

Solving small spaces: investigating the use of landmark cues in brown capuchins (*Cebus apella*)

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Abstract Some researchers have recently argued that humans may be unusual among primates in preferring to use landmark information when reasoning about some kinds of spatial problems. Some have explained this phenomenon by positing that our species' tendency to prefer landmarks stems from a human-unique trait: language. Here, we test this hypothesis—that preferring to use landmarks to solve such tasks is related to language ability—by exploring landmark use in a spatial task in one non-human primate, the brown capuchin monkey (*Cebus apella*). We presented our subjects with the rotational displacement task, in which subjects attempt to relocate a reward hidden within an array of hiding locations which are subsequently rotated to a new position. Over several experiments, we varied the availability and the salience of a landmark cue within the array. Specifically, we varied (1) visual access to the array during rotation, (2) the type of landmark, (3) the consistency of the landmark qualities, and (4) the amount of exposure to the landmark. Across Experiments 1 through 4, capuchins did not successfully use landmarks cues, suggesting that non-linguistic primates may not spontaneously use landmarks to solve some spatial problems, as in

this case of a small-scale dynamic spatial task. Importantly, we also observed that capuchins demonstrated some capacity to learn to use landmarks in Experiment 4, suggesting that non-linguistic creatures may be able to use some landmarks cues in similar spatial tasks with extensive training.

Keywords Non-human primate · Spatial cognition · Rotational displacement · Landmarks

Introduction

Imagine the following scenario:

I'm in the foyer of my house getting ready to leave in the morning. I suddenly remember I must bring a book to a colleague, and before going into the house to retrieve the book, temporarily set down my keys. Not a minute later, I re-enter the foyer, and pause to remember where I've set my keys. Fortunately, I remember I put them next to the potted plant on the table. I grab my keys and go.

Most adult humans have probably had experiences like the common one described above. Indeed, the idea of locating an object relative to another landmark object, such as the potted plant, is a common strategy in human spatial reasoning. What is surprising, though, is the fact that individuals of other species sometimes struggle with this sort of spatial solution. A number of comparative studies have found that non-human primates (hereafter, primates) tend to rely on landmarks to solve spatial problems less than humans do (Gouteux et al. 2001a; Haun et al. 2006; Okamoto-Barth and Call 2008). Although primates do in

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fact use landmarks¹ to solve spatial problems (Deipolyi et al. 2001; Dolins 2009; Garber and Brown 2006; Garber and Paciulli 1997; Gouteux et al. 2001a; Herman and Wallen 2007; Kanngiesser and Call 2010; MacDonald et al. 2004; Marsh et al. 2011; Poti et al. 2005, 2010; Sutton et al. 2000), some have argued that primates are less likely to use landmarks to solve more dynamic spatial problems, in which relationships between the actor, objects, and space change (e.g., Haun et al. 2006; Okamoto-Barth and Call 2008). Hints as to why primates would have difficulty prioritizing landmarks in such spatial tasks are provided by the human developmental literature on the subject. While younger children, like primates, struggle with landmarks cues in some dynamic spatial tasks, there is evidence that by early to middle childhood, this difficulty disappears (Gouteux et al. 2001b; Haun et al. 2006; Hermer and Spelke 1994, 1996; Learmonth et al. 2002; Okamoto-Barth and Call 2008). These results have led some researchers (e.g., Haun et al. 2006; Okamoto-Barth and Call 2008) to argue that increased ability to utilize landmarks in some spatial tasks is linked to an important human character: the use of language.

Over the last few decades, a number of researchers have attempted to explore this language hypothesis and better articulate the relationship between language ability and landmark use. Earlier, cognitive accounts postulated that spatial representations were the product of dedicated spatial module that was shielded from landmark information (Cheng 1986; Hermer and Spelke 1994, 1996; Hermer 1997; Hermer-Vazquez et al. 2001; Wang et al. 1999). This idea was supported by studies with rats (*Rattus norvegicus*, Cheng 1986), and human toddlers and adults (Hermer and Spelke 1994, 1996; Wang et al. 1999) that used a reorientation task. In reorientation tasks, participants are shown the location of a goal in a rectangular arena, disoriented, and then allowed to retrieve the goal. Initially, studies using this task suggested that rats and human toddlers were unable to use a landmark to guide their search while adult humans readily used such cues (Cheng 1986; Hermer and Spelke 1994, 1996; Wang et al. 1999). Based on this pattern of performance, researchers argued that language allowed adult humans (but not toddlers and rats) to verbalize and thus encode landmark information, which could not otherwise be represented by the spatial module. More recent studies, however, have provided evidence against an isolated geometric module incapable of integrating landmark information. Subsequent investigations of the reorientation task demonstrated that non-linguistic participants

can also use landmarks cues to reorient (toddlers: Learmonth et al. 2001, 2002, 2008; Lourenco et al. 2011; rhesus monkeys *Macaca mulatta*: Gouteux et al. 2001a; black-capped chickadees *Poecile atricapillus* and mountain chickadees *Poecile gambeli*: Batty et al. 2009; domestic chicks *Gallus gallus* Vallortigara et al. 2004; redbill splitfin fish *Xenotoca eiseni*: Sovrano et al. 2007). Additionally, it seems that landmark information is not cognitively isolated from other spatial information as these two types of information can interact in spatial learning through overshadowing and potentiation (review in rats: Cheng 2008). However, even these new findings suggest that non-linguistic creatures may not prioritize landmark information as much as humans do when solving such tasks. In the only study of a primate in a reorientation task, Gouteux et al. (2001a) found that rhesus macaque could use both geometry and landmarks to solve the task; however, while macaques' use of geometry was always robust, the use of landmarks was less so and required that landmarks be a certain size and type. Additionally, numerous studies with other non-linguistic populations have found that the reliance on landmarks decreases as the size of the space decreases (human toddlers: Learmonth et al. 2002; domestic chicks *G. gallus* Vallortigara et al. 2005; Chiandetti et al. 2007; Sovrano and Vallortigara 2006; redbill splitfin fish *X. eiseni*: Sovrano et al. 2007). Interestingly, these behavioral tendencies disappear in older linguistic humans who become less likely to ignore landmark information no matter the experimental manipulation with increasing age (e.g., Learmonth et al. 2002).

This tendency of some populations not to prioritize landmark information is not limited reorientation tasks, but has also been observed in other small-scale spatial tasks. In one such example, Gouteux et al. (2001b) investigated the behavior of 3- to 5-year-old children in a tabletop version of the reorientation task: a reward was hidden in one corner of a rectangular arena that sat atop a table and was rotated while the subject was blinded. Gouteux and colleagues then varied whether landmark information was present. At 3 years of age, children failed to use landmark information to solve this tabletop reorientation task, but by 4 years of age, children's use of landmarks dramatically increased. In fact, 4-year-old subjects preferred landmarks cues and paid less attention to geometry cues (the shape of the arena) when both cues were available to relocate the reward (for a similar result with 4 year olds: Hupbach and Nadel 2005). The authors attributed this change to greater language ability for 4 year olds (for similar changes across child development, see Haun et al. 2006; Okamoto-Barth and Call 2008). This effect, which is similar to what is observed over human development in the reorientation task, was elicited even though the Gouteux task differs from the reorientation task in several characteristics: scale, movement of the

¹ In this paper, we use the term landmark to refer to non-geometric properties of landmarks and features, a category that excludes geometrical landmarks such as the overall shape of a testing apparatus or its edge (e.g., Huttenlocher et al. 1994).

subject, and movement of the object to be tracked. This set of studies strongly suggests that the difficulty non-linguistic creatures sometimes experience with landmarks is not limited to the reorientation task, but might be a characteristic of reasoning about a certain class of spatial problems—dynamic spatial tasks that require mental transformation of spatial information such as reorientation or changes in perspective (for a similar definition, see Call 2000).

