

Rotational Displacement Skills in Rhesus Macaques (*Macaca mulatta*)

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Rotational displacement tasks, in which participants must track an object at a hiding location within an array while the array rotates, exhibit a puzzling developmental pattern in humans. Human children take an unusually long time to master this task and tend to solve rotational problems through the use of nongeometric features or landmarks as opposed to other kinds of spatial cues. We investigated whether these developmental characteristics are unique to humans by testing rotational displacement skills in a monkey species, the rhesus macaque (*Macaca mulatta*), using a looking-time method. Monkeys first saw food hidden in two differently colored boxes within an array. The array was then rotated 180° and the boxes reopened to reveal the food in an expected or unexpected location. Our first two experiments explored the developmental time-course of performance on this rotational displacement task. We found that adult macaques looked longer at the unexpected event, but such performance was not mirrored in younger-aged macaques. In a third study, we systematically varied featural information and visible access to the array to investigate which strategies adult macaques used in solving rotational displacements. Our results show that adult macaques need both sets of information to solve the task. Taken together, these results suggest both similarities and differences in mechanisms by which human and nonhuman primates develop this spatial skill.

Keywords: object-tracking, rotational displacement, rhesus macaques

All primates, including humans, successfully track objects through movements, disappearances, and different angles of approach. How do different species solve these complex spatial problems? Researchers have gained much insight into this problem through a suite of experimental tasks known as object-tracking tasks. The advantage of object-tracking tasks is that they allow researchers to simplify complex spatial problems into their essential features: a desired object, its visibility, and its motions. The use of object-tracking tasks has a long history, beginning with the development of object permanence tasks by Piaget (1954) over a half-century ago. Since that time, new methods have raised additional questions about the nature of object-tracking abilities, both in their evolutionary and developmental origins and in their un-

derlying cognitive mechanisms. Here, we focus on one object-tracking task—the rotational displacement task—that has played a key role in the generation of new ideas about object cognition (Barth & Call, 2006; Okamoto-Barth & Call, 2008).

Rotational displacement tasks require the participant to track an object hidden within an array while the substrate supporting that array is rotated. Although the rotational displacement task at first glance appears to involve a simple spatial problem, human children find this task relatively difficult (Barth & Call, 2006; Okamoto-Barth & Call, 2008). For example, while 30-month-old children perform well on most other object-tracking tasks (Acredolo, 1978; Bremner, Knowles, & Andreasen, 1994; Call, 2001; Collier-Baker, Davis, Nielsen, & Suddendorf, 2006; Lasky, Romano, & Wenters, 1980; Piaget, 1954), they are still unable to track a hidden object through 180° rotation, performing below chance when the hidden object is moved to a new location (Barth & Call, 2006). Three-year-old children can successfully track a hidden object across an 180° rotation, but only if obvious landmark¹ information is present in the array (Bremner, 1978; Okamoto-Barth & Call, 2008). What is interesting is that children of this age perform equally well on the rotation task when the rotation itself is hidden, bringing into question whether children are actually tracking the hidden movement of the object across the rotation or merely associating the location of the object with a landmark. By age 5, children become fully proficient on rotational displacement tasks, correctly locating an object that has been

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¹ In this study, we use the terms *features* and *landmarks* interchangeably to denote any nongeometric perceptual cues in the display that indicate where the object was hidden; we distinguish these cues from geometrical landmarks such the overall shape or an edge of a testing apparatus (e.g., Huttenlocher, Newcombe, & Sandberg, 1994).

hidden and then rotated to a new position. Nevertheless, even at age 5, children's performance is bolstered by the presence of featural information (Lasky et al., 1980; Okamoto-Barth & Call, 2008).

Children's performance on the rotational displacement task illustrates two unique features of this spatial skill, and each raises interesting questions. First, children take a very long time to develop rotational displacement skills. Indeed, this capacity appears to be one of the latest emerging object-tracking skills, emerging years later than successful performance on problems involving invisible displacement (Call, 2001; Collier-Baker et al., 2006; Piaget, 1954) or transpositions (i.e., when an object is hidden at one location in an array and is later switched with another hiding location (see Sophian, 1984). This late development of rotational displacement performance is a bit puzzling, as in many respects this task is similar to other earlier developing object-tracking tasks. Second, when young children do solve this task, they tend to rely on landmark information (Okamoto-Barth and Call, 2008). This pattern of attending to landmark information is also seen in other related object-tracking tasks, in which children tend to rely on featural cues to solve a variety of spatial problems (Gouteux, Vauclair, & Thinus-Blanc, 2001; Haun, Call, Janzen, & Levinson, 2006). Of note, these same researchers have argued that children's focus on landmarks in these spatial tasks could be at least in part related to the development of language skills (see Hermer-Vazquez, Moffet, & Munkholm, 2001; Hermer & Spelke, 1994, 1996; Learmonth, Nadel, & Newcombe, 2002; Wang, Hermer, & Spelke, 1999, for additional examples), forcing the question whether and to what degree language plays a role in the ability to use landmarks in select spatial tasks, such as rotational displacement. Here, we attempt to gain more insight into these two aspects of rotational displacement skills by exploring the mechanisms underlying rotational displacement skills from a comparative perspective.

Our work builds on previous comparative work in nonhuman primates (e.g., Barth & Call, 2006; Beran, Beran, & Menzel, 2005; Call, 2003; Okamoto-Barth & Call, 2008) that has begun to address whether the unusual aspects of human rotational displacement capacities have evolutionary continuity. Although these previous studies have provided important insights into the mechanisms underlying rotational displacement performance across primates, there are still several open questions about the speed of the development of this capacity in primates as well as the kinds of strategies other primates tend to rely on to solve rotational displacement problems.

