

A Test of Object Permanence in a New World Monkey Species, Cotton Top Tamarins

(*Saguinus oedipus*)

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ABSTRACT

Cotton top tamarins were tested in visible and invisible displacement tasks in a method similar to that used by de Blois, Novak and Bond (1998) to test squirrel monkeys and orangutans. All subjects performed at levels significantly above chance on visible (n=8) and invisible (n=7) displacements, wherein the tasks included tests of the perseverance error, tests of memory in double and triple displacements, and “catch” trials which tested for the use of the experimenter’s hand as a cue for the correct cup. Performance on all 9 tasks was significantly higher than chance level selection of cups, and tasks using visible displacements generated more accurate performance than tasks using invisible displacements. Performance was not accounted for by a practice effect based on exposure to successive tasks. Results suggest that tamarins possess Stage 6 object permanence capabilities, and that in a situation involving brief exposure to tasks and foraging opportunities, tracking objects’ movements and responding more flexibly are abilities expressed readily by the tamarins.

162 words.

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The phrase “object permanence” is used to mark a demonstration of the cognitive capacity to attribute to disappearing objects continued existence. In children, this capacity may originate as an innate skill (see Baillargeon, 1995) but it is certainly not a unitary one, for the type of details represented about an absent object seem to change with experience and development within the first 2 years of life (Piaget, 1936/1952). Development through the last two stages of Piagetian object permanence is particularly interesting, because the tests of those stages identify response inhibition problems (Stage 4- 5), and problems in generating inferential knowledge about the invisible movements of disappeared objects (Stage 6). The transition from Stage 4 to Stage 5 (often referred to as 4b) involves hiding an object repeatedly in a single location, and then suddenly shifting to a new location. Successful retrieval with a location shift means that the subject can overcome the perseverence error (Diamond, 1991), or can inhibit a highly probable response in deference to the cognitive representation of the correct location of the disappeared object. This kind of success is found in human infants by 12 months of age (Piaget, 1954). Further tests of Stage 5 involve using random locations for hiding, and successively hiding an item across 2 or more sites.

The skill tested in Stage 6 is tracking invisible displacement. Subjects watch an object disappear into a container, watch the container move to a hiding location, and then see that the container is now empty. By this method, subjects receive incomplete information about the demise of the hidden object, and must infer from the visual clues that it must have traveled with the container and been deposited at the location at which the container paused. Humans have demonstrated this inference by 2 - 3 years of age, but recent evidence (Hood, Cole-Davis, and Dias, 2003) suggests that 2-year olds continue to have some problems with inferring invisible displacement in certain tasks.

It should be noted that these ages of progression were determined by responding defined as physical searches. More recent work using look rates as the dependent variable have found that infants by 4 months of age show increased looking if physical objects which are hidden lose their physical characteristics while hiding (for a review, see Baillargeon, 1995). Still, the

inferences that are required in invisible displacement seem to occur later in development, and require some utilizing of knowledge of predictable events in the world (Diamond, 1988).

It is commonly accepted that tests of object permanence are an ecologically valid means to test the representational capacities of different species of animals (Dumas, 1992; Dumas and Wilkie, 1995; Etienne, 1984; Goulet, Dore´, and Rousseau, 1994; Pepperberg, Willner, and Gravitz, 1997; de Blois, Novak and Bond, 1998; and Call, 2001). All seeing animals (including humans) live in a world in which objects appear, move in space, disappear, and reappear. The capacities to recognize an object as the same through repeated appearances over time, and to search for and find a desirable object once it has disappeared, are clearly both of great adaptive value. A recent review of the criticisms levied against the use of Piagetian tasks to study animals' abilities by Pepperberg (2002) identifies important methodological considerations for any study, including insuring that enculturation, learning, memory, and cueing cannot account for the representational stage represented by the subjects' behavior.

Past studies have demonstrated successful searching with visible displacements, captured by Stage 4 and 5 of Piagetian development, in birds such as ring doves (Dumas and Wilkie, 1995, although doves failed when multiple hiding spots are used) and in parrots (Pepperberg, Willner, and Gravitz, 1997); in various mammals such as cats (Dore´, 1986, 1990; Dumas and Dore´, 1989, 1991; Goulet, Dore´ and Rousseau, 1994), and dogs (Gagnon and Dore´, 1992, 1993, 1994; Triana and Pasnak, 1981); in new world monkeys such as squirrel monkeys (Vaughter, Smotherman and Ordy, 1972; de Blois, Novak, and Bond, 1998), and cebus monkeys (Dumas and Brunet, 1994; Natale and Antinucci, 1989; Schino, Spinozzi, and Berlinguer, 1990; Mathieu, Bouchard, Granger, and Herscovitch, 1976); in old world monkeys such as crab-eating macaques (Natale and Antinucci, 1989), Japanese macaques (Natale and Antinucci, 1989), rhesus macaques (de Blois and Novak, 1994; Hauser, 2001; Natale, Antinucci, Spinozzi, and Poti´, 1986); and in great apes, such as gorillas (Natale, Antinucci, Spinozzi, and Poti´, 1986; Redshaw, 1978; Spinozzi and Natale, 1989), orangutans (de Blois, Novak, and Bond, 1998) and chimpanzees (Call, 2001; Wood, Moriarty, Gardner, and Gardner, 1980; Mathieu, Bouchard, Granger, and Herscovitch, 1976; Mathieu and Bergeron, 1981). The tracking of an object moved visibly to a