Several researchers have claimed that primates' and toddlers' problems using landmark information are the result of a lack of linguistic competence. Gouteux et al. (2001b) attributed the developmental change they observed in their tabletop reorientation task to the greater language ability of 4 year olds. Other researchers have also recently suggested that such changes in the use of landmarks across human development are supported by language learning (Haun et al. 2006; Okamoto-Barth and Call 2008). In this way, several researchers have argued for a more nuanced version of the language hypothesis, in which all individuals are capable of using landmarks, but language ability is related to increased use of landmarks when solving particular spatial problems. Given the types of tasks that seem to elicit this deficit of landmark use, the connection between landmark use and language development may be particularly relevant for *dynamic spatial tasks*.

Evidence from primate studies also shows poorer performance in dynamic spatial tasks when using landmark information compared with other types of spatial cues. In one example, Haun et al. (2006) investigated the spatial strategies of apes (*Pongo pygmaeus*, *Gorilla gorilla*, *Pan paniscus*, and *Pan troglodytes*), pre-linguistic 1-year-old human toddlers, and 3-year-old children in an occluded transposition task. In normal transposition tasks, subjects must track an object that is first hidden in one container among an array of containers and then the container is switched with one of the others bringing the hidden object to a new position. In Haun's *occluded* version, after the object-to-be-tracked was hidden, the array of containers was occluded and the switch happened out of the subjects' sight. Importantly, subjects could potentially solve the task because each container had unique features, and subjects could use a container as a landmark for the location of the desired object. Three-year-old children succeeded in using the container like a landmark to find the position of the hidden object, but apes and 1-year-old children only performed at chance in the occluded version of this task. Haun and colleagues argued that the difference in performance between apes and 1 year olds compared to 3 year olds could be language ability. They postulated that increasing language ability influenced 3 year olds to favor featural information to solve the spatial task rather than using a place-based strategy.

In a very similar study with landmarks and an object-tracking task, Okamoto-Barth and Call (2008) presented apes (*P. pygmaeus*, *G. gorilla*, *P. paniscus*, and *P. troglodytes*) and children with the rotational displacement task, in which subjects attempted to track an object at a hiding location within an array while the array rotated. Landmark cues (such as a sticker on the hiding container or differently colored containers) were always available to indicate the new location of the hidden reward, but in some conditions, subjects were prevented from watching the displacement. As one might predict, apes were unable to use landmark information to solve the task when the rotation was occluded, although children 3 years of age and older performed successfully. The conclusion from these studies is that primates and non-linguistic toddlers are less able to use landmarks than older children, at least in some tasks, just as one might predict if such landmark use relied on sophisticated linguistic capacity.

However, one primate study to date does not fit the general pattern in which primates show difficulty with landmarks in dynamic spatial tasks. Potì (2000) found that capuchins (*Cebus apella*) could use landmarks to relocate a hidden reward in an occluded rotational displacement task. At first glance, these results seem to pose a serious challenge to the language hypothesis; capuchins do not have linguistic capacity yet they were able to use landmarks to solve a dynamic spatial task.

Why might the capuchins in Potì's study succeed where other primates failed? One possibility is that there are species differences in primates' ability to use landmark information. Perhaps, capuchin monkeys have a species-specific capacity to use landmarks which make their performance better than the apes who have been tested to date. This would suggest that language might not be as essential for landmark use in dynamic spatial tasks as was suggested in the ape studies. Indeed, there are examples of such species-specific landmark preferences among bird species. When black-capped chickadees (*P. atricapillus*) and mountain chickadees (*P. gambeli*) completed a reorientation task, mountain chickadees relied more on landmarks cues than black-capped chickadees to solve the task (Batty et al. 2009). Although such species differences have been documented in avians, few primate species have been thoroughly tested in their use of landmarks in dynamic spatial tasks, which makes it difficult to know how plausible a species difference might be. A second possibility is that the experimental design used in Potì (2000) differed from other studies in a subtle yet significant way. Previous studies on landmark use in a variety of other populations have shown that the characteristics of the landmark affect whether subjects successfully use it as a spatial cue (e.g., in 3-year-old children: Okamoto-Barth and Call 2008; in rhesus macaques *M. mulatta*: Gouteux et al. 2001a). More

specifically, failures by apes in the study by Haun et al. (2006) could be due to difficulty in discriminating among landmarks rather than an ability to use a singular landmark, as Potì (2000) used. A final possibility is that the Potì (2000) design might have provided capuchins with more time to learn to use the landmark cue, while other studies did not afford their primate subjects this opportunity. Potì (2000) provided 144 trials to capuchin subjects while Okamoto-Barth and Call (2008) and Haun et al. (2006) provided less than a third of this number to their ape subjects. Thus, capuchins' successful use of landmarks in Potì (2000) could be explained by differences in learning opportunities rather than general tendency to use landmarks to solve dynamic spatial problems.

Differentiating among these possibilities is important for a better understanding of the possible role of language in representing landmarks in dynamic spatial tasks. If capuchins truly differ from apes in their ability to use landmarks in dynamic spatial tasks, than this is evidence against the hypothesis that language is necessary for spontaneous and successful use of landmarks in small-scale dynamic spatial tasks. In contrast, if capuchins are only able to use particular kinds of landmarks or only do so after substantial opportunity for learning, than capuchins' performance would not represent strong evidence against the language hypothesis. Indeed, such evidence would be consistent with the idea that language ability is linked with greater ability to attend to or differentiate among landmarks, as has been suggested by others (e.g., Haun et al. 2006). The best way to distinguish between these possibilities is to continue to investigate landmark use in dynamic spatial tasks in brown capuchins.

In the current study, we build on the work started by Potì (2000) by presenting brown capuchins with a new version of the rotational displacement task. Furthermore, we blend aspects of both the Okamoto-Barth and Call (2008) and Potì (2000) designs in an effort to understand the differences between these studies. To do so, we experimentally varied landmark type, visual access to the rotation, consistency in the use of a particular landmark, and the amount of exposure each subject had to landmarks. By combining and comparing these different factors, we aimed to create a more in-depth analysis of landmark use in the rotational displacement task that could allow us to clarify some difference in the results observed in previous studies.

In the present study, we started by using the type of landmark used in Okamoto-Barth and Call (2008): differently colored hiding locations. Apes tested in Okamoto-Barth and Call (2008) were not able to use this cue to relocate rewards, but given capuchins' success in using a different type of landmark in the Potì (2000) study, we explored whether capuchins could succeed where apes had failed. As in Okamoto-Barth and Call (2008), we frequently changed the relevant cue color and provided a

limited number of trials, compared to Potì (2000), to curtail the effects of learning. Thus, in Experiment 1, we addressed whether capuchins could make use of differently colored hiding locations to improve their performance on a visible rotational displacement. In Experiment 2, we took these same landmarks and assessed whether capuchins would use this cue when there were no other cues to rely on, namely when the rotation was occluded. Then, in Experiment 3, we switched to a second kind of landmark: a large visible token was placed next to the hiding location. This sort of token landmark mirrored the landmark cue that capuchins successfully used in Potì (2000) and is similar to the type of landmark cue used by the youngest children tested by Okamoto-Barth and Call (2008). In addition, matching the Potì design, in Experiment 3, we no longer switched the type of the landmark between trials, creating a more stable cue. In Experiment 4, we extended Experiment 3 to investigate how learning affected the ability to use landmark information.

