strategy) × 3 (Position) × 2 (Order) analysis of variance (ANOVA) on the % of correct responses, separately for the two conditions. Position was within-subjects variable and Age, Strategy and Order of conditions were between-subjects variables. To compare children's performance against chance (33%), we conducted a one-sample t-test; to compare the performance on the two conditions, we used paired-samples t-test (two-tailed); and to compare individual performance against chance, we used a binomial test.

Apes in Hribar et al.'s study (2011) tended to use the landmark strategy in the One line condition, even though they were always rewarded only for the aligned strategy. Therefore, we were interested to see, whether the children from the Aligned group also tended to choose cups following the landmark strategy (even though they were not rewarded for it). We coded Aligned group's responses irrespective of their success and compared their percentage of choices following the landmark strategy against chance (33%) with a one-sample t-test.

RESULTS

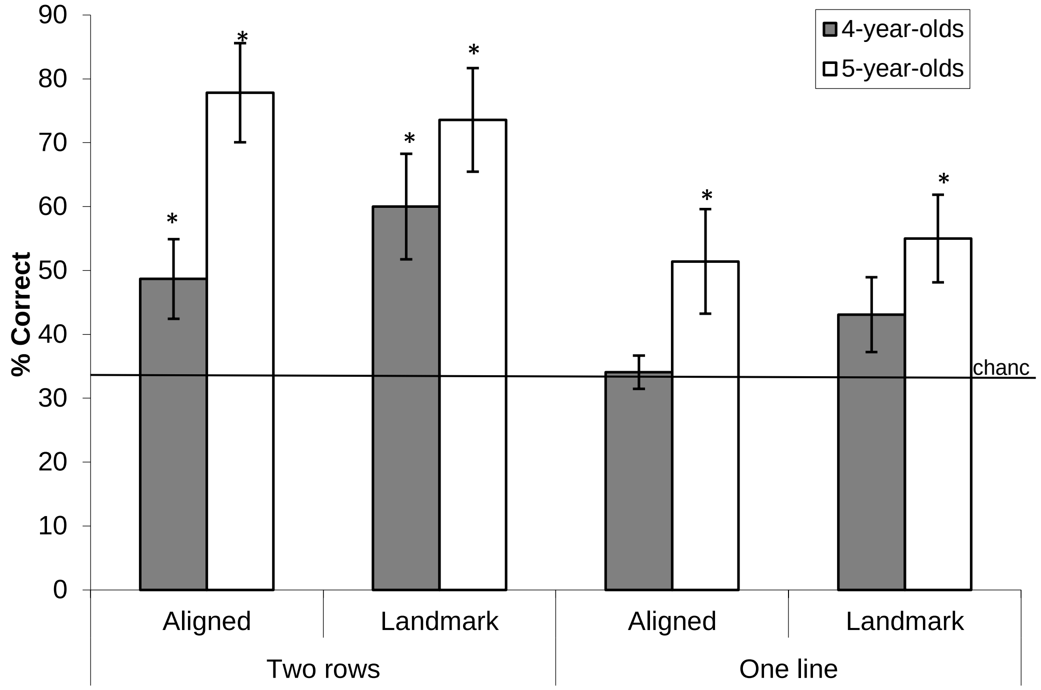

Fig.2. The percentage of correct responses for each condition and rewarded mapping strategy as a function of age. * - denotes above chance performance (p<0.05). Bars represent *standard error.*

Figure 2 presents the percentage of correct responses for each condition and strategy group as a function of age. In the Two rows condition 4-year-olds from both strategy groups chose the correct cup more often than expected by chance (Aligned group: 48.6%, $t(11) = 2.454$, $p = 0.032$; Landmark group: 60.4%, $t(11) = 3.228$, $p = 0.008$). In the One line condition, on the other hand, 4-year-olds from both strategy groups performed at chance levels (Aligned group: 34%, $t(11) = 0.267$, $p = 0.795$; Landmark group: 43.1%, $t(11) = 1.654$, $p = 0.126$). Five-year-olds from both strategy groups performed above chance in both conditions (Aligned group: Two rows condition, 77.8%, $t(11) = 5.722$, $p < 0.001$; One line condition, 51.4%, $t(11) = 2.203$, $p = 0.050$; Landmark group: Two rows condition, 73.5%, $t(11) = 4.954$, $p < 0.001$; One line condition, 54.9%, $t(11) = 3.148$, $p = 0.009$). Children's retrieval accuracy was higher in the Two rows condition than in the One line condition ($t(47)= 5.160$, $p < 0.001$).