The first open question about nonhuman primates' rotational displacement performance concerns whether adult primates perform this task using the same strategies as humans. To date, several studies have shown that adult nonhuman primates can succeed on a rotational displacement problem (Barth & Call, 2006; Beran et al., 2005; Call, 2003; Okamoto-Barth & Call, 2008). Comparatively less work to date has explored the specific strategies that nonhuman primates favor when solving this task. In one important study, Okamoto-Barth and Call (2008) compared the strategies that great apes and children used when tested on a standard rotational displacement problem. First, they found that both great apes and children were able to successfully solve the rotational displacement task when they were given visual information about the rotation. Second, and perhaps more important,

Okamoto-Barth and Call found that the great apes did not rely as heavily on landmarks as children did when solving this task. When tested with invisible displacement problems, the apes in this study did not spontaneously use landmark information, performing below chance during 180° rotations when the rotation was occluded. Although apes' performance on this task does not exclude that landmark information was encoded to some extent, these results suggest that apes rely more heavily on visual information about the rotation than they do on the landmark information available inside the array. The apes' relative weighting of the visual movement information over featural information is mirrored in the performance observed by Haun et al. (2006) on a slightly different spatial task. Haun et al. presented apes, prelinguistic infants, and 3-year-old children with a task in which food was hidden in one of three distinct containers that were then moved behind a screen. Haun et al. found that different populations used different strategies to solve this task. Although 3-year-old children favored a feature-based strategy (searching the same object under which the food was originally hidden), the great apes and human infants preferred a more spatially based strategy, searching the original place in which the food was hidden. Like Okamoto-Barth and Call (2008), Haun et al.'s results suggest that apes do not spontaneously favor featural information when trying to successfully relocate a hidden item after it had been moved to a new location. Indeed, Haun et al.'s results suggest that adult apes do not tend to favor the same strategies that older children use to solve this task.

Although the apes tested by Okamoto-Barth and Call's (2008) tended to use visual information about the rotation of the array more readily than they used featural information, it is worth noting there is evidence that nonhuman primates can use landmark cues, at least for some other kinds of spatial tasks (e.g., Deipolyi, Santos, & Hauser, 2001; Dolins, 2009; Garber & Brown, 2006; Gouteux, Thinus-Blanc, & Vauclair, 2001; Herman & Wallen, 2007; Poti, 2000; Poti, Bartolommei, & Saporiti, 2005; Poti et al., 2010; MacDonald, Spetch, Kelly, & Cheng, 2004; Marsh, Spetch, & MacDonald, 2011; Sutton, Olthof, & Roberts, 2000). Nonhuman primates' ability to use featural information on other spatial tasks raises the question why apes do not seem to spontaneously favor this strategy when solving rotational displacement problems to the same extent as older human children (Okamoto-Barth & Call, 2008).

The second open question about nonhuman primates' rotational displacement performance concerns the developmental trajectory of this capacity. To date, there has been little investigation into the developmental of rotational displacement skills outside the human species. Specifically, there are no comparative developmental data that speak to how primates perform on the rotational displacement task across different ages. However, a few studies have investigated developmental trends in nonhuman primates' performance on other object-tracking tasks (Antinucci, 1990; Diamond, 1990a, 1990b; Doré & Goulet, 1998). The studies typically suggest that nonhuman primates tend to achieve developmental milestones in the same sequence but at an earlier age than humans (see Gómez, 2005). For example, growing rhesus macaques (*Macaca mulatta*) and capuchin monkeys (*Cebus sp.*) achieve the most basic levels of object permanence, retrieving a hidden object, at 100 and 125 days, respectively (Antinucci, 1990), while developing humans achieve this ability at around eight months (Piaget, 1954). From this perspective, we might expect nonhuman primates to succeed

on rotational displacement tasks more quickly than their human counterparts. Alternatively, there is reason to suspect that nonhuman primates might develop the ability to solve rotational displacement tasks more slowly than humans. Given the difficulty of rotational displacement tests for younger human children (e.g., Bremner, 1978; Okamoto-Barth & Call, 2008), one could hypothesize that nonhuman primates may require more developmental time to succeed on this task. There is evidence that even some adult primates have great difficulty with more advanced object-tracking tasks, such as the invisible displacement task (de Blois, Novak, & Bond, 1998, 1999; Natale, Antinucci, Spinozzi, & Poti, 1986). As such, one might also expect that younger populations of nonhuman primates might do poorly on this task for longer periods than humans do.

Furthermore, several studies have demonstrated that although adult apes can often successfully complete rotational displacement problems (Beran et al., 2005; Call, 2003; Okamoto-Barth & Call, 2008; but see Barth & Call, 2006), these subjects tend to perform worse on rotational displacements as compared to other advanced object-tracking tasks (Barth & Call, 2006; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; but see Albiach-Serrano, Call, & Barth, 2010). This pattern of performance across different advanced spatial tasks suggests that the relative difficulty of rotational displacements compared to other object-tracking tasks may be roughly similar across humans and other apes, and, for this reason, we might expect a late developmental emergence of rotational displacement ability in primates as well.

In these ways, there remain open questions about the extent to which nonhumans share human-like mechanisms for processing rotational displacement problems. Although there is some evidence that apes appear to struggle with this task relative to other spatial tasks in the same way as human children, there is also evidence that they rely less on landmark information than one might expect based on children's performance. In addition, no work to date has investigated whether nonhuman primates share other human-like characteristics of rotational displacement task performance, such as the long developmental time course that children regularly exhibit. Here, we attempt to gain more clarity on the nature of rotational displacement skills by addressing these questions. Specifically, our experiments extend this task to a previously untested nonhuman primate population—rhesus monkeys. Much evidence has shown that monkeys are likely less capable of solving object-tracking tasks, such as invisible displacement, than apes (de Blois et al., 1998, 1999; Natale et al., 1986; but see Fillion, Washburn, & Gulledge, 1996; Mendes & Huber, 2004; Neiworth et al., 2003). Therefore, exploring rotational displacement performance in a monkey species should provide an even stricter test of the difficulty of this spatial problem relative to other tracking tasks. Given children's difficulty with rotational displacement problems, we might expect that rhesus monkeys would perform poorly when tested on a version of the rotational displacement task. Experiment 1 tests this question directly by testing for rotational displacement skills in a macaque.

In addition, the present study aimed to overcome some of the limitations of previous comparative studies of rotational displacement by directly testing both of the two unusual aspects of children's performance on rotational displacement tests—its long developmental trajectory and its reliance on featural information—in a nonhuman species. Experiment 2 investigated the developmental

time-course of macaques' rotational displacement skills. As reviewed above, several studies have explored the nature of rotational displacement skills in adult apes, but no work has investigated the development of performance on rotational displacement tasks in any nonhuman species. In the current studies, we examined rotational displacement skills not only in adult macaques, but also in infant and juveniles. We succeeded in this developmental approach by testing a large free-ranging population of macaques at the Cayo Santiago field site. Cayo Santiago is unique in that it maintains a large population of macaques into which a new cohort of infant macaques is born every year. In this way, we could use the multiple age classes available in Cayo Santiago to perform a developmental analysis of macaque rotational displacement skills. Finally, Experiment 3 directly tested what strategies macaques use to solve rotational displacements, by investigating visual tracking of the array and featural information within the array as potential cues. Thus far, experiments exploring the use of landmarks and features by primates in object-tracking tasks have tested only a small subset of species. To truly understand whether primates do not spontaneously use featural or landmark information to reliably solve rotational displacements, it is better to test a wider set of primate species on this task. In this way, our three experiments investigated whether macaques shared both of the unusual features of children's performance on rotational displacement tests.