Experiment 1

Methods

Subjects

Six brown capuchins (*C. apella*) housed at the Comparative Cognition Laboratory at Yale University served as subjects in Experiment 1 (Table 1). Five individuals were adults (3 males and 2 females) and 1 was a juvenile female. All of the individuals were born in captivity, either at the Yerkes Primate Center or at the Comparative Cognition Laboratory. All individuals have been maintained since birth in group-housed populations maintained for the purposes of noninvasive cognitive experiments. Currently, the capuchins are maintained in a single social colony in a large indoor enclosure. The monkeys are provisioned with monkey chow and a daily mix of vegetables and fruits, and water is available ad libitum. All had previous experience with a variety of cognitive tasks (Barnes et al. 2008; Chen et al. 2006; Egan et al. 2007, 2010; Lakshminarayanan et al. 2008, 2011; Lakshminarayanan and Santos 2008, 2009; Phillips et al. 2009; vanMarle et al. 2006), although older individuals have had more experience than younger individuals. No subject had previous experience with spatial cognition tasks. For this task, testing occurred over a period of 4 months, with individuals tested between 1 and 3 times a week. Subjects were tested when they choose to enter the testing chamber at their own volition.

Apparatus

The apparatus (Fig. 1) consisted of a base (56.25 cm × 38.13 cm × 42.5 cm) with a flat, table-like, circular

Table 1 List of subjects in Experiments 1–4

Name	Sex	Age (years; in 2010)	Experiment (group)
AG	M	15	1, 2, 3, 4 (N)
FL	M	14	1, 2, 3
HG	F	10	1, 2, 3, 4 (V)
JM	F	14	1, 2, 3, 4 (N)
NN	M	15	1, 2, 3, 4 (V)
MP	F	3	1

surface on top (50 cm diameter). The table could be rotated by hand, up to a full 360°. Centered on the top of the table were two flat panels (24.4 cm across \times 17.5 cm deep); these could be placed so that they looked as though they constituted one long plank (48.8 cm across \times 17.5 cm deep, Fig. 1a). On top of each panel was a single colored cup, which served as a hiding location for object tracking. The two cups were always in the same location, equidistant from each other and the outer edge of the panel. Two sets of two opaque cups (10.0 cm across \times 10.0 cm deep \times 5.3 cm tall) were used during Experiment 1. One of these sets differed in color (one set consisted of a red and green cup) while the other was the same color (two blue cups). Each panel sat on a track that ran the length of the table. This track allowed the panels to be pushed forward to the edge of the table; in the experimental procedure, this movement was key to allow the contents of the panels (cups and hidden object) to be placed within reach of the subject (Fig. 1b). Once a subject had touched one cup, indicating a selection, the other panel could be withdrawn from the subject, negating it as a choice (Fig. 1c).

The entire apparatus was placed on top of a portable metal table outside a testing chamber connected to the main enclosure. When a subject was present in the testing chamber, the apparatus (and the experimenter operating the apparatus) would sit directly opposite the subject. Subjects could thus reach through an opening in the testing chamber to overturn one of the two cups when these were within reach. A single piece of Cheerio brand cereal was used as a reward on each trial. A metronome was used to measure time during trials so that each movement and the entire length of each trial was the same across trials.

Procedure

All training and testing sessions were run by two experimenters. One experimenter operated the apparatus while a second experimenter recorded the choices made by the subject. All sessions were videotaped. All subjects received two training phases followed by an experimental test phase.

Training phase 1

The first training phase allowed subjects to become familiar with the mechanics of the apparatus in the absence of any rotations. A session began when a subject entered the testing chamber alone. The apparatus was then placed outside the subject's reach, but within full view. Next, the presenting experimenter placed one set of cups—either the green cup and red cup or two blue cups—on top of the plank. She then flipped the cups on their sides with the open bottom facing the subject, showing there was nothing under the cups. While the subject was watching, the presenter then placed one food reward on top of a panel and in front of one of the cups. She then flipped both cups over at the same time, covering the food item with one of the two cups. Immediately after the reward was hidden, the experimenter slid the plank forward within reach of the subject. The subject's response was recorded as the first cup that was touched. As soon as one cup was touched, the panel with the other cup was pulled backward so that only the chosen cup remained within reach of the subject. The subject was then allowed to overturn the chosen cup and retrieve the reward if she chose correctly. After the subject retrieved the reward, the entire apparatus was reset for the next trial. If the subject did not choose accurately, the panel was pulled back after the subject turned over the incorrect cup. In this case, while resetting the apparatus, the experimenter surreptitiously removed the hidden food item from the array. The presentation of the reward was counterbalanced for color of cup, side, and cup set. In order to move on to the next training phase, subjects needed to select the correct cup at above chance levels over two full sessions of 18 trials each as determined by a binomial test.

Training phase 2

The procedure in training phase 2 was similar to that of training phase 1 except for one feature. In training phase 2, after hiding the reward, the experimenters waited 6 s before allowing a subject to indicate a choice; this additional delay ensured that subjects could remember the location of a reward across a short time delay. We chose this amount of delay because it was equivalent to how long a subject would have to wait during a rotation event used in the test condition. In order to move on to the next training phase, subjects needed to select the correct cup at above chance levels over two full sessions, each of 18 trials, as determined by a binomial test. Trials were counterbalanced for side, color, and cup set.

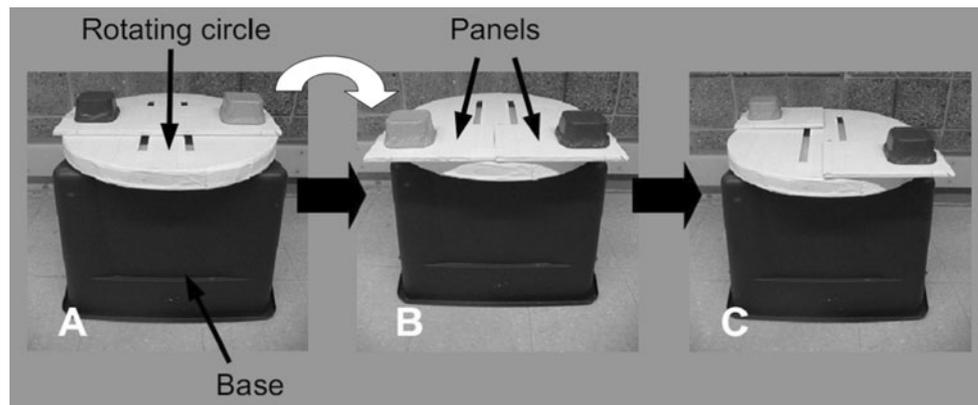


Fig. 1 **a** Starting position for the apparatus, which consists of a base and a *rotating table*, on top of which sit two *panels*. Each *panel* sits in a track and can be moved forward and backward independently, but the *panels* can also be placed together to look as though they constitute one plank. *Inverted cups* served as hiding locations, placed

opposite each other on the two *panels*. After a reward is hidden under one *cup*, the table may be rotated, depending on condition. **b** Next, the two *panels* are pushed forward so that a subject can choose the contents of one *cup*. **c** Finally, after a choice is made, the unchosen *cup* is retracted

Testing phase

The procedure for the test phase was similar to phase 2 training except that on some trials the experimenter rotated the circular base underlying the panels and cups. There were three rotation conditions: 0° (control), 180°, and 360°. After hiding the food, the presenter rotated the circular table in the 180° and 360° conditions. To rotate the table, the experimenter gripped the table surface at the back of the apparatus, not touching the panels or cups, and rotated the table in a clockwise direction. On 0° rotations, the experimenter gripped the back of the rotating table, but made no rotating motion. Using a metronome, the presenter ensured that all three degrees of rotations took the same amount of time (6 s). The placement of the food reward was counterbalanced for side, color, and cup set. The subjects completed five sessions of 18 trials each.