A 2 (Age) × 2 (Strategy) × 3 (Position) × 2 (Order of condition administration) ANOVA of the Two rows condition revealed main effects of Age (4-year-olds: 54%, 5-year-olds: 76%; $F(1, 40) = 8.422$, $p = 0.006$) and Order (Two rows condition presented first: 56%, Two rows condition presented second: 74%; $F(1, 40) = 5.925$, $p = 0.019$) and no significant interactions. The ANOVA of the One line condition revealed main effects of Age (4-year-olds: 38.5%, 5-year-olds: 53%; $F(1, 40) = 5.207$, $p = 0.028$) and Position (Left: 37%, Middle: 57%, Right: 44%; $F(2, 80) = 6.625$, $p = 0.002$). There was also a significant interaction between Strategy and Position ($F(2, 80) = 3.165$, $p = 0.048$). To investigate the pattern of the interaction we conducted an ANOVA, with a baited cup's position (Position) as within-subject factor, separately for the two Strategy groups. The performance of the Aligned group differed on the three cups: Left 33%, Middle 62%, Right 33% ($F(2, 46) = 8.455$, $p = 0.001$), whereas the performance of the Landmark did not: Left 40%, Middle 53%, Right 54% ($F(2, 46) = 1.148$, $p = 0.326$).

Table 1

Percentage of correct choices for the two conditions when presented as first or second.

	Aligned group		Landmark group	
Order of Presentation	Two rows	One line	Two rows	One line
First				
4-year-olds	41.7 (0)	37.5 (0)	48.6 (1)	41.7 (1)
5-year-olds	73.6 (4)	52.8 (2)	61.0 (3)	47.2 (2)
M	**58**	**45**	**55**	**44**
Second				
4-year-olds	55.6 (4)	30.6 (0)	72.2 (3)	44.4 (1)
5-year-olds	81.9 (5)	50.0 (2)	86.1 (5)	62.5 (3)
M	**69**	**40**	**79**	**53**

Note. Numbers of children that passed the condition are in parentheses.

Individual analysis revealed that in the Two rows condition, eight 4-year-olds (four from each rewarded strategy group) and 17 5-year-olds (9 from aligned group and 8 from landmark group) selected the baited cup above chance, and that in the One line condition two 4-year-olds (both from the Landmark group) and nine 5-year-olds (4 from the Aligned and 5 from the Landmark group) selected the baited cup above chance (Binomial test, $P < 0.05$).

We were interested in whether children's performance became better over the trials in each condition. We compared the success on the first 6 trials with the success on the last 6 trials of each condition. There was no learning effect for the Two rows condition (*t*(47) = 1.881, *p* = 0.066), but there was a learning effect for the One line condition (*t*(47) = 4.228, *p* < 0.001).

Table 2

Percentage of correct choices across the three positions

		Position of the reward		
		Left	Middle	Right
Aligned strategy				
Two rows	4-year-olds	38	54	54
	5-year-olds	77	79	77
	M	**56.5**	**65.5**	**64.5**
One line	4-year-olds	23	50	29
	5-year-olds	44	73	38
	M	**33.5**	**61.5**	**33.5**
Landmark strategy				
Two rows	4-year-olds	54	56	70
	5-year-olds	67	90	65
	M	**60.5**	**73**	**67.5**
One line	4-year-olds	29	52	48
	5-year-olds	50	54	60
	M	**39.5**	**53**	**54**

The ANOVAs did not show a difference in the overall performance between the Landmark and Aligned groups in neither of the conditions, but there was a difference between the strategy groups in their success on the three cups in the One line condition. The difference between the aligned and landmark strategies can be seen only in the One line condition, more specifically, only when the Left or the Right cup were baited (the aligned strategy would lead in the Search array to the Left and the Right cup, respectively; and the landmark strategy would lead to the Right and the Left cup, respectively; see Figure 1); when the Middle cup was baited, both strategies led to the same cup – the Middle cup. Therefore, we decided to exclude the trials where the Middle cup was baited, and to compare the two strategy groups in the One line condition again. The results showed that now the difference in the performance of the Landmark and Aligned groups approached significance (*t*(46)= 1.965, *p* = 0.056).

Moreover, as already mentioned above, when all trials were included in the analysis, then the 5-year-olds from both strategy groups performed above chance in the One line condition. However, if we exclude the Middle trials, then the Aligned group's performance in the One line condition is not above chance anymore (*t*(11)= 0.815, *p* = 0.432), whereas the Landmark group still found the reward more often than expected by chance (*t*(11)= 3.622, *p* = 0.004).