To explore the rotational displacement abilities in our unique study population at Cayo Santiago, we developed a new method for testing rotational displacement skills. Because monkeys in the Cayo Santiago population were free-ranging, they could not be tested on the rotational displacement test that is typically used with captive primate populations. More specifically, we were unable to train animals on the kind of rotational displacement task that has typically been used, which requires both lengthy training and multiple sessions of testing (e.g., Okamoto-Barth & Call, 2008). In addition, the rules of this field site limit the extent to which individual animals can be provisioned with food rewards, which also prevented us from running a standard task. To deal with these methodological issues, in Experiment 1 we developed an expectancy-violation looking-time version of the rotational displacement task. Looking-time studies work from the premise that individuals look longer at unexpected or novel outcomes. This approach has been useful to investigate cognitive abilities in human infants (Baillargeon, 1986, 1987; Baillargeon & DeVos, 1991; Spelke, Kestenbaum, Simons, & Wein, 1995; Xu & Carey, 1996) as well as in nonhuman primates (Cherries, Newman, Santos, & Scholl, 2006; Munakata, Santos, Spelke, Hauser, & O'Reilly, 2001; Santos & Hauser, 2002; Santos, Miller, & Hauser, 2003), but to date has not been applied to examine rotational displacement skills. In our study, monkeys were allowed to watch as a human experimenter placed a desirable food item into one of two hiding locations that sat opposite each other on a substrate that could rotate. The experimenter then rotated the hiding locations 180° from their original location, and opened the hiding locations to reveal the food in either the correct or incorrect location. We predicted that if adult macaques could successfully track objects across 180° rotations, they should look longer when a piece of rotated food was revealed in the wrong location than when it was revealed in the correct location.

Experiment 1

Methods

Subjects. We finished Experiment 1 with a sample size of 50 adult rhesus macaques aged 4 years and older ($M = 8.38$ years, $SD = 3.28$).² Additional subjects ($n = 144$) were approached but did not complete testing due to subject inattention, subject approach toward the apparatus, or secondary interference from other monkeys. This number of incomplete sessions is typical for studies using similar methods in this population (e.g., Mahajan et al., 2011). The cameraperson, who was blind to testing condition, made all decisions to abort a session. An additional nine sessions were discarded after testing completion because it was learned that the monkey tested had served as a subject in this experiment previously. One final session was discarded because the individual monkey could not be positively identified (and therefore his age could not be determined). Later, during coding of the sessions, 11 additional sessions were discarded due to the poor quality of the videos (see Data Analysis below).

Our macaque subjects were from the Cayo Santiago colony, a free-ranging population living on an island off the coast of Puerto Rico. The macaques in this population live in naturally formed groups and engage in many natural social interactions (Rawlins & Kessler, 1986). Although monkeys forage for foods occurring naturally on the island, about 50% of their diet consists of monkey chow. The rhesus macaques in this population are identifiable through unique tattoos and ear notches. Records of subjects' birth dates and ages are maintained by the University of Puerto Rico.

Apparatus. The apparatus (Figure 1) consisted of a stage (30 × 30 cm) with high walls (20 cm) and a front screen (30 cm). The screen could be opened and closed to reveal the contents of the stage.

The stage had a rotating table on top of which were two differently colored boxes (red and green), placed opposite each other. Each box was fixed to its position on the rotating table, and had a front and back door that could be opened to reveal its contents. In addition, each box actually had a false back, so that the box was not as deep on the inside as it appeared on the outside. This allowed an experimenter to hide an item behind the false back of the box and to control the perceived outcome of the test event.

Several identical plastic strawberries were used as stimuli for the subjects to track. The Cayo macaques are not specifically familiar with strawberries, but they consume similar berries (e.g., small, red berries) that grow naturally on the island. In addition, previous experimental work at Cayo suggests that the monkeys are visually attracted to and are keen to retrieve both real and artificial brightly colored fruits (Flombaum, Junge, & Hauser, 2005; Flombaum, Kundey, Santos, & Scholl, 2004; Flombaum & Santos, 2005; Phillips & Santos, 2007; Phillips, Shankar, & Santos, 2010; Santos, Hauser, & Spelke, 2001; Santos, Sulkowski, Spaepen, & Hauser, 2002; Santos & Hauser, 2002; Santos, 2004; Santos, Nissen & Ferrugia, 2006).

Design and procedure. We developed an expectancy-violation looking-time version of the rotational displacement task. Our between-subjects design followed that of previous looking-time studies at Cayo Santiago (e.g., Cheries et al., 2006; Munakata et al., 2001; Santos & Hauser, 2002; Santos et al., 2003).

Two experimenters ran each session. A presenter handled the stage and the stimuli, while a cameraperson recorded the subject's looking using a digital video camera. To begin a session, the presenter chose a subject opportunistically, focusing on monkeys who were seated, alone, and attentive. The presenter then set the apparatus between 2 and 3 m from the subject, and randomly selected the condition to be run. The cameraperson stood about 1 m behind the presenter and immediately began recording the session, capturing a tight portrait shot of the subject's face. Recording only stopped when the session was aborted or completed. The cameraperson was responsible for aborting a session; she could do so without bias because she remained blind to condition. The cameraperson could easily remain blind to the testing condition because she could not see the condition that was being performed from her position behind the display.

Each session consisted of one *familiarization* trial, in which the subject was familiarized with the apparatus, followed by one *test* trial, in which the subject observed an action followed by a critical test outcome. The familiarization trial began when the presenter dropped the screen in front of the stage to reveal the table and the two boxes. She then opened the two boxes simultaneously, revealing a strawberry that had been hidden previously in one of the two boxes (see Figure 1, Slide 1). The presenter then said "now," at which time the cameraperson recorded the monkey's looking for the next 10 s; the trial ended when the presenter said "stop." The presenter then shut the boxes and lifted the front screen to cover the apparatus. While the screen was shut, the presenter surreptitiously baited the boxes based on the test conditions described below.