Data analysis

The results were first recorded live by the second experimenter. Later, videos of the trials were processed (with M-PEG Streamclip Software: Cinque 2007), to be coded by a naive experimenter. In this way, 20 % of data were coded twice; agreement between the two sets of data was perfect, $\kappa = 1.0$.

For statistical analysis, we used two approaches. First, we computed binomial tests to determine whether individual subjects succeeded at levels above chance in each condition. Second, to understand whether rotation condition and presence/absence of landmark information affected the probability that subjects chose correctly, we used a generalized estimating equation (GEE) in PASW (version 18) to perform a binary logistic regression with repeated

measures. ID was added to the model to control for the effects of individuals, and we chose an independent working correlation matrix to model the relationship of data points within each subject. Choice was the dependent variable (correct = 1, incorrect = 0, reference category), and our independent variables were rotation and cup color set. Because the independent variables were categorical, they were recoded into dummy variables, one for cup color set (labeled *D*; same color = reference category) and two for rotation (labeled 180 and 360; zero rotation = reference category). We also tested for significant interactions between the independent variables using two interaction variables, $D * 180$ and $D * 360$.

Results

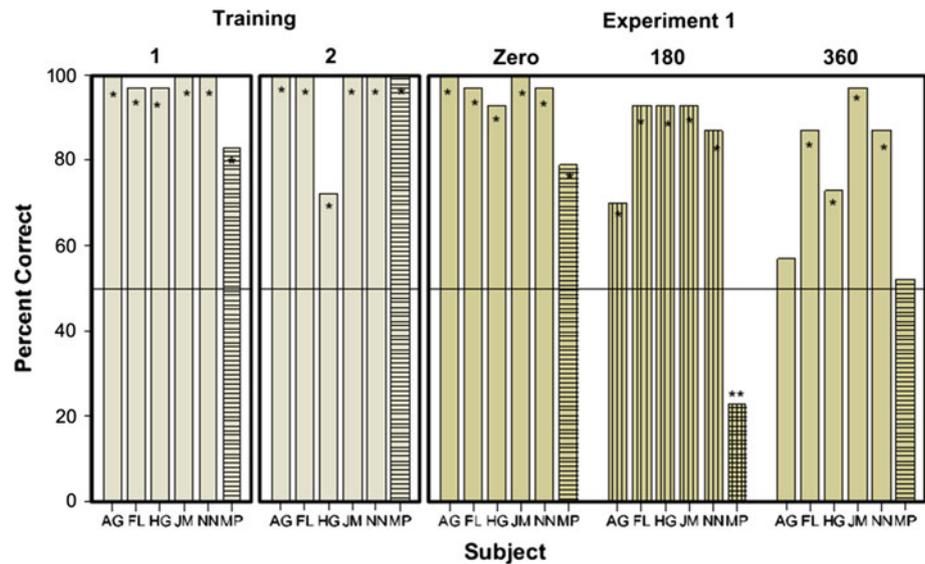
Training phases 1 and 2

The results for the performance on training phases 1 and 2 are illustrated in Fig. 2. All subjects performed significantly above chance (Training 1: $M = 96$ % correct; Training 2: $M = 95$ % correct; $p = 0.01$ or smaller for each test) and passed the training levels required for participation in the test sessions of Experiment 1.

Test

All five adult subjects completed 90 trials, and the juvenile subject completed 81 trials (she stopped participating halfway through the last session). We first assessed whether each individual was successful at performing above chance for each rotation condition (Fig. 2). Using two-tailed binomial tests, we found that four adults performed significantly above chance on all rotation conditions

Fig. 2 Results of binomial tests for Training 1 and 2, and Experiment 1 per individual, with 180° condition in *vertical-hatched bars* and with the juvenile subject (MP) in *horizontal-hatched bars*. Results: *statistical difference from chance in the correct direction as determined by a binomial test, **statistical difference from chance in the incorrect direction as determined by a binomial test



($M = 91\%$ correct, $p = 0.016$ or less), while adult male AG was significantly above chance for the zero and 180 conditions (100% correct, $p < 0.001$ and 70% correct, $p = 0.043$, respectively), but not for the 360 condition (57% correct, $p = 0.585$). Thus, for the most part, the adults successfully completed the rotational displacement task. However, the juvenile differed markedly from the adults; she performed at chance in the 360° condition (52% correct, $p = 1.0$) and significantly chose incorrectly in the 180° condition (23% correct, $p = 0.009$). Because the performance of this younger individual seemed to markedly differ from that of the adult capuchins, we dropped MP from the rest of the group analysis.

We conducted the GEE with data from only the adult subjects (Fig. 3). Cup color set was not significantly related to the odds of observing a correct choice ($D: B = -1.650E-15$, Wald $X^2 = 0.000$, $df = 1$, $p = 1.0$), but the odds were negatively affected by nonzero degree rotations (180: $B = -1.836$, Wald $X^2 = 4.935$, $df = 1$, $p = 0.026$; 360: $B = -2.292$, Wald $X^2 = 7.854$, $df = 1$, $p = 0.005$). Although these results seemed to indicate that cup color set did not affect subjects' choice, we anticipated that any effect of color might only be detectable in an interaction because opportunity to improve performance in the zero rotation condition was limited because scores in this condition were already very high. However, we did not find a significant interaction effect ($D * 180: B = 0.364$, Wald $X^2 = 0.079$, $df = 1$, $p = 0.778$; $D * 360: B = 0.167$, Wald $X^2 = 0.017$, $df = 1$, $p = 0.895$), indicating that the capuchins did not use cup color to bolster performance in the rotation conditions.