We also investigated whether the children from the Aligned group tended to choose cups following the landmark strategy. Indeed, in the One line condition, children that were rewarded for the aligned strategy chose the cups in the Search array following the landmark strategy more often than expected by chance (*t*(23)= 2.623, *p* = 0.015). Individual analyses revealed that three 5-year-olds from the Aligned group selected the cups after the landmark strategy at above chance levels ($P < 0.05$). Similarly, we tested whether the children from the Landmark group preferred to choose the cups after the aligned strategy, and we found no significant result (*t*(23)= 1.011, *p* = 0.323). Moreover, none of the children from the Landmark group preferentially chose the cups following the aligned strategy.

DISCUSSION

Children were presented with a spatial mapping task, where the two spatial arrays could be positioned in two rows or in one line. We rewarded them for two different types of mappings: aligned and landmark mapping. There were four main findings: First, similar to prior results in the other great apes, children's retrieval accuracy was higher, when the two arrays were positioned in two rows, compared to when they were forming a line. Second, against our expectations, the experience with the Two rows condition did not increase children's performance in the One line condition. Third, in the One line condition, children tended to performed better when they needed to use the landmark mapping – the mapping spontaneously applied by the other great apes in almost identical situation – than when needed to use the aligned mapping. Moreover, even some children that were rewarded for the aligned mapping chose the cups following the landmark mapping, whereas none of the children rewarded for the landmark mapping preferred to use aligned mapping. Finally, even the younger group performed above chance in the Two rows condition without any verbal scaffolding; however, they failed in the One line condition. Moreover, 5-year-olds outperformed 4-year-year-olds in both conditions.

We propose three possible explanations (that could also work in a combination) for the first major finding: why children's performance was higher in the Two rows condition than in the One line condition. In the Two rows condition, the Search array could be considered more similar to the Hide array than in the One line condition. The two arrays in the Two rows condition had almost identical surrounding (e.g., on their left the table ended and on their right the table continued), whereas the arrays in the One line condition did not. Moreover, a similarity between two spatial scenes that need fewer changes to become identical is higher than between two scenes, which require more change (Bruns & Egenhofer, 1997). Surface similarity has been shown to have an effect on children's performance in relational mapping tasks (Chen, 1996; Chen, Sanchez, & Campbell, 1997; Holyoak, Junn, & Billman, 1984; Paik & Mix, 2006). Therefore, the higher similarity between the arrays, the better performance became. Another explanation could be that in the Two rows condition the two arrays were perfectly aligned one behind the other. Studies have shown that children's mapping success was higher when the two comparing scenes were aligned or oriented in the same direction (Blades & Cooke, 1994; Bluestein & Acredolo, 1979; Paik & Mix, 2008; Presson, 1982; Vasilyeva & Bowers, 2006). Blades and Cook (1994) obtained similar results that 4-year-olds succeeded in the spatial mapping task when the spatial layouts were aligned, but not when the target layout was rotated in respect to the base layout. Some authors have suggested that this alignment allowed children to potentially use the help of egocentric cues to solve the task and therefore, the trials with non-aligned scenes provided a more reliably measure of the ability to map spatial relations (Blades & Cooke, 1994; Vasilyeva & Bowers, 2006). Lastly, in the Two rows condition the corresponding cups from the two arrays were also the most proximate cups and therefore the children might have chosen the cup from the Search array that was closest to the picture reward they saw hidden in the Hide array. The proximity of the corresponding cups have been shown to have an effect on children's spatial mapping (Haun & Call, 2009). However, children did not show a preference to pick the closest cup in the One line condition, which would be always the same cup, the Right cup, irrespective of the position of the baited cup in the Hide array. Thus, the higher overall similarity of the arrays, their alignment one behind the other, and the proximity of the corresponding cups might have increased children's performance in the Two rows condition, compared to the One line condition.

The second major finding was that we did not find any order effect for the One line condition, meaning that presenting the children with a simpler problem (the Two rows condition) did not help them to solve the harder problem (the One line condition). Surprisingly, children performed better in the Two rows condition, after they were presented with the One line condition. This is the opposite result found in other studies that have shown that presenting children with a simpler task first, improved their performance in the subsequent more difficult task (Kotovsky & Gentner, 1996; Loewenstein & Gentner, 2001). We propose the following explanation for these results. As we mentioned earlier, children might have solved the Two rows condition by using egocentric or proximity cues rather than the relational mapping, and as a consequence, this strategy was not beneficial to them later, when they were presented with the One line condition. On the other hand, if they started with the One line condition, there was no (easier) alternative strategy available to them. This might have caused them to spend more time comparing the two arrays in search of a "game rule". Indication for this would be children's improvement over trials in the One line condition, and their increased performance on the Two rows condition, if it was presented after the One line condition. Vasilyeva and Bowers (2010) found that when children compare scenes that are to some degree different, are more likely to focus on common relations than on common surface features. In contrast, when they are comparing highly similar scenes, they are more likely to focus on common features.