Monkeys were then presented with a test trial. With a between-subjects design, each subject saw either an *expected test event* or an *unexpected test event* for their critical test trial. Before the testing event, while the screen in front of the apparatus was still closed, the presenter baited the false back of one box with one strawberry so that she could artificially determine the location the strawberry would appear to be in after a rotation. This allowed for "expected" and "unexpected" outcomes. Next, to start a test event, the presenter lowered the screen and opened the front of the boxes, showing the subject that the boxes appeared to be empty (see Figure 1, Slides 2a–2d). She next took out a strawberry and placed it into one of the boxes as the subject watched. She then closed the boxes and began spinning the table, turning it 180°. The table was always rotated clockwise, in the same manner. To rotate the table, the presenter started by placing a hand on each box and pushing the left box (from her perspective) forward. As the right hand box approached the back of the apparatus, the experimenter used both hands on this box to push the rotation. As the other box (previously the left-hand box) approached reachable distance after passing the front of the apparatus, the presenter again put a hand on this box to guide the rotation. As the rotation was completed, the subject saw that the presenter had a hand on the back of each box. Once complete, the presenter opened the boxes to reveal the location of the strawberry, which, in reality, was the prebaited strawberry

² Unfortunately, the archived video files for 16 successful trials (14 for Experiment 1, two for Experiment 2) were lost in a hard drive failure. However, data from these files were coded before the clips were lost and thus we still included these trials in our analysis.

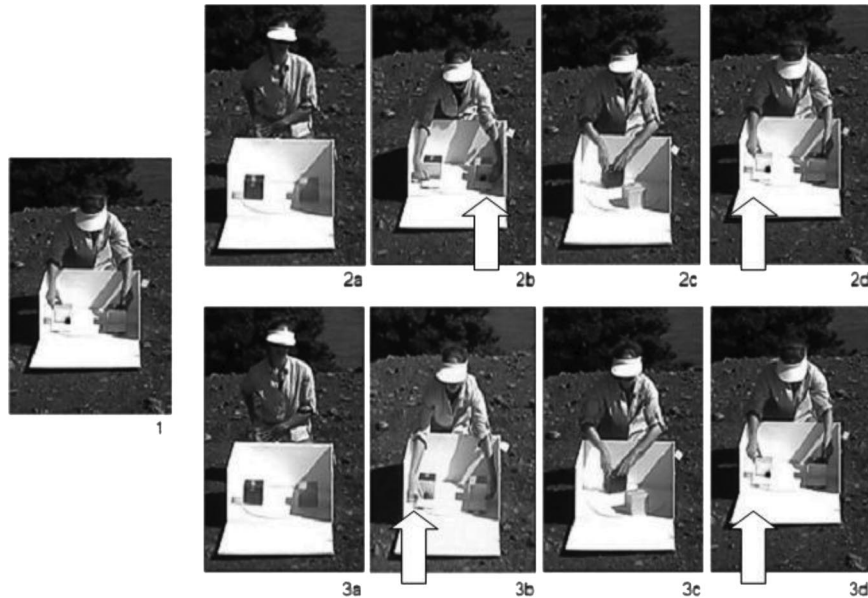


Figure 1. Experimental procedure used throughout Experiments 1–3. Subjects were exposed to two looking-time events. In the first familiarization event (Slide 1), subjects were shown a strawberry revealed in one of the two hiding locations. In the second test event, the strawberry was hidden in one of two hiding locations, then the array was rotated and the hiding locations reopened to reveal the final location of the strawberry. Subjects tested in the expected condition witnessed the strawberry revealed in the correct location (Slides 2a–2d). Subjects tested in the unexpected condition witnessed the strawberry revealed in the incorrect location (Slides 3a–3d).

hidden in the false back of one of the boxes. In the expected test event, the strawberry was revealed on the opposite side of where it had been originally placed (i.e., the correct location after the rotation). The unexpected test event was identical to the expected test event except the strawberry appeared to stay where it was originally placed (see Figure 1, Slides 3a–3d). After revealing the strawberry, the presenter called “now” to start the next looking-time event, which again lasted 10 s. If subjects form correct expectations about the location of the rotationally displaced strawberry, then subjects shown the unexpected test event should look longer than subjects shown the expected test event. Sessions were counterbalanced for side and color.

Data analysis. Video footage was digitized using MPEG Streamclip, Version 1.2 software (Cinque, 2008). All 10-s clips of looking time were then coded to determine how long subjects watched the event in frames (30 frames per 1 s) by an experimenter who was blind to condition. As in previous studies (e.g., Santos & Hauser, 2002), coders watched the videos frame-by-frame and determined “looking” as the direction in which the subject was looking when the experimenter said “now,” which had to be clearly audible on the recording. From that point, looking time was recorded whenever the subject appeared to be looking in that direction. At this stage, the coder (who was blind to condition) chose to discard an additional 11 completed sessions due to poor filming quality, that is, the video or audio resolution was not sufficient for accurate coding.³ A second blind coder coded the looking time of 20% of sessions to establish reliability ($r = .937$). Statistics were completed using the PASW 18 statistics package.

Results

We first explored macaques’ looking times during familiarization trials. We observed no difference in looking across familiarization trials for monkeys tested in the expected ($M = 143.70$ frames) and the unexpected conditions ($M = 156.52$ frames), $t(48) = 0.706$, $p = .483$. In contrast, we observed a significant difference in monkeys’ durations of looking times during the test events, $t(48) = -2.255$, $p = .029$, $d = 0.63$ (Figure 2) with monkeys tested in the unexpected condition looking longer at the test event ($M = 114.83$ frames) than monkeys tested in the expected condition ($M = 79.52$ frames).⁴

Discussion

Adult rhesus macaques looked significantly longer in the unexpected as compared to the expected conditions, suggesting that adult macaques form correct expectations about where the food should be located after the rotation. These results provided evidence that monkey species can successfully track objects in a

³ The majority of these sessions are discarded due to wind, which obscured the verbal cues of the presenter. This problem was difficult to detect at the time of filming.

⁴ We also ran the analysis without the video files that were lost in the hard drive error. Again, the differences between conditions in the familiarization trials were not significant (expected $M = 160.11$, unexpected $M = 166.94$), $t(34) = -0.337$, $p = .738$, but the results of the test trials were significant (expected $M = 76.44$, unexpected $M = 127.28$), $t(34) = 2.882$, $p = .007$.