Within the GEE analysis, we also conducted Bonferroni corrected pairwise statistical tests among the three rotation conditions. Performance on the zero condition was significantly better than on the 360° condition ($p = 0.018$) and

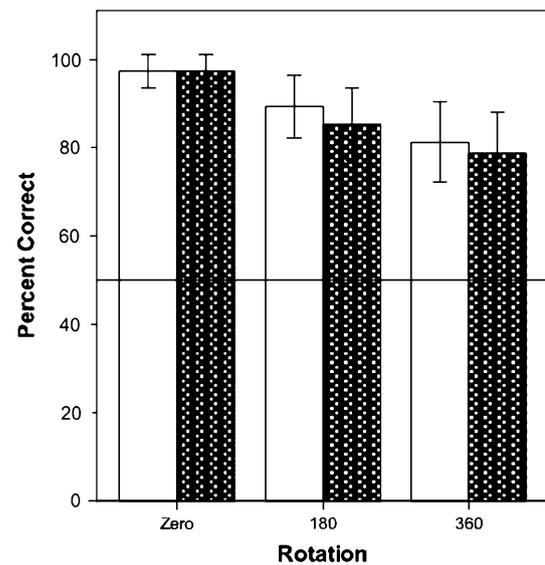


Fig. 3 Results from Experiment 1: Pooled performance of group, for each rotation condition, for both cup color set conditions. *White bars* same colored cups, *dark bars* differently colored cups (error bars 95% CI)

marginally better than on the 180° condition ($p = 0.089$), but the difference between the 180° and 360° condition was not significant ($p = 0.177$), suggesting that rotation *per se* significantly increased the difficulty of tracking the hidden object.

Discussion

Adults performed successfully at levels above chance on all rotation conditions, indicating the capuchins were more than capable of successfully completing the rotational

displacement task when the rotation was visible. However, their performance was significantly poorer on the 180° and 360° conditions than on the zero condition, indicating that the rotation provided at least somewhat of a challenge. Notably, the 360° condition was as difficult as, if not more difficult than, the 180° condition. Because the reward moved in the 360° case, but ended where it started, this indicates that the rotation itself, not the movement of the hidden reward to a new final position, increased the difficulty of the task. Finally, the set of cups used during rotations did not affect performance, indicating that including landmark information in the array (red and green cups) did not benefit the capuchins when the rotations were visible. This was even true in the 180° and 360° conditions, where the capuchins had opportunities to improve their performance by using the landmarks.

An unanticipated finding from Experiment 1 was the behavior of the one juvenile tested, MP, which was strikingly different from that of adults. While the adults were competent on both the 180° and 360° conditions for the most part, MP was unsuccessful on both and her performance was even worse than chance in the 180° condition. Due to the evidence we collected in this study, we cannot know much about the causes of MP's performance. MP has participated in other cognitive studies (e.g., Furlong and Santos, in preparation) and easily passed the training trials, suggesting that her difficulties were specific to the present test and not due to general confusion with experimental methods per se. Beyond this, it is unclear why MP found the task to be difficult, and there are many possibilities including immature spatial cognition, or attentional and executive function capacity. Some evidence in favor of the interpretation that this deficit is specific to spatial ability is the fact that MP showed above chance performance during training and also during the zero condition during testing. This pattern of performance suggests MP's difficulties were specific to the rotation portion of the test. Overall, we felt the MP's performance reflected immature cognitive development and did not represent the abilities of the other adult capuchins we tested. As we were unable to investigate the role of development further in this study (since we only had one juvenile individual in our sample), we chose to exclude MP from Experiments 2 through 4.

The results of Experiment 1 showed that the rotational displacement task is excellent for investigating the questions we posed. Our results suggest that our adult capuchin monkeys understood the rotational displacement mechanism, although it did present some challenges for them. These initial results suggest that capuchins could have taken advantage of a landmark cue (i.e., cup color) to improve their performance on some trials, but our results suggest that capuchins were unable or did not do this. Among the adult subjects, the percentage of correct choices

on actual rotation conditions (180° and 360°) was not statistically distinguishable between the landmark (green and red cups) and no landmark (two blue cups) conditions.

One possibility is that our capuchin subjects might not have used the landmark cues in Experiment 1 because simply tracking the hiding location visually as it was rotated within the array was more efficient. Somewhat similar findings have been reported in studies of rats in other dynamic spatial tasks (reviewed in Cheng 2008). Such studies have found that rats encode some landmark information in spatial tasks, but that other types of spatial information, such as geometry, sometimes overshadow landmark information in spatial representations. When these alternative cues are removed, subjects are better able to use landmark cues. Given this possibility, we designed Experiment 2 to remove visual access to the array during rotation. In this case, the only clue the subjects had that the array had moved would be the cup color and subjects would need to attend to this to retrieve the reward. This is especially tested in the 180° condition, as this is the only condition in which the final location of the reward has changed.

Experiment 2

Methods

Subjects

The subjects used in Experiment 2 were the same five adult capuchins (3 males and 2 females) who participated in Experiment 1. There was a 1-month break in testing between Experiment 1 and Experiment 2. All testing for Experiment 2 was completed in a month and a half, during which subjects were tested between 1 and 3 times a week.

Apparatus, design, procedure, and data analysis

The experimental apparatus was the same as in Experiment 1 except for three changes. First, we used only one cup color set, red and green, as hiding locations. Second, an occluder was used to hide the apparatus from the subject's view during rotations (50 cm × 90 cm piece of stiff board colored black); this occluder was manipulated by a third experimenter. Lastly, the surfaces of the testing chamber that faced the apparatus but were not directly in front of it were covered with screens so that a subject could not look at the apparatus from an angle above the apparatus. Together, these changes allowed the experimenters to hide the motion of the rotation from subjects.

The procedure was identical to the test conditions of Experiment 1, except for two changes. First, one second

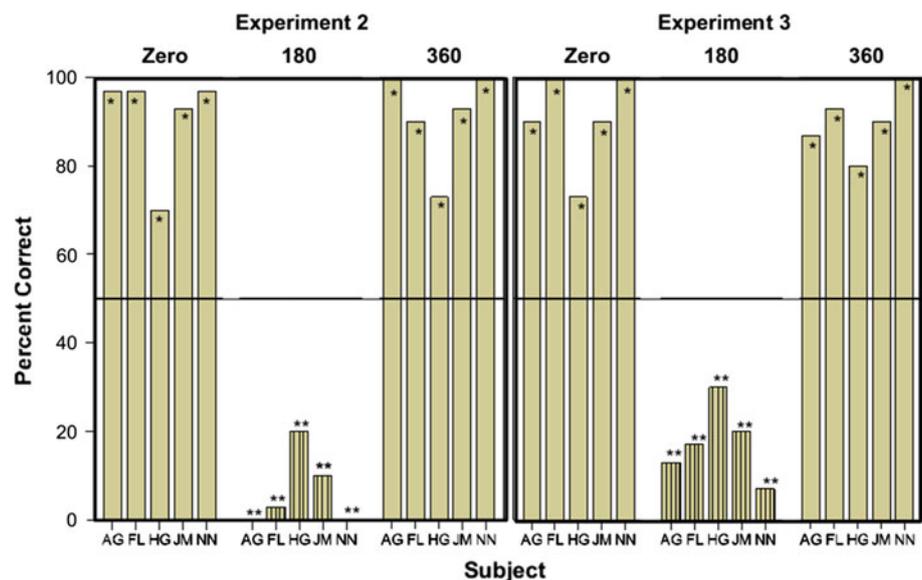
after the food was hidden, the third experimenter moved the occluder in front of the display to block the rotation. The apparatus was then rotated according to condition. The occluder was removed immediately after the rotation was completed, allowing the panels to be pushed forward so that the subject could make a selection. Even with these additions, the food was occluded for 6 s. as in Experiment 1.

Data were first recorded by hand during the experiment. Later, 20 % of these data were checked against the video recording for accuracy; there was a high level of agreement between the data, $\kappa = 0.81$. For statistical analysis, we used the same approaches as in Experiment 1, although our GEE regression contained only one independent variable, rotation, which was recoded into two dummy variables (labeled 180 and 360; zero rotation = reference category).