hiding location seems to be a capacity shared by most vertebrates tested, including avians, nonprimate mammals, and primates.

More advanced object permanence abilities involving invisible displacements have been reported consistently in a small group of birds (in parrots, primarily, Pepperberg et al., 1997), in dogs (Gagnon and Dore', 1992; Watson et al., 2001), and in the great apes, (including chimpanzees, orangutans, for example, Call, 2001; orangutans, in de Blois, Novak and Bond, 1998, 1999; and gorilla, for example, Natale et al., 1986).

Early studies of invisible displacement reported success by old world monkeys such as rhesus macaques (Wise, Wise and Zimmermann, 1974), and new world monkeys such as squirrel monkeys (Vaughter, Smotherman, and Ordy, 1972). Still, de Blois, Novak, and Bond (1998) pointed out and Pepperberg (2002) reiterated that in most of these early studies of monkeys, too many trials were used to test subjects to rule out the possibility that they learned how to respond more locally from practice. A variety of species of macaques and the new world species, squirrel monkeys, have failed subsequent tests of invisible displacement with fewer trials (for rhesus macaques, de Blois and Novak, 1994; for crab-eating macaques, Natale and Antinucci, 1989; for squirrel monkeys, de Blois, Novak and Bond, 1998). Monkeys as a group perform inconsistently in this area, with new world monkeys generally failing to represent objects invisibly hidden, and old world monkeys, specifically rhesus monkeys, failing most of the time they are tested (for example, a recent study by Hauser, 2001, obtained a striking failure at representing invisible displacements specific to displacements of falling objects). The most common strategy monkeys show when they fail is to repeat a search at a favored location (de Blois, Novak, and Bond, 1998 for new world monkeys; 1999 for old world monkeys).

Still, with all this inconsistency in the abilities demonstrated of monkeys, Call (2000) could find no clear differences in representational skills in space and for objects between monkeys and apes. He examined the use of features in the environment to remember spatial locations, the use of dynamic representations to imagine the trajectories of moving objects, and the encoding of properties of objects in relation to others, and in all 3 cases, there was no clear differentiation between monkey and ape abilities.

In this study, a species of new world monkey not tested before on traditional tests of object permanence is exposed to a method similar to that used to study apes and a different species of new world monkey. The cotton top tamarin is an excellent candidate for this type of testing because individuals of the species have demonstrated abilities that predict success and failure in object permanence. Their reported ability to understand limited aspects of invisible displacement (Hauser, Williams, Kralik and Maskovitz, 2001), to use tools in sophisticated ways (Hauser, Kralik and Botto-Mahan, 1999; Hauser, 1997), to show self-directed behaviors to mirrors (Hauser, Kralik, Botto, Garrett, and Osser, 1995; Hauser, 2000; Neiworth, Anders, and Parson, 2001), and tamarins' ability to hold feeding sites in spatial memory (Milton, 1988) suggest a higher level of object representation in space and inferences about those objects. Cotton top tamarins' inability to extrapolate the final location of an object moved invisibly and against the obvious path dictated by gravity in an opaque tube (Hauser, Williams, Kralik and Maskovitz, 2001), and their reported problems in inhibiting a more readily available response (Hauser, Kralik, and Botto-Mahan, 1999) suggest limits on extracting invisible movements of absent objects and a limit on their ability to act on cognitive representations rather than making ready responses. For cotton top tamarins, we expected a high rate of success in visible displacement tasks, as other tested primates have shown. We expected increased errors in tasks with the following: a) a bigger memory load (i.e., when items are hidden successively across two or more locations), b) a requirement to inhibit a previously successful response (i.e., when the location of hiding has been repeated at one spot and then suddenly switches), and c) in invisible displacements, most likely because of a lack of ability to infer the location from the incomplete information provided. In sum, our aim is to test cotton top tamarins' ability to represent objects in a more traditional set of object permanence tasks. These animals have had no enculturation, and their testing will occur over 9 trials per task, thus there will be little chance for learning or memorizing the correct response. Moreover, the possibility of cueing is controlled in "catch" trials placed within particular tasks in which the experimenter touches a final cup which does not contain the hidden item.