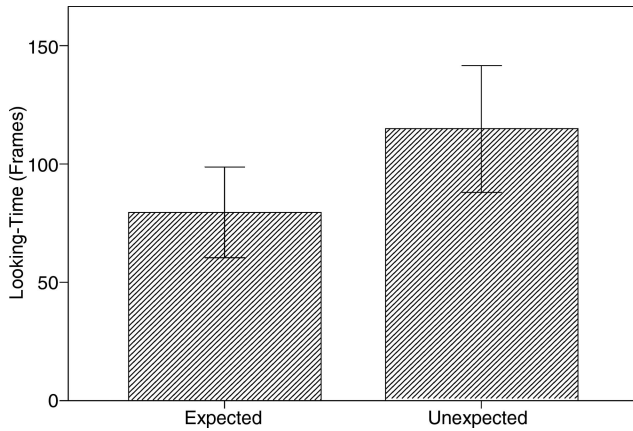


Figure 2. Subjects' duration of looking (in frames) across expected and unexpected test conditions (error bars = 95% confidence intervals) in Experiment 1.

rotational displacement task. By extension, this indicates that the capacity to solve rotational displacements, at least as a mental representation, is evidenced in at least one monkey species and is not only found among apes. In addition, the results of Experiment 1 validated our looking-time method for testing rotational displacement.

Having established that adult macaques can track objects across rotational displacements, Experiment 2 sought to explore the developmental origins of this capacity. Using the same looking-time procedure as in Experiment 1, Experiment 2 tested rotational displacement skills across the macaque life-course. Specifically, we compared adults' performance on this looking-time task to that of macaques at infancy, 1 year of age, 2 years of age, and 3 years of age. We predicted that, like human children, macaques may succeed on this task only after a long developmental time period.

Experiment 2

Methods

Subjects. We tested an additional 131 rhesus macaques from the same population, and used 19 sessions originally gathered at the same time as Experiment 1,⁵ for a total of 150 immature subjects. These monkeys were from four different age classes: infants ($n = 42$; $M = 1.75$ months, $SD = 0.59$), 1-year-olds ($n = 40$; $M = 1.78$ years, $SD = 0.15$), 2-year-olds ($n = 33$; $M = 2.73$ years, $SD = 0.19$), and 3-year-olds ($n = 35$; $M = 3.85$ years, $SD = 0.16$). Other monkeys ($n = 254$) were approached but did not complete testing due to subject inattention, approaching the apparatus, interference from other monkeys, or experimental error. The cameraperson who was blind to condition made the decision to drop any aborted session. An additional 28 sessions were discarded because subjects had already participated in this study, and 26 sessions were later discarded in the video-coding process (see below).

Apparatus, design, and procedure. We used the same apparatus, design, and procedure as in Experiment 1.

Special care was taken when approaching infant macaques as subjects. We did not test any individuals younger than 10 days

because these very young infants cling to their mothers and are significantly less interactive with the larger world. After 10 days, infants will leave their mother for short periods to explore. We tested such infants either while they were in their mother's lap or as they sat by themselves a short distance from their mother. The experiment was started when the infant was facing and attending to the experimenter, and we additionally discarded trials (blindly) in which the mother interfered with the infant in some fashion.

Data analysis. The data analysis procedure was the same as in Experiment 1. Twenty-six sessions were discarded in this process by a blind coder because the video or audio resolution was insufficient for accurate coding. Again, a second coder, who also was blind to condition, coded the looking time of 20% of clips to establish reliability, with a high degree of correlation ($r = .817$).

Results

A quick visual inspection of the data (Figure 3) suggested the possibility of three different developmental stages of performance in the task. Although infants appeared, on average, to be looking longer at the expected condition, the other four age classes (including the adult data from Experiment 1) tended to look longer at the unexpected condition. Additionally, adults appeared to have more marked differences between the two conditions compared to the four other age classes. To study these differences, we pooled age classes 1–3 years into a juvenile age-class group that was distinct from the infant and adult class. From this point, we first assessed whether there was any significant difference between the expected and unexpected conditions in the familiarization trials. We conducted a 2×3 (Condition [expected, unexpected] \times Age Classes [infant, juvenile, adult]) analysis of variance (ANOVA) on subjects' familiarization trial performance, and found no significant main effects for age class, $F(2, 194) = 2.150$, $p = .119$, partial $\eta^2 = 0.022$, or condition, $F(1, 194) = 0.070$, $p = .791$, partial $\eta^2 < 0.000$, nor a significant interaction effect, $F(2, 194) = 0.565$, $p = .569$, partial $\eta^2 = 0.006$. We then conducted the same 2×3 (Condition [expected, unexpected] \times Age Classes [infant, juvenile, adult]) ANOVA on subjects' test trial performance. This ANOVA revealed a main effect of age, $F(2, 194) = 8.803$, $p < .001$, partial $\eta^2 = 0.083$. In general, younger individuals generate longer looking times regardless of the condition on which they were tested; this is especially notable for the long looking times observed in the infant group. We saw no main effect of condition, $F(1, 194) = 0.387$, $p = .535$, partial $\eta^2 = 0.002$, which was not surprising because the infant age group trended in the opposite direction of all other age groups. For this reason, we also included an interaction effect, to understand whether significant results could be detected in some age classes, but not in others. However, we observed only a marginal interaction between condition and age class, $F(2, 194) = 2.591$, $p = .078$, partial $\eta^2 = 0.026$. Likely, the marginal effect was driven by the successful performance of adults (Experiment 1), but was here found to be nonsignificant due to the performance of infant and juvenile individuals.

⁵ These were pilot data for Experiment 2, which we collected at the same time we completed Experiment 1. The difference between these collection times was 6 months.

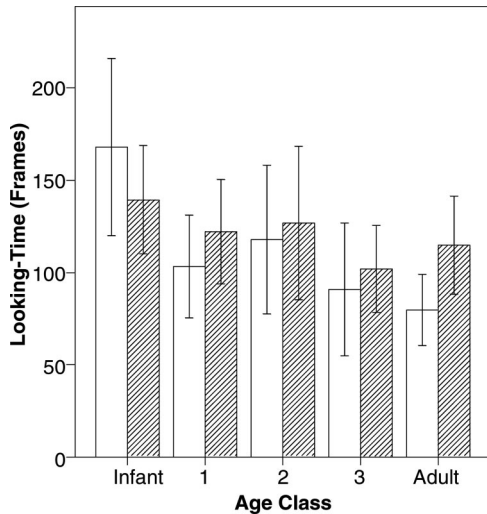


Figure 3. Subjects' duration of looking (in frames) across expected (open bars) and unexpected (hatched bars) test conditions and age classes (error bars = 95% confidence intervals) in Experiment 2.