Results

All five subjects completed all sessions, for a total of 90 trials per subject. The performance of all individuals in each rotation condition differed significantly from chance as determined by a two-tailed binomial test (Fig. 4). However, while all succeeded more often than expected by chance in the zero and 360° conditions ($M = 91\%$ correct, $p = 0.043$ or less per test), all monkeys made significantly more errors than expected by chance in the 180° condition ($M = 6.6\%$ correct, $p = 0.001$ or less per test). The GEE confirmed these results: the 180° condition had a significant negative effect on the odds of observing a correct choice on the task ($B = -4.913$, Wald $X^2 = 20.833$, $df = 1$, $p < 0.001$), while the effect of the 360° condition was nonsignificant ($B = 0.081$, Wald $X^2 = 0.151$, $df = 1$, $p = 0.698$).

Fig. 4 Results of binomial tests for Experiments 2 and 3 per individual per rotation condition, with the 180° condition in *vertical-hatched bars*. Results: *statistical difference from chance in the correct direction as determined by a binomial test, **statistical difference from chance in the incorrect direction as determined by a binomial test



Discussion

Experiment 2 revealed above chance performance in the zero and 360° conditions but capuchins failed to perform well in the 180° condition on the occluded rotational displacement task. In fact, the capuchins performed at levels significantly below chance in the 180° condition.

In our version of the occluded rotational displacement task, the 180° condition becomes the critical test condition because it is the only condition in which the final position of the hidden reward is at a different location from which it started. In this rotation condition, the only way to solve the task reliably is by attending to the color of the cup as a relevant cue for the hidden item. The capuchins did not succeed in this condition, so we can conclude that they did not use cup color as a relevant landmark to track the hidden item.

That subjects reliably searched in the incorrect location in the 180° condition further suggests that they simply looked for the reward in the last position in which they had seen it. This interpretation is further supported by the high number of correct choices in the zero and 360° conditions, in which the final position of the hidden item was the same as the starting position. This result is consonant with the findings of Okamoto-Barth and Call (2008) and Haun et al. (2006), in which primate subjects privileged position information over landmark information when the movement of the objects was hidden.

Taken together, the results of Experiments 1 and 2 suggest that capuchins, like other primates, fail to successfully use landmark cues in dynamic spatial tasks. However, there remains an alternative explanation for these results. Some research suggests that the qualities of a landmark itself (Gouteux et al. 2001a; Okamoto-Barth and

Call 2008) can affect its use in spatial representations. Okamoto-Barth and Call (2008), for example, found that 3-year-old children did not use some kinds of featural landmark information, such as cup color, to relocate rewards in the occluded rotational displacement task. However, when the researchers made the landmark “more salient” by placing a sticker on the cup where the reward had just been hidden, this age group was capable of using this more salient landmark information to locate a rotationally displaced reward. Along similar lines, Gouteux et al. (2001a, b) found that rhesus macaques tested in a reorientation task could use large two-dimensional landmark cues ($\sim 50 \text{ cm}^2$) placed in the corners of the reorientation arena, but not smaller landmark cues ($\sim 20 \text{ cm}^2$). Both of these studies show that properties of the landmark cue can increase its salience and integration into spatial representations.

To explore this possibility, Experiment 3 presented the monkeys with the same occluded rotational displacement task but used what we thought to be a more salient landmark: a token placed next to the hiding location. It is worth noting that the positive result obtained by Potì (2000) used a similar type of landmark. To maximize subjects' probability of success, we also made other changes to our experimental design. First, we started testing with occluded rotations instead of visible ones, so that from the beginning, there were fewer competing cues to influence any strategy the subjects developed to solve the task. Secondly, we stabilized landmark qualities by only using one type of token in all trials, which differs from our previous experiments in which the color of the relevant cup changed among trials. This means that subjects only had to track the presence and location of the landmark, not any of its specific featural properties (e.g., color).

Experiment 3

Methods

Subjects

The same five adult capuchins (3 males and 2 females) that participated in Experiment 2 served as subjects in Experiment 3. Testing began 45 days after the completion of Experiment 2, and all testing was completed within a month. Subjects experienced between 1 and 3 testing sessions per week.

Apparatus, design, procedure, and data analysis

The apparatus for Experiment 3 differed from that used in the previous two experiments in two ways: (1) only the

blue pair of cups was used as hiding locations, and (2) a bright orange cylindrical landmark (10 cm tall \times 5 cm diameter) was placed next to one of the hiding locations. The landmark was always attached to the panel, adjacent to the outer edge of one of the hiding location cups. As in Experiment 2, the occluder and screens were used to block visual access to the rotation of the apparatus.

To initiate the experimental procedure, the experimenter took the landmark and placed it next to the location where the food reward would be hidden. Then, while the subject was attending, the experimenter placed the food reward on the panel and initiated the test sequence. Location of the food reward was counterbalanced for side. Subjects completed five sessions of 18 trials each.

Data were first recorded during the experiment and were checked later by an experimenter naive to the study; agreement between the two sets of data was perfect, $\kappa = 1.0$. Statistical analysis was the same as in Experiment 2, and again, our GEE regression contained one independent variable, rotation, recoded into two dummy variables (labeled 180 and 360; zero rotation = reference category).

Results

All five subjects completed all sessions, for a total of 90 trials per subject. The choice patterns of all subjects differed significantly from chance for each rotation condition (Fig. 4). However, as in Experiment 2, we observed that subjects made more errors than expected by chance in the 180° condition ($M = 17\%$ correct, $p = 0.043$ or less per test), in stark contrast to their positive performance on the zero and 360° conditions ($M = 90\%$ correct, $p = 0.016$ or less per test). The GEE procedure confirmed that the 180° condition had a significant negative effect on the odds of observing a correct choice on the task ($B = -3.836$, Wald $X^2 = 27.363$, $df = 1$, $p < 0.001$), but the effect of the 360° condition was nonsignificant ($B = -0.076$, Wald $X^2 = 0.097$, $df = 1$, $p = 0.756$).

Discussion

As in Experiment 2, our subjects' performance on the 180° rotation was the true indicator of whether they could use the token landmark in Experiment 3 to relocate the hidden reward. Given that subjects reliably chose the incorrect location on the 180° condition, we can conclude that the capuchins did not use the token landmark as a cue to the location of the reward, and that switching to a new “easier” landmark type did not change the capacity of the capuchins to be able to solve this spatial problem. In this way, our subjects performed poorly even when given access to a landmark similar to that used in Potì (2000).

There are two final possibilities that could explain the lack of landmark use by our capuchins in this study. One of these possibilities is that capuchins do not spontaneously use landmark cues to solve an occluded rotation task, but that subjects can learn to use such cues when they have sufficient opportunity to learn the association between the cue and the reward. This could explain why Potì (2000) obtained positive results, whereas the results of Experiment 3 were negative. Indeed, Potì (2000) also observed a learning trend across experimental sessions, suggesting that some degree of learning was needed. A second possibility is that the capuchins were simply not motivated to solve the 180° condition because they could easily receive rewards on the zero and 360° trials, which represent the majority of trials. We decided to explore these possibilities by conducting a final Experiment 4, in which we provided additional time for the capuchins to learn to use the landmark. If the capuchins showed some evidence of learning in this fourth experiment, then we can conclude that capuchins can use landmark cues under some circumstances and that they remained motivated throughout the experiment to try and solve the 180° trials.