METHODS

Subjects

A total of 8 cotton top tamarins (*Saguinus oedipus*), 5 females and 3 males, participated. Six of the animals, 4 females and 2 males, were socially housed in pairs, and studied in their home cages. The remaining two adults (one male, Dante, age 4, and one female, Caitlin, age 12) were housed in a family group of 4 and studied in their home cage. The pairs of adults included females Oprah (age 13), Fozzy (age 7), Olympia (age 5), and Ophelia (age 7) and males Mac (age 11) and Zhivago (age 8). All subjects had been family-reared in lab settings, and had been socially housed as non-breeding couples (Oprah and Mac, and Fozzy and Zhivago), as mother and son (Caitlin and Dante) and as sisters (Ophelia and Olympia).

The 2 living in a group of 4 lived in a cage 1.8 X 3.0 X 2.3 m in size, while the remaining pairs were housed in three 0.85 X 1.5 X 2.3 m pair cages located in an adjoining room. Opaque sheets visually separated all cages. The subjects were on a twelve-hour light/dark cycle and had free access to water. All animals were maintained on a complete diet consisting of a yogurt and applesauce breakfast, a lunch of Zupreem Marmoset chow, Mazuri New World Monkey dry chow, fruits and vegetables, and a protein snack (e.g., eggs, hamburger, mealworms) daily.

Four of the subjects (Caitlin, Dante, Olympia, and Ophelia) had prior experience with an experiment requiring them to tip over one of two cups in a gaze-following experiment to obtain a food reward (Neiworth, Burman, Basile, and Lickteig, 2002). In the previous experiment, the baiting did not occur in front of the animals. Rather, baiting occurred within a large cardboard box, so no presentation of objects moving, being displaced, or being hidden was shown before this experiment. The other 4 (Oprah, Mac, Fozzy, and Zhivago) were naïve to any tasks involving food baiting in cups at the time of this study.

Apparatus

Three opaque cups, measuring 9.3 cm in height with a width of 8.7 cm at the base, were used in an inverted orientation during acclimation and testing. The cups were placed on a cart (1.17 m height, 0.4 X 0.5 m top) separated such that the distance center to center was 14.5 cm between each pair of cups. The cups were placed 24.5 cm from the front (subject side) of the cart and the outer cups were placed 10.25 cm from the sides of the cart. Holes measuring 3.81 cm X

3.81 cm were made along the bottom rear of the base of each cup, and then covered with 2 layers of opaque cloth with vertical slits cut in them to form a curtain. Each cup was taped to the cart such that the covered openings faced the experimenter, and so that the subjects had to flip the cups back toward the experimenter to receive a food reward. Food rewards were the objects hidden, and they consisted of individual pieces of fruit sugar cereal (Fruity Pebbles or Fruit Loops). The specific type used was varied throughout acclimation and testing depending on the subject's preferences. In prior studies with monkeys (e.g., de Blois, Novak, and Bond, 1998), food rewards were often used as the objects to hide. An aluminum tea strainer, 18 cm long, with 2 opaque aluminum cups, 3 cm in diameter and glued on each end, was used as a displacer during the invisible displacement trials.

Procedure

There were two phases of the experiment: an acclimation phase and a testing phase. The acclimation phase was intended to insure that subjects knew the particular response for the experiment (i.e., tipping a cup) and they knew that reinforcers were available for emitting a response. The subjects were not in any way trained in a Piagetian task in this phase in the sense that objects were not moved and hidden for them to find. In fact, the baiting of all 3 cups occurred on every trial in acclimation, and baiting was done without subjects' attention being drawn to the baiting. It was necessary in an experiment with very few trials per task that subjects learned a priori to approach the test equipment and to emit a response, or such very basic issues as failure to approach or failure to emit any response would be interpreted as a failure to represent objects later.

Acclimation. The acclimation phase familiarized the subjects with the apparatus (cart, cups, and displacer) and required a demonstration of the search response distributed among the 3 cup locations twice each in 6 consecutive trials in a session for the testing phase to begin. A total of 20 trials were conducted per session, with trials lasting 30 seconds in duration. A search response was marked either if a cup was tipped over by the subject, revealing the reward, or if a cup was touched by the front hands of the subject, which suggested a choice to that cup, but did not always lead to the cup tipping over. If the reward was not obtained by the subject following a search response, the experimenter tipped the chosen cup over revealing the reward, and either

waited for the subject to take it, or if the subject had moved from the cart, handed the reward to the subject.