Discussion

Our developmental study revealed that only adult rhesus macaques were able to successfully represent the location of hidden objects in an expectancy-violation rotational displacement task. Both infant and juvenile age groups showed no difference in looking between the expected and unexpected test events, suggesting these test groups made no prediction about where the strawberry was likely to end up after the rotation.

This pattern of performance suggests that rotational displacement skills may be late emerging for both humans and macaques. We must, however, be somewhat cautious when interpreting this similarity across the developmental timeline of humans and monkeys. First, humans and macaques were tested on different versions of this task. Although humans were tested on a choice version of this task (e.g., Okamoto-Barth & Call, 2008), we tested macaques using an expectancy-violation design with a looking measure. It is possible that a looking-time task might reveal a different developmental pattern in humans than the typical search version of this task (e.g., Okamoto-Barth & Call, 2008). Indeed, other research has shown that humans sometimes demonstrate more abilities when tested on looking measures than when tested on corresponding active choice tasks (see Santos, 2004, for a review of this discrepancy across tasks). Despite the differences across the tasks used to test humans and macaques, however, our looking-time results provide the first evidence to date that rotational displacement may be rather difficult for younger primate subjects. The pattern of performance we observed across Experiments 1 and 2 clearly suggest that rotational displacement may be more difficult for subadult macaques than it is for adult monkeys, at least when testing using looking-time methods.

Having investigated the difficulty of rotational displacement across different aged rhesus macaques, we next turned to *how* rhesus macaques solve this task. According to Okamoto-Barth and Call (2008), there are two key sources of information a subject may use to successfully track objects that are rotationally dis-

placed. Our adult macaque subjects may solve our rotational displacement task simply by associating a landmark or distinguishing feature—in this case, the color of the box—with the presence of the reward. Under this account, our macaques may not be mentally representing the invisible movement of the hidden item as the array rotates. Alternatively, our adult macaques may be ignoring featural information and may instead be mentally reconstructing the movement of the hidden item while they view the rotation. Finally, they may be using a combination of these strategies. These alternatives are difficult to distinguish from the current findings because Experiment 1 presented adult subjects with both types of information during the rotational displacement. In Experiment 3, however, we systematically varied the presence and absence of features and visible access to the rotation movement to address which cues rhesus macaques use to solve rotational displacement.

Experiment 3

Methods

Subjects. We completed Experiment 3 with a sample size of 99 additional adult rhesus macaques ($M_{\text{age}} = 8.26$ years, $SD = 4.22$). We also approached an additional 240 monkeys, but these sessions were discarded by the cameraperson, who was blind to condition, due to subject inattention, approach, interference from other monkeys, or experimental error. An additional 21 sessions were discarded because the subject was already represented in another experiment in this study, and 26 sessions were later discarded due to video quality during data analysis.

Apparatus, design, and procedure. Experiment 3 tested animals on two different conditions (Experiments 3A and 3B). The apparatus, design, and procedure for both conditions of Experiment 3 were very similar to those of Experiments 1 and 2, except for the changes described below.

Experiment 3A: Occluded rotation. Half of the monkeys ($n = 49$) were tested on an *occluded rotation* condition. This condition differed from that of Experiment 1 in that an occluder was used to block the subjects' visual access to the array. We used a 20×30 cm piece of heavy black cloth as an occluder that could be suspended over the front of the stage while the screen was open. During the test condition, the presenter again hid the strawberry in one of the two hiding locations and then closed the boxes. She then placed the occluder in front of the stage and rotated the table. The subject could see the presenter reaching into the stage area, but could not see the lower portion of the presenter's arms or any aspect of the rotating parts of the apparatus. It is worth noting that because these subjects were naive to the experiment (i.e., they had not participated in another condition), they would be unlikely to infer that the experimenter was performing a rotation behind the screen. Immediately after the rotation was completed, the presenter removed the occluder, and then opened the boxes as in Experiment 1, revealing either expected or unexpected test events. If macaques can use featural information (i.e., the color of the boxes) alone as a cue to the location of the rotated food, then monkeys who see the unexpected event should look longer than those who witness the expected event. In contrast, if monkeys primarily use visual access to the rotation to solve rotational displacements, then monkeys should look longer when presented with the "expected" condition,

because they would have no information that the array had been moved and thus should expect to see the food in its original location.

Experiment 3B: Same-colored boxes. In Experiment 3B, we prevented subjects from using any featural information to determine the location of the hidden strawberry. To do so, we changed the color of the two boxes that served as hiding locations so that both boxes were the same color (red). All other aspects of the procedure were identical to those of Experiment 1, and thus subjects could fully watch the rotation as they had in the first study. If macaques primarily use visual access to the rotation to solve this task, then their performance should be similar to Experiment 1. However, if macaques require some featural information to solve the rotational displacement task, then subjects' performance in Experiment 3B should differ from that of Experiment 1.

Data analysis. Data analysis procedure was the same as in Experiment 1. Twenty-six sessions were discarded by a blind coder because the video or audio quality of the recording did not allow accurate data collection. Again, a second coder, who also blind to condition, coded the looking time of 20% of clips to establish reliability ($r = .935$).

Results

We observed no differences across familiarization trials for monkeys tested on expected and unexpected conditions (pooled Experiments 3A and 3B), $t(97) = -1.296, p = .198, d = 0.57$. We then analyzed subjects' performance on the test trials (Figure 4). We conducted a 2×2 (Experiment [3A, 3B] \times Condition [expected, unexpected]) independent ANOVA. The results of this ANOVA found a significant effect for experiment, $F(1, 95) = 5.335, p = .023$, partial $\eta^2 = 0.053$, but, more importantly, did not reveal a significant effect of condition, $F(1, 95) = 0.629, p = .430$, partial $\eta^2 = 0.007$. There was also no significant interaction effect, indicating that there was no difference in the effect of condition

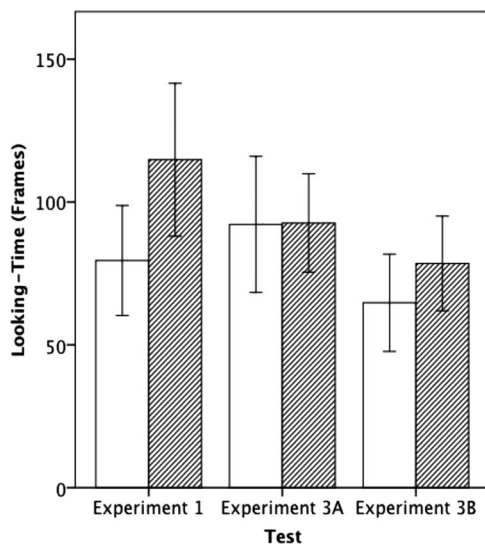


Figure 4. Subjects' duration of looking (in frames) across expected (open bars) and unexpected (hatched bars) test conditions (error bars = 95% confidence intervals) in Experiments 1, 3A, and 3B.

across experiments, $F(1, 95) = 0.542, p = .463$, partial $\eta^2 = 0.006$.