Experiment 4

Methods

Subjects

One adult male (FL) no longer choose to participate in the study, leaving four adult capuchins (2 males and 2 females) to complete Experiment 4. Testing started immediately after Experiment 3 and was conducted over 2.5 months; as before, individuals were tested 1–3 times a week.

Apparatus, design, procedure, and data analysis

The goal of Experiment 4 was to see whether capuchins could learn to use a token landmark in our rotational displacement task. To explore this, we investigated two potential sources of learning. First, we gave each individual capuchin 10 more sessions to learn relevant cues. This allowed us to see whether more training trials alone could increase subjects' performance. However, we also considered that our subjects had never seen the token cue used in a visible rotation, and so they might have had limited understanding of how it functioned during the rotation. To control for this possibility, we split the subjects into two groups: *the visible group* (one female HG and one male, NN), which worked through a block of five sessions in which the rotation was visible followed by a second block of five sessions in which the rotation was again occluded,

and *the non-visible group* (labeled N, one female JM and one male AG) in which subjects worked through all 10 sessions without seeing the rotation.

If the capuchins had difficulty solving Experiment 3 because they had never seen the working apparatus with the token landmark, then we would expect the visible group subjects, but not non-visible group subjects, to solve the problem once the rotation was again occluded. However, if subjects simply needed more trials to learn to associate the landmark with the reward, then both groups should have been able to solve the landmark problem by the end of Experiment 4. If neither group could use the landmark, this would be further evidence that landmark use in such dynamic spatial tasks is particularly difficult for primates.

We considered the first five sessions of the 10 sessions run for Experiment 4 to be an additional round of training that differed between the visible and non-visible groups. In contrast, we considered the last five trials critical test trials in which subjects in both conditions experienced the same experimental test, which was also directly comparable to the trials of Experiment 3. Given this, we concentrated our statistical analysis on these last five trials.

Date recorded at the time of the experiment and later coded by a second experimenter from video had a high level of agreement, $\kappa = 1.0$. To test our hypotheses, we used a GEE binary logistic regression analysis with repeated measures to compare performance in the 180° condition across Experiment 3 and the last five sessions of Experiment 4. The first five sessions of Experiment 4 were not included in this analysis because any significant effects they generated would not have been relevant to our experimental questions. We examined the effects of two categorical variables on the probability of a correct choice: group membership (dummy variable G , non-visible group = 1, visible group = 0, reference category) and experiment (dummy variable E , Exp. 4 = 1, Exp. 3 = 0, reference group). We also included a $G * E$ interaction term in our model.

Results

All 10 sessions of 18 trials each were successfully completed for each of our four subjects, giving a total of 180 trials per individual. In the first block of five sessions, the visible group performed above chance in all three rotation conditions ($M = 94\%$ correct, all $p < 0.001$ for each test). In contrast, the non-visible group performed above chance in the zero and 360° conditions ($M = 88\%$, all $p < 0.001$ for each test), but were below chance in the 180° condition (AG: 23% correct, $p = 0.005$; JM: 33% correct, marginally significantly below chance, $p = 0.099$). Given our previous results, these findings were much as expected.

Results from the second block of testing were quite different. Again, all individuals succeeded at levels above chance in the zero and 360° conditions ($M = 93\%$ correct, all $p < 0.001$ for each test). However, in contrast to results from the first block, those in the visible group performed at levels below chance on the 180° condition (HG: 23% correct, $p = 0.005$; NN: 3% correct, $p < 0.001$), while those in the non-visible group performed at chance levels (AG: 37% correct, $p = 0.20$; JM: 53% correct, $p = 0.856$).

Binomial analyses and visual inspection of the data (Fig. 5) suggested that any significant effects for group (visible, non-visible) or experiment (Experiments 3 and 4) would be driven solely by the increase in performance in a single cell: the non-visible group in Experiment 4. As such, the GEE analysis with three factors (group, experiment and $G * E$) would likely be problematic in that our factors would be highly correlated. In this case, the statistics associated with the various parameters can be unreliable. The GEE analysis revealed a nonsignificant effect of group (G : $B = -0.116$, Wald $X^2 = 0.040$, $df = 1$, $p = 0.841$), but a significant effect of experiment (E : $B = -0.378$, Wald $X^2 = 38.466$, $df = 1$, $p < 0.001$). The B -coefficient associated with the effect of experiment thus indicates that Experiment 4 had a negative impact on the odds of obtaining a correct response. Since this is obviously not the case, we checked the correlation of this factor with the other factors and found a very high degree of correlation between group and experiment ($r = -0.956$), and as such, the statistics for the effect of experiment may be unreliable. More importantly, we observed a significant interaction term ($G * E$: $B = 1.787$, Wald $X^2 = 380.574$, $df = 1$, $p < 0.001$), indicating that membership in Experiment 4, non-visible group increased the odds of observing a correct choice. The correlations of this parameter with the other parameters were lower: Experiment and $G * E$ ($r = -0.665$), Group and $G * E$ ($r = 0.856$).

Discussion

The results of Experiment 4 must be approached with caution. Given our small sample size, teasing apart the effects of individual performance from those of treatments is difficult. However, if our findings are representative, they would support an interpretation that capuchins can learn to use landmarks in the occluded rotational displacement task. We found a significant effect of experiment on performance in the 180° condition, with individuals performing better in the last five sessions of Experiment 4 than in the five sessions of Experiment 3. This change in behavior also suggests that subjects remained motivated to try to perform better on this study over time, and as such, that motivation was likely not the

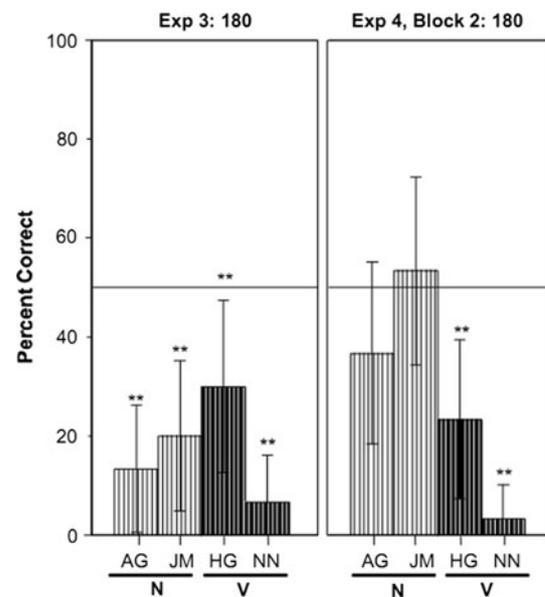


Fig. 5 Results per individual of Experiment 3 contrasted with the last five sessions of Experiment 4 for the 180° condition only. Light bars non-visible group members (N), dark bars visible group members (V; error bars 95% CI)

reason capuchins continued to do poorly in previous experiments.

The learning we observed was modest—monkeys' performance switched from significantly below chance to chance performance. Although we did not observe above chance performance, we still believe this our results provide evidence of learning on this task. Prior to Experiment 4, capuchins did not discriminate between the 180° condition and the zero or 360° conditions as evidenced by the fact that they applied the same strategy—a positional strategy—to all rotation conditions. However, in Experiment 4, some capuchins modulated their behavior on the 180° condition and only this condition. This finding suggests that capuchins came to recognize that the 180° condition was a unique situation that required a different strategy. Since landmark cues were the only indication that the 180° condition differed from the zero and 360° conditions, capuchins must have learned to use landmark information specifically to discriminate between conditions. In the end, our capuchin subjects learned that landmarks were in some way relevant to solving the task, but their modest improvement indicates that they still did not fully grasp the associative quality of the landmark, even after quite a few trials.