It is important to note here that the acclimation phases were conducted at a rapid pace, and criterion was met often within 1 session. The subjects did not persist in selecting the same cup once they had obtained reward at that location, but rather seemed more inclined to try other locations (possibly a foraging strategy, assuming that the prior location was depleted). This generated a flexible moving response pattern in the animals which was very different than the response repetition problems found by Hauser, et al., 1999, but this was also a different type of task, in which multiple sites were available for food reward.

Testing. The tamarins participated in nine different tasks involving visual displacements (Tasks 1 – 5) and invisible displacements (Tasks 6 – 9). All subjects were presented the tasks in the same order, starting with Task 1. Any effects of learning that might have occurred because of any prior exposure on earlier tasks was statistically analyzed as a practice effect. Task 1 through Task 9 were limited to 9 completed trials for each, with 3 samplings at the 3 distinct search locations for any task involving randomly selected final locations. Several studies from which this method was developed used comparably small sets (i.e., de Blois, Novak and Bond (1998) used 3 or 6 trials per task with 3 locations tested (with 1 or 2 uses of each location, respectively), and Call (2001) used between 8 and 12 trials per task with 3 locations tested).

A completed trial was defined as one in which the subject made any search response, defined as the front hands touching a cup, or the subject tipping over a cup. Trials lasted for 60 seconds, or until a response was made, whichever occurred first.

Each trial began with all three cups inverted, with their removed side openings covered with curtains and facing the experimenter. Food items were eventually hidden in single but different locations throughout testing, and olfactory cues left by subjects touching the cart, the cups, scent marking the cart and cups, and olfactory cues left by previously placed food were left to linger for each subject.

Each trial began when the experimenter obtained the attention of the subject being tested by showing him or her a reward, stating the name of the subject repeatedly, and noting that the subject's head orientation and gaze orientation was toward the experimenter and the reward. The

reward was eventually placed in a predetermined cup through the covered opening, however tasks varied in terms of how that was done (by hand or with the displacer) and whether visits to other cups preceded the final hiding. Once a cup was baited, the subject was allowed 60 seconds to make a search response. A single search response was allowed when the hiding was completed, and once that was made, no other responses were allowed. The subject was made to leave the cart area after his/her first search response, but was allowed to obtain the food reward first if the response was correct. If the response was incorrect, the experimenter would tip over the cup (if that had not been done by the subject) revealing that no food was hidden at that location. The correct location was not shown following an incorrect response.

Trials were aborted if a) the subject's attention was disrupted, defined as his/her visual orientation shifting from the task to elsewhere in the cage environment during the hiding process, b) the subject attempted to make a search response before the baiting process was completed, c) the subject's cage mate interfered with the searching process by also climbing onto the cart, or d) the subject failed to make a search response within 60 seconds following the baiting process. Trials, either completed or aborted, were separated by intertrial intervals of 10 seconds duration. During the search process within trials, and during the intertrial interval between trials, the experimenter doing the baiting gazed at a fixation point in the room such that the experimenter's head orientation and eye orientation were never directed at any cup on the cart.

A second experimenter was present for all tasks in the testing phase. He or she identified to the experimenter in the cage the cup displacement order and final hiding location for each trial, timed the search period, recorded the subject and first search response or called for an aborted trial if 60 seconds passed with no response, and timed the intertrial intervals. The recording experimenter kept his/her head oriented downward toward a clipboard throughout the 60-second search time period, and used quick upward glances to observe the subject's search behavior. This tactic was used in case the subject attempted to use the recording experimenter's direction of gaze (only tracked by tamarins if the head and eyes are oriented toward a location, see Neiwirth, Burman, Basile, and Lickteig, 2002) to find the hidden reward.

Sessions were limited to 30-minute durations, and usually produced 9 completed trials per subject per session, with a varying number of aborted trials. The maximum number of

completed trials that were allowed in any session was 18, or the testing of two tasks. The tasks are graphically represented in Table 1a, for visible displacement, and Table 1b, for invisible displacement.

In visible displacement tasks, the experimenter's hand was used to displace the object hidden. The object was held to be visible to the subject, except when it disappeared under a cup. The visible displacement tasks became progressively more time-consuming and complex, as the item was first hidden in a single location repeatedly (Task 1), then hidden in a new location (Task 2),¹ then hidden at random sites (Task 3), and finally hidden successively in 2 locations (Task 4) or 3 locations (Task 5). Catch trials were imbedded in Task 5 such that the hand moved the object to two hiding places, depositing the object in the 2nd of the two places, and then the hand touched the top of the cup in a 3rd location. If subjects were simply following the hand and selecting the cup last touched, they should consistently respond incorrectly in the Task 5 Catch trials.