The third finding was that the Landmark and the Aligned group differed in their retrieval accuracy in the One line condition (recall that this analysis does not apply to the Two rows condition, because there both strategies led to the same cups). The Aligned group needed to identify a relation the hiding cup held to the other two cups in the Hide array, and then find a cup with the same relation in the Search array. Interestingly, the Aligned group was successful when the Middle cup was baited, but failed when the Left and Right cups were correct. Nevertheless, we do not believe that children mapped the middle relation, but had problems with the left and right relations. A more plausible explanation would be that the Middle cup had a special feature that made it unique and distinctive from the other two cups – i.e., it was the only cup that was surrounded by two other cups. In Lee et al.'s study (2006), when 4-year-olds had been disoriented after observing an object being hidden in one of three hiding containers (one distinctive and two identical) forming a triangle, they found the hidden object only if it was hidden in the distinctive container and failed when the object was in one of the identical hiding places. These findings suggest that 4-year-olds did not encode spatial relationship between the three hiding places. Blades and Cooke (1994) found similar results with a model room task. They tested children's mapping ability between two model rooms, which had two unique and two identical hiding places. To differentiate between the identical hiding places, children had to take spatial relationships into account – something that 4-year-olds were only able to do when the two models were aligned. We believe that in the One line condition the Aligned group of children did not encode the baited cup' relative position in the array, and that they were highly successful on the Middle cup, because they matched the unique cups.

The Landmark group was expected to use the "landmark" strategy - to map together the cups placed at the table's edge, the middle cups, and the cups in the middle of the table - as great apes were suggested to do (Hribar, et al., 2011). If 4-year-olds are presented with two identical objects placed on a platform, they can encode the target object's location in respect to its distance to a nearby landmark, or to a platform's edge, and they can also transfer this information to another identical spatial layout and indicate to an object in the same location (Vasilyeva, 2002). Nardini et al. (2006), however, showed that when children were presented with 12 identical hiding places, only 5-year-olds and older could encode a location of the hidden toy in respect to the surrounding landmarks on the platform, the platform edges and the configuration of the array. Thus, they encoded a hiding cup in a relation to nearby special features. In our study, the platform's edge could serve as a nearby special feature. The platform's edge or a boundary and the symmetry axis (i.e., the middle of the platform) are very salient cues, and affect adults' and children's spatial recall (Batty, Spetch, & Parent, 2010; Bullens et al., 2010; Huttenlocher, Newcombe, & Sandberg, 1994). Therefore, it is conceivable that children in our study in the One line condition (possibly in the Two rows condition as well) encoded the hiding cup from the Hide array in a relation to nearby special features and that they then mapped this relation to the Search array.

However, children could solve this task, by using other strategies as well. For example, children could map together the cups that held a similar relation to themselves as a central landmark – i.e., the cups that were furthest away from them, the cups that were closest to them, and the cups that were halfway. Alternatively, if in the One line condition, children saw the two arrays as one continuous line, they might have mapped together the two endings of the line (the Right cup in the Hide array and the Left cup in the Search array) and the two middle parts of the line, for example. However, note that before the children were allowed to choose a cup, the Search array was pushed forward, and so the continuous line that the two arrays formed was broken.

To summarize, without any verbal instructions to do so, 4- to 5-year-old children spontaneously used information about the location of a picture hidden in the Hide array to locate the picture in the Search array. However, children of both ages were affected by the constellation of the arrays – they performed better when the two arrays were aligned in two rows. Interestingly, their experience with the Two rows condition did not improve their performance in the One line condition. Moreover, children tended to perform better, when they were rewarded for the landmark mapping – mapping together the cups, which held the same relation to the nearby table's special features. Overall, children's performance was very similar to apes' performance on a very similar task (Hribar et al., 2011), which shows intriguing parallels in ape and children spatial mapping abilities.

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Erklärung

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Ich erkläre, dass ich die vorgelegte Dissertation selbstständig angefertigt, nur die angegebenen Hilfsmittel benutzt und die Zitate gekennzeichnet habe.

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