Improvement of scores resulted entirely from performance by individuals in the non-visible group, as indicated by the significant interaction effect between group and treatment across experiments; by the second block of five sessions in Experiment 4, individuals in the non-visible group performed better than those in the visible group.

Thus, capuchins' tendency to learn to use landmarks seems to require two factors: adequate time to learn plus exposure to the occluded rotation. The importance of occluding the rotation was surprising, as we expected that a period of visual access would actually increase learning on the occluded rotational displacement task. Overshadowing is one explanation of this outcome, that is, visual access to the rotation might have allowed the capuchins to track the movement of the array visually thereby eliminating any need for subjects to attend to other cues, such as the presence of the token landmark. The introduction of additional cues made the encoding of landmark information less likely.

It is of note that our capuchins were not as successful as those in the Potì (2000) study. Some learning occurred in our study, but only some individuals' performance increased to chance. In contrast, the subjects in Potì's study solved 180° occluded rotations at levels significantly above chance. There is a chance that Potì's design differed slightly from ours in ways that might have scaffolded the learning process for capuchins more effectively. Potì's (2000) sessions fell closer together in time, and this design used more rotation conditions, including 90° and 270°. Differences in natural ability or previous testing history among individuals might also help to explain the differences in results, but as both studies relied on a small number of primates, it is difficult to assess this possibility. However, the current study supports the interpretation that capuchins are much like other primates in that they have a relatively limited capacity to spontaneously utilize landmark information in select dynamic spatial tasks.

General discussion

The series of studies in this paper demonstrated that capuchins do not easily use landmarks to solve the occluded rotational displacement task. Across all four of our studies, which involved different types of landmarks and varied spatial cues, we observed little spontaneous successful use of landmarks. Instead, we found that capuchins were best able to use landmarks when they had received many trials over which to learn the nature of these cues and when subjects had no other alternative cues to indicate the location of the reward. It should be noted that the present experiments were conducted with relatively small samples sizes which may not be the representative of capuchins or primates in general. However, this work aligns with other published accounts of primates' non-preference for landmarks in small-scale dynamic spatial tasks (Gouteux et al. 2001a; Haun et al. 2006; Okamoto-Barth and Call 2008), and strongly contrasts with the ability of older children and adult humans who readily use landmark information in

such tasks (Gouteux et al. 2001b; Haun et al. 2006; Okamoto-Barth and Call 2008).

Our study did not identify whether some landmark cues are easier for capuchins, and perhaps other primates, to use in the rotational displacement task. Capuchins failed to spontaneously use either the landmark of cup color or the token to solve this displacement task. Moreover, although Experiment 4 showed that capuchins could eventually learn to use the token landmark as an indicator of the reward location, this involved a long training period. Without a similar training period, it is unclear whether capuchins would also be able to learn to use cup color in this way. Future work could therefore help to determine more specifically the types of landmarks or featural information that primates might encode in spatial tasks.

When the rotation was occluded and subjects could not track the hiding location visually, we found that capuchins spontaneously used position information. This allowed the capuchins to solve the rotational displacement problem when the reward returned to where they had last seen it, but led to errors when it had moved. This is similar to the results of Haun et al. (2006) and Okamoto-Barth and Call (2008), who found that apes and pre-linguistic children respond preferentially to position information rather than landmark cues when solving occluded object-tracking tasks. That capuchins, apes, and pre-linguistic toddlers use position-based strategies when solving dynamic spatial tasks suggests that this is a phylogenetically ancient and widespread default strategy among primates.

The present work is in agreement with the argument made by Haun et al. (2006) and Okamoto-Barth and Call (2008) that spontaneous, and perhaps preferential, use of landmarks to solve some kinds of spatial tasks is related to the capacity to use language. More specifically, it is consonant with the hypothesis that the likelihood of using landmark information in spatial tasks increases with linguistic ability. According to this hypothesis, primates and non-linguistic toddlers are not incapable of using landmark information; instead, they are less likely to use landmark information spontaneously in solving spatial tasks, perhaps because learning to use featural/landmark information is more difficult than learning to use other cues. This newer more nuanced version of the language hypothesis (Haun et al. 2006; Okamoto-Barth and Call 2008) replaces a more conservative version in which the representation of space was thought to be modular and insulated from featural or landmark information (Cheng 1986; Hermer and Spelke 1994, 1996; Hermer 1997; Hermer-Vazquez et al. 2001; Wang et al. 1999).

Although the results we observed are consistent with this newer language hypothesis, more investigation will be necessary to establish that language affects the encoding of landmarks when forming spatial representations. Other

areas of cognitive developmental research may provide answers. For example, some researchers have hypothesized that the process of becoming linguistic may train children to attend more to features in order to contrast the meaning of different object labels (Booth and Waxman 2008; Jones et al. 1991; Landau et al. 1988; Markson et al. 2008; Smith et al. 1996). Such focused featural attention has been shown experimentally in children; when learning words for object categories based on shape, even when these categories are artificial, individuals are later better at extending labels to novel objects (usually on the basis of shape), likely because children have better learned to attend to the relevant discriminating features (Smith et al. 2002). Hopefully, further integration of such ideas with studies of the ability of non-linguistic populations to recognize objects in spatial tasks will generate fruitful research.

One possible critique of the present study is that the rotational displacement task is unnatural and therefore more difficult than similar spatial tasks. The strange behavior observed on rotational displacements may be due to specific difficulties associated with this task. Indeed, some studies have documented that primates (Barth and Call 2006) and humans of all ages (Huttenlocher and Presson 1979; Presson 1982; Wraga et al. 2000) have difficulty solving rotational displacements relative to other object-tracking tasks. However, other research has shown that greater difficulty with rotational displacements is not always the case, especially among mature individuals (primates: Albiach-Serrano et al. 2010; humans: Presson 1982; Wraga et al. 2000). Further complicating the matter is the fact that the difficulty adult humans experience on rotational displacements is easily modulated by changes in the framing of the task or the stimuli used (e.g., Presson 1982; Wraga et al. 2000). This pattern of findings strongly suggests that animals may use a variety of strategies to solve the rotational displacement task, each perhaps with its own level of difficulty. Since we did not investigate the precise spatial representations that capuchins used to solve our rotational displacement task and instead focused on how that spatial representation interacted with landmark information, we cannot know whether this species used (or attempted to use) more difficult strategies.

It is likely that the language hypothesis alone cannot explain our subjects' failure to use landmarks in this task. In Experiment 3, we used a landmark that could be encoded as present or absent, and its specific featural characters were not relevant to solving the task, yet we still observed difficulty or reluctance in using it as an associative cue to the reward location. Additionally, since it is well established that primates can differentiate among objects based on featural properties (e.g., Mishkin 1982), it is odd that primates cannot do so in certain kinds of spatial tasks. The full answer to why primate do not use landmarks in spatial

tasks may lie more in the realm of difficulty in understanding the relationship of the cue to the reward. Only future work will be able to assess the validity of these different possibilities.

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