In invisible displacement tasks, the displacer with occluded spoon-ends was used to move the object, once it was hidden in it at the beginning of each trial in Tasks 6–9. The displacer was then moved to the hiding location, or through successive hiding locations, and placed inside the cup for 1–2 seconds. If successive hidings occurred in the trial (as in Tasks 8 and 9) the displacer was opened in between cup visits to show whether it still contained the object or not. This part of the invisible movement is a clear deviation from other procedures (i.e., Call, 2001; and de Blois, Novak and Bond, 1998) wherein a displacer was used for successive hidings but was not shown as still carrying the object or empty after cup visits. The problem caused by the lack of viewing the displacer between visits is that it is truly and logically ambiguous whether the displacer deposited the item in any one of the visited locations, thus “chance –level” responding must be adjusted to account for the possibility of 2 or more legitimate hiding spots. While the current method allows chance to remain at 33%, it also allows the subjects a reminder of the object by allowing a “peek” into the displacer between visits. There remains the required inference that the object is being moved invisibly, and if the displacer suddenly appears empty,

¹ The switch from Task 1 to Task 2 was made to occur within 1 session, so that the tendency to repeat the prior visited location would be salient. If a session was ended at the end of Task 1, the next session began with 3 trials of Task 1 before Task 2 was initiated.

that it deposited the hidden object inside the former visited location, and thus the cognitive work remains similar to that in original Piagetian tasks.

One exception to the procedure occurred if a subject started to show a strong location bias despite a lack of reinforcement acquired there, which occurred with a few subjects. If a subject seemed to perseverate at choosing one location despite no reward being obtained there for 3 or more trials in a row, the experimenter would offer a single “remedial” visible displacement trial at another location, just to determine if the subject was willing to choose a different cup under more simple circumstances. In all cases, a correct response occurred to the single visible displacement trial, and the experimenter then re-engaged the subject in the task at hand. This practice did not change the coding of data, all incorrect prior trials were counted as incorrect, and the “correct” remedial trial was not counted at all. The remedial step was imposed to insure experimenters that the subject in question understood the rules of the game. It was imposed only twice each within Tasks 6 – 9 for 3 subjects (Ophelia, Oprah, and Dante).

Percent correct scores were calculated per task as correct responses out of 9 completed trials. Percent correct scores were subjected to a series of repeated measures analyses of variance (ANOVA's), and t-tests for matched groups using SPSS 10.0. One-sample t-tests against a hypothetical mean of 33%, or chance level responding, were conducted using SPSS 10. An alpha level of significance was set at 0.05.

RESULTS

All 8 subjects completed the visible displacement tasks (tasks 1 – 5), but one subject, Oprah, became ill and did not participate in the invisible displacement tasks. The remaining invisible displacement tasks 6 – 9 were successfully completed by 7 subjects. Individual performances per task are presented in Table 2. Most scores were based on 9 completed trials, with the exception of Task 5 (5 trials), Catch Task 5 (4 trials), and Catch Task 9 (4 trials).

Figure 1 depicts the mean percent correct score for all subjects (n=8 for visible displacement tasks, n=7 for invisible displacement tasks) for each task, and the standard deviation for each illustrates the range of scores the subjects emitted. The percent correct scores were subjected to a repeated measures ANOVA with task (n=11, including 9 tasks and two sets of catch trials) as the independent variable, and the result was a significant difference in

performance across tasks, $F(10, 60)=3.94$, $p < 0.01$. Pairwise comparisons using paired-sample t tests adjusted for unequal n 's were conducted for tasks with similar methods across visible and invisible displacement testing. A significant difference was found between scores from Tasks 3 and Tasks 8, or between visible and invisible displacements when the hidden object was placed in randomly selected single locations ($t(6) = 2.49$, $p = 0.05$), with performance much more accurate in visible displacement with random locations (mean = 72.3, $sd = 10.7$) than for invisible displacement with random locations (mean = 59.7, $sd = 10.7$). A nonsignificant result ($t(6) = 2.32$, $p=.059$) emerged between scores from Tasks 4 and 9, or between visible and invisible displacements using double-hiding, with the mean for visible displacement (mean = 69.1, $sd=16.45$) higher than that for invisible displacement (mean = 48.7, $sd = 10.7$). Other comparisons did not show accuracy differences between visible and invisible displacements, including Task 1 and Task 6 ($t(6)=1.51$, $p=0.17$); and Task 2 and Task 7 ($t(6)=0.98$, $p=0.37$). Since there were no invisible counterparts to the catch trials (5 and 9) nor to the triple hiding (Task 5), no pairwise comparisons were made.