Discussion

The goal of Experiment 3 was to explore whether adult macaques could successfully represent an object that been rotationally displaced when they lacked either featural information about the object's hiding location (Experiment 3B) or visual access to the rotational movement of the object (Experiment 3A). Although macaques tested in Experiment 1 performed well in representing rotational displacement when both of these types of information were available, macaques tested in Experiments 3A and 3B failed to successfully track a piece of food when they lacked either featural information or visual access to the motion of the locations. This difference in performance between Experiment 1 and the two conditions of Experiment 3 suggests that adult macaques depend *both* on the presence of featural information within the array and on visible access to the rotation movement to solve rotational displacements. When we removed either of these aspects from the test display, as we did in Experiment 3, macaques' performance on the task decreased.

The performance of the macaques in Experiments 3A and 3B revealed behavior both like and unlike the behavior of apes when tested with the rotational displacement task previously (see Okamoto-Barth & Call, 2008). Like apes, rhesus macaques could not form the representations to successfully solve the task when the rotation was occluded. Apes tested in Okamoto-Barth and Call (2008) performed at high levels when the rotations were observable, but dropped to just below chance performance in 180° rotations when the rotation was not visible (they were required to use features alone to solve the task). Taken together, these results suggest that both species perform worse on a rotational displacement when they lack visual information about the substrate's rotation. In addition, both apes and macaques may be affected by the availability of featural cues in this task. Okamoto-Barth and Call (2008) observed that apes performed just below chance on an invisible rotation task in which landmark cues are available. This nonzero level of performance raises the possibility that apes may use landmark cues at some level. Monkeys also appear to benefit from the presence of featural cues in this task. Our adult macaque subjects performed better on a visible rotation in Experiment 1, when featural cues were present, than they did in Experiment 3B, when no features were available. This common use of features at some level suggests that both apes and monkeys are sensitive to features in the display, even though neither group appears to weight using this strategy very highly. In contrast to apes, however, macaques' performance seems to be more negatively affected when featural information is *removed* from the display, as in Experiment 3B. At least across different studies, it seems that apes do equally well in successfully solving a visible rotational displacement when landmarks are present (Okamoto-Barth and Call, 2008) as when they are not (Call, 2003). Our monkeys, in contrast, were unable to correctly represent a visible rotational displacement event when featural information was absent, as in Experiment 3B. This pattern of performance suggests that monkeys may get more benefit from the presence of features in an array than apes do, at least when tested specifically in the context of a looking-time task.

Our macaques' sensitivity to the absence of features contradicts the hypothesis that language skills are tied to increase reliance on featural information in spatial tasks, as some developmental researches have historically hypothesized (e.g., Hermer-Vazquez et al., 2001; Hermer-Vasquez, Spelke, & Katsnelson, 1999). Instead, as in previous primate studies (e.g., Gouteux, Thinus-Blanc, et al., 2001), we found that our adult macaques used the featural information in the display, at least to some degree. Our rhesus macaques subjects performed worse when featural information was absent, despite the fact that they are a nonlinguistic species. Our results provide further comparative support for the idea that, although language ability may be linked to a greater ability to attend to and integrate landmarks for humans, it is not a necessarily capacity for successfully using feature and landmark information.

General Discussion

Across three experiments, we provide evidence that a monkey species, the rhesus macaque, can sometimes accurately represent a hidden object that has been rotationally displaced. Macaques' success in Experiment 1 is especially noteworthy because our looking-time method allowed subjects only to see a single exposure of the rotation. Although primate subjects sometimes have trouble with rotation problems, even with training (e.g., Barth & Call, 2006; Poti, 2000), our macaque subjects were able to successfully discriminate the two test outcomes in Experiment 1 in only one exposure, looking longer when the food was revealed in an unexpected location after the rotation. In addition, previous experiments that have tested monkey species on other object-tracking tasks have shown that monkeys tend to have a difficult time reconstructing the movements of hidden objects (de Blois et al., 1998, 1999; Natale et al., 1986). For example, monkey species are known to fail the invisible displacement task, which is often considered an easier task than rotational displacement (Barth & Call, 2006; Okamoto-Barth & Call, 2008). Historically, researchers have also claimed that the ability to solve such higher-order object-tracking tasks evolved only in the ape lineage (de Blois et al., 1998, 1999; Natale et al., 1986). In this way, our study demonstrates that the capacities required to solve rotational displacements, and to represent the hidden movements of hidden objects, are more prevalent among primate species than previously thought. Indeed, our findings suggest that rotational displacement abilities are shared among monkeys, apes, and humans.

It is worth noting, however, that monkeys' success on our rotational displacement task may be due at least in part to the fact that we used a different kind of experimental task than is typically used in tests of monkeys' object-tracking capacities. Specifically, although other studies typically use training and choice-based measures of primates' spatial skills, we tested macaques using a looking-time test. We must therefore be very cautious in interpreting our monkeys' looking-time performance in comparison to other primates who were tested on similar problems using choice-based methods. Previous work both in human development and other primates has shown that performance on looking-time studies sometimes surpasses that of choice-based methods (developmental work: Baillargeon, 1986, 1987; Baillargeon & Graber, 1987; Baillargeon & DeVos, 1991; Berthier, DeBlois, Poirier, Novak, & Clifton, 2000; Berthier et al., 2001; Hofstadter & Reznick, 1996; Hood, Carey, & Prasada, 2000; Hood, Cole-

Davies, & Dias, 2003; nonhuman primates: Santos & Hauser, 2002; Santos, 2004; Santos, Seelig, & Hauser, 2006). Largely, these investigations have shown that when solving problems of object movements and interactions, infants and primates sometimes demonstrate understanding of objects in looking behavior even though they fail to employ this knowledge through searching behavior. It is possible that the same discrepancy may apply to the results of our study. More specifically, it is possible that macaques may perform well on our looking-time rotational displacement task even though they may not perform as accurately when tested with a choice-based version of this task. Although we were unable to test our macaque population on a choice study due to the constraints of a free-ranging subject population, future work would certainly profit from testing a different population of macaques on a choice measure to compare performance across measures. Similarly, it would be interesting to see whether great apes show similar performance on a looking measure as they have previously shown when tested using other choice-based methods (Beran et al., 2005; Call, 2003; Okamoto-Barth & Call, 2008).