A total of 4 of the subjects (Caitlin, Dante, Ophelia, and Olympia) had been in a previous experiment involving finding food under cups (Neiworth, Burman, Basile, and Lickteig, 2002), and a separate mixed model ANOVA was conducted with experience (naïve vs. in prior experiment) as a fixed factor, and task ($n=11$, including catch tasks) as the repeated measure, and percent correct scores as the dependent variable. The repeated measure task remained a significant main effect, $F(10, 50) = 3.66$, $p < 0.01$, while the main effect of experience was not significant, $F(1, 5) = 2.36$, $p = 0.18$) and the interaction between experience and task was not significant, $F(10, 50) = 0.59$, $p = 0.81$. The experienced subjects are presented as the first 4 subjects in Table 2, with the naïve subjects, the last 4.

A determination of accurate performance for each task was made by pitting the percent correct scores for all subjects at each task against an hypothetical chance level of success, or 33% correct (based on selection from 3 cups). By One Sample t -tests, subjects were found to perform at levels significantly higher than chance in single visible displacement ($t(7)=17.0$, $p<0.01$), in A not B visible displacement ($t(7)=7.19$, $p < 0.01$), in random single visible displacement ($t(7) = 10.69$, $p < 0.01$), in double visible displacement ($t(7)=6.62$, $p < 0.01$), in triple visible displacement ($t(7) =$

4.27, $p < 0.01$), in the catch trials in triple visible displacement ($t(7) = 3.86$, $p < 0.01$), in single invisible displacement ($t(6) = 3.93$, $p < 0.01$), in A not B invisible displacement ($t(6) = 3.87$, $p < 0.01$), in random invisible displacement ($t(6) = 6.58$, $p < 0.01$), and in double invisible displacement ($t(6) = 3.87$, $p < 0.01$). Performance was not different from chance level responding in the catch trials in double invisible displacement ($t(6) = -0.08$, $p = 0.938$). On the whole, these results indicate that performance was significantly more accurate than chance through all standard visible and invisible displacement tasks. Performance dropped to chance levels for catch trials in double invisible displacement when a 2nd irrelevant cup was manipulated by the experimenter before subjects were allowed to make a choice. However, performance was significantly higher than chance levels in a similarly tricky task in triple visible displacement, in trials in which the experimenter hid the visibly displaced item in the 2nd container of 2 visited, and then touched a 3rd container.

Performance on visible displacement tasks was predicted to be better than performance on invisible displacement tasks. A matched pairs t-test for averaged percent correct scores per subject for visible displacement tasks and for invisible displacement tasks (with Oprah removed since she was not tested in invisible displacement) revealed that there was significantly more accurate performance for visible displacement tasks (mean = 68.94, $sd = 7.76$) than for invisible displacement tasks (mean = 53.8, $sd = 8.42$; $t(6) = 4.14$, $p < 0.01$).

Another expectation was that tamarins would show decreased accuracy with shifts from the prior single hiding location to a new one (A not B Tasks 2 and 7). Paired t- tests for matched groups indicated no significant difference between performances to single visible displacement, Task 1 and the A not B test when the single location was suddenly switched, Task 2 ($t(7) = 1.31$, $p = 0.23$). Moreover, there was not a significant effect of switching to a new location in the invisible displacement task (from Task 6 to Task 7) ($t(6) = 1.11$, $p = 0.31$). Thus, the tamarins did not show difficulty in inhibiting a response to a previously reinforced location.

Since subjects were tested in social circumstances, it was possible that the 2nd subject in a pair acquired some knowledge about the tasks by watching, and thus would show enhanced performance and inflate the accuracy scores overall. To examine this effect statistically, a t-test for matched pairs was conducted to compare original subjects' scores across tasks (Fozzie, Mac,

Caitlin, and Olympia) with the 2nd subject of a pair who was tested (Zhivago, Oprah, Dante, and Ophelia, respectively). The comparison between original subjects (mean = 69.4, $sd=7.91$) and 2nd subjects (mean = 61.8, $sd=7.44$) was not significantly different ($t(3)=1.39$, $p = 0.21$). If anything, the original subjects' scores were, on the whole, slightly higher than the 2nd subjects' scores, showing a lack of facilitation in doing after watching.

An issue of concern was whether the subjects could perform accurately on increasingly difficult displacement problems because there may have been some learning across the earlier tasks (i.e., from task 1, single visible displacement, to task 9, double invisible displacement.) In contrast, the mean percent correct scores appeared to decrease with increased exposure to the tasks (see bars of histogram, Figure 1). A linear trend analysis was performed on averaged accuracy per trial starting on trial 1 of Task 1, single visible displacement, and for each of 9 consecutive trials for each of the 9 tasks. The resulting averaged accuracies, shown in Figure 2, are constructed of a total of 77 trials, with 9 consecutive trials from Tasks 1 – 4, 5 consecutive standard trials across subjects for Task 5 (i.e., without the catch trials included), and 9 consecutive trials from Tasks 6 – 9. The correlation between trial order and accuracy revealed a correlation of -0.394 , with $R^2 = 0.15$, which was significant ($F(1, 75) = 13.76$, $p = 0.0004$). The best-fitting line across all tasks is shown in Figure 2, and has a negative slope, -0.334 , with an intercept of 79.79. Accuracy generally started quite high in Task 1, showed a wide range across tasks, and generally decreased across tasks.

Separate linear regression analyses were conducted for consecutive accuracy scores within each task, and the results are shown in Table 3. The only significant positive linear trends were in Task 3 (random visible displacement) and Task 6 (single invisible displacement). For both, the best-fitting lines were positive in slope, indicating some learning within the 9 trials of each of these tasks. The initial averaged score to Task 3 was 37.5, and the final averaged score was 87.5. It appears as though Task 3, which involved hiding the object randomly in all of the 3 locations across 9 trials, marked a more difficult task for the subjects, but one which they could respond to with greater accuracy as the 9 trials progressed. The increase within 9 trials either indicates an acquisition of better object representation (i.e., search where the object is hidden) or

an acquired inhibition of location bias (i.e., don't search in the same location all the time, even though that produced good results before).

The averaged score for the first trial of Task 6, invisible displacement, was 62.5, which is much higher than 33% chance levels from the start, while the final averaged score by Trial 9 in Task 6 was 87.5. In Task 6, the linear trend suggested that subjects performed very well from the beginning of the task, but performed better as they progressed through the 9 trials.

All other linear trends of standard versions of the tasks were not significant and did not show systematic trends in the data. Most visible displacement tasks (with the exception of Task 3) show a y-intercept for accuracy that was quite high, suggesting high accuracy projected from the start and throughout each task. Invisible displacement tasks show slightly lower y-intercepts. Still, none showed systematic significant upward trends within its 9 trials of testing.

The strategy "pick the cup the experimenter touched last" would lead to accurate performance in all standard tasks, and is a simpler interpretation than the inference that subjects were representing the movement and successive hiding of objects now absent. The "catch" trials were intended to test for this, for a final cup was touched in those trials and the final cup was incorrect. A closer examination of the errors made in both sets of catch trials (following visible displacement, in Task 5; and following invisible displacement, in Task 9) does not support the notion that subjects were following a last cup touched strategy. Hypothetically, errors could be split between 2 incorrect locations, since the third location was correct. For both tasks, there was a slight tendency to select the last cup touched over the other incorrect cup (i.e., 53.75% of the time, and 60% of the time errors were made, respectively), but the distribution of errors across it as compared to the other cup was not different from chance ($\chi^2(1)=0.25$, $p=0.62$ for Task 5, $\chi^2(1)=0.8$, $p=0.37$ for Task 9). The subjects' accurate performance on standard trials cannot be explained by a last cup touched strategy, or the same subjects should perform at near 0% accuracy on catch trials, and should favor the last cup touched a significant portion of the time. These latter characteristics were not substantiated by the data.

DISCUSSION

This study utilized 9 separate tasks and 2 sets of "catch" trials to examine object representation by tamarins in visible and invisible displacement tasks. The results were that all

subjects chose the correct cup at rates significantly higher than chance in both visible and invisible displacement tasks, with the exception of a final set of catch trials utilizing double invisible displacement. More importantly, tamarins were successful at finding objects in most invisible displacement tasks, and this success stands in contrast to recent tests of another new world monkey, the squirrel monkey (de Blois, Novak, and Bond, 1998).

There were direct indications that the tamarins were doing cognitive work in the object permanence tasks. First, tamarins selected accurately at significantly higher levels when items were visibly displaced than when they were invisibly displaced, a tendency found in prior studies with primates (de Blois, Novak and Bond, 1998; Call, 2001). The fact that invisible displacement was more difficult to track implies that the object representation was more fragile under those conditions. Conversely, if subjects simply selected the last cup touched by the experimenter regardless of the “show” that preceded this event, there should have been no differences in accuracies between visible and invisible displacement tasks.

Secondly, tamarins did not show a perseverance error, in that they did not persistently emit a previously reinforced response when the hidden object was suddenly placed in a new hiding location (the A not B error tests). In the prior study, de Blois, Novak and Bond (1998) found that squirrel monkeys and orangutans did not commit perseverance errors with visibly displaced items, and orangutans did not commit them with invisibly displaced items. The squirrel monkeys actually performed at *below* chance levels across Tasks 6 and 7 (the invisible displacement task, and the switch to a new location), and it is unclear from the data whether that inaccuracy was caused by a perseverance error or some other strategy for response. The data from tamarins show successful performance in Tasks 6 and 7, and a lack of perseverance error in invisible displacement with location shifts as well.