There are, however, some advantages to using a looking-time measure like the one we developed in the present study. First, because expectancy violation studies involve no training, looking-time measures like the one we used here can capture subjects' spontaneous responses to different cognitive problems and the strategies they would naturally bring to solving a problem. More specifically, our looking-time approach can test how macaques think about rotational displacement in a situation in which there is little or no opportunity for learning. Finally, our looking-time measure allows us to test a number of different age ranges, which can be trickier using the typical choice-based task. Using looking time, we were able to provide the first-ever developmental test of rotational displacement in a nonhuman primate.

Although rhesus macaques may be capable of rotational displacements, our findings also demonstrated that this is a difficult task for them. Across Experiments 1 and 2, we observed that the capacity to solve rotational displacement tasks emerges only in a macaque's adulthood. Our results are thus similar to results found in human children, in which rotational displacement skills are observed to be relatively late emerging in childhood (Lasky et al., 1980; Okamoto-Barth & Call, 2008). In some cases, apes also find this to be a more difficult task than many other object-tracking tasks, as evidenced by higher error rates on rotational displacement tasks relative to other kinds of spatial tasks (Barth & Call, 2006). Our study therefore adds to the literature and supports the conclusion that, on a gross level, the difficulty of rotational displacements are intrinsic to the task and that such difficulty is observed both across primate taxa and different methodological formulations of this problem.

For rhesus macaques (and potentially other primates), the late developmental emergence of the rotational displacement skill is an outlier compared to the known developmental timing of other object-tracking skills in primates. In absolute time, nonhuman primates seem to develop object-tracking skills in less than half the time it takes their human counterparts (Gómez, 2005). However, the present set of experiments shows that rhesus macaques succeed at the rotational displacement problem at approximately the same absolute age as human children (about 4 years old) and, thus, at a comparatively much older relative age (adulthood in rhesus macaques and middle childhood in humans). If we pool this new

information with existing information on object-tracking development in nonhuman primates, a logarithmic developmental trajectory is suggested, with a number of easier object-tracking skills developing quite quickly at the beginning of life, and then more difficult skills developing at progressively later intervals. Although the late developmental timing of the rotational displacement skill in rhesus macaques is perhaps surprising considering how early macaques develop other object-tracking skills, it is not unexpected considering that rotational displacement has been identified as a more difficult task in both humans and nonhumans (e.g., Barth & Call, 2006).

Why rotational displacements are difficult, however, remains to be investigated. Previous accounts have posited that all object-tracking tasks rely on highly similar cognitive capacities, and that, as these capacities grow, individuals are able to complete more difficult tasks, with rotational displacements being the most difficult of all tasks (Barth & Call, 2006; Call, 2003). Monkeys' success on rotational displacement in our studies combined with their failure in other object-tracking tasks (de Blois et al., 1998, 1999; Natale et al., 1986) hints that rotational displacements are not necessarily the most difficult object-tracking task, although it is possible that our results differ from previous results due to our looking-time methodology. Regardless, future work will need to more clearly identify which underlying cognitive capacities are required to solve each object-tracking task and when such capacities mature.

Our experiments also examined what strategies—featural cues or visual tracking—rhesus macaques use to solve rotational displacements. We found that rhesus macaques required both sets of cues to solve the task, suggesting they encode both when watching rotational displacements. Although we have observed that macaques do in some way attend to featural cues in this task, there is a possibility that our macaques may not use featural cues in the same manner as humans do. In arrays with landmark information, a further improvement in performance is not obtained in 3-year-old human children if the rotation is made visible. This pattern is unlike that we observed in macaques, in which the combination of featural cues with visual tracking bolstered the representation of hidden objects. Thus although it is likely that 3-year-old children solve the rotational displacement problem by associating a landmark with a reward, at present, we do not know whether macaques also associate the reward with a particular landmark or whether the addition of features in the visual field helps structure it in a way that simply allows for more accurate visual tracking (see Butterworth, Jarrett, & Hicks, 1982, for a similar idea in children).

Finally, our results do not support the hypothesis that language is necessary for humans to spontaneously attend to featural and landmark information in object tracking. Our results demonstrate that nonlinguistic rhesus macaques spontaneously take into account featural information when representing rotational displacements. This presents two future challenges for research. One challenge will be to more accurately assess whether there is a gradient of ability or preference to successfully use featural or landmark information in spatial representations among primate species. Such an investigation will bring to attention whether there are any ecological and evolutionary reasons why “preferences” in strategies to solving spatial problems might vary. A second, larger, future challenge will be to continue to understand how language ability may affect featural and landmark use in spatial problem-

solving in general (see also Haun et al., 2006). This topic is an evolving debate, which continues to work on a complex problem: if nonlinguistic populations are known to use landmarks in spatial tasks (primates: Deipolyi et al., 2001; Dolins, 2009; Garber & Brown, 2006; Gouteux, Thinus-Blanc, et al., 2001; Herman & Wallen, 2007; MacDonald et al., 2004; Marsh et al., 2011; Potì et al., 2005; Potì et al., 2010; Sutton et al., 2000; prelinguistic infants: Bushnell, McKenzie, Lawrence, & Connell, 1995; DeLoache & Brown, 1983; DeLoache, 1986; Gouteux & Spelke, 2001; Learmonth, Newcombe, & Huttenlocher, 2001), why do these same populations tend to make less use of landmark information in select spatial tasks (Gouteux & Spelke, 2001; Gouteux, Vauclair, et al., 2001; Haun et al., 2006; Hermer & Spelke, 1994, 1996; Okamoto-Barth & Call, 2008)? Future research will thus surely profit from exploring the extent to which language abilities change the spatial strategies organisms favor when solving different spatial problems.

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