The accurate performance by the tamarins across all 9 tasks could not be explained by a practice effect, for across successive tasks, performance actually became worse. The pattern of increased errors is more fitting with the increased complexity of the tasks, assuming one is attempting to represent the hidden object in increasingly difficult circumstances. A strategy of selecting the last cup touched by the experimenters could not explain the data because the catch trials in which experimenters touched an incorrect final cup failed to lure subjects substantially to

the cup last touched. Still, the catch trials involving the fake hiding of the object in a final 2nd location using the displacer and following a “peek” in which the displacer was shown as empty generated chance level responding by the subjects. The subjects did not consistently simply select the last place the displacer went, however, but rather seemed to lose the ability to track the object under these circumstances, and reverted to selecting an object location randomly.

Another subtle indication that the tamarins were sensitive to the increased difficulty that multiple hiding and invisible hiding caused was the rate of participation we observed. Subjects were much more likely to disengage from the task, or fail to respond within 60 seconds, in the later tasks (tasks 8 and 9) than they were in the earlier tasks of the experiment. This unwillingness to participate was not a result of lack of motivation, for the subjects would eagerly receive free reinforcements both before and after a session of work. It corresponded with task difficulty, the lack of acquired reinforcers with successive hidings, and particularly, the complexity of invisible displacement tasks.

It is possible that the results mean that cotton top tamarins have particular cognitive capacities, previously demonstrated by Hauser’s group in studies of problem solving and tool use, that allow them specialized abilities in object representation. Still, Hauser and others (Hauser, Kralik and Botto-Mahan, 1999) found that tamarins would often persist in responding in a trained or “ready” way despite the lack of reward for doing so, which should have caused problems in the current experiment when the final reinforced location was suddenly switched to a new one. The fact that the tamarins in this study did not persist in selecting an old reinforced location is most likely due to the kind of “thinking” induced by the method used here. Note that the tamarins were ready to alternate their choice of cups from the beginning of the experiment in the acclimation period, and this reveals a foraging mode that they used naturally in this task which seemed more typical of “win-shift” or of trying new locations once a prior location’s food was obtained. Moreover, the method did not require many responses at any particular location, and in fact, the switch to a new location occurred after 9 trials, or at most, 1 day of exposure. Without over-training at a particular location, tamarins may move more flexibly to new locations, especially if the task is set up as a foraging opportunity. Finally, it is possible that the task itself,

that of tracking an object visibly seen to a destination, controlled responding more than the tendency to choose a previously reinforced location.

Hauser and others (Hauser, Williams, Kralik, and Moskovitz, 2001) have also found a failure in tamarins to track invisible displacements, and the success in this experiment seems in contrast to those results. Upon closer examination though, the task used in which tamarins failed to track objects involved objects being forced to move in paths in occluded tubes which violated “natural” movements in the real world in the sense that they violated how objects would fall if gravity were at work. In the present experiment, the objects were moved mostly in a horizontal plane, and the hiding started out visibly, so that tracking was easier to do. When Hauser’s group trained tamarins to track visible movement of objects first, and then followed such training with invisible movements (which remain in conflict with gravity), tamarins could successfully track the final location of the object. In the present case, with few trials per task, no violations of natural movement, displacement mostly along a horizontal plane, and visible movements preceding invisible displacements, the tamarins were able to attend well and track objects’ movements readily. By this method then, their cognitive ability to represent objects was tapped without the obstacles associated with conflicts in natural movements or ready responses that needed to be inhibited.

It remains difficult to fully interpret the invisible displacement success found, because the current methodology was modified in order to control chance level responding. The deviation occurred only in the double hidings in invisible displacement, where the displacer was opened in between location visits. This “peeking” could have served as a cue to remind subjects of the object, or the lack of it. There are two reasons why the deviation in methodology does not preclude an interpretation that tamarins were succeeding in invisible displacement tasks. First, the subjects succeeded from the beginning, in *single* invisible displacement trials which did not include successive hiding and peeking. The other new world monkey tested before, squirrel monkeys failed to accomplish *single* invisible displacement in deBlois, Novak, and Bond (1998). Secondly, if the “peeking” subtracted the invisible nature of double hiding and thus made the double hiding in invisible displacement more like single hiding, then performance to the double invisible displacement tasks (Task 9) and the “catch” trials (Catch Task 9) should have been

similar to that in invisible displacement, or even in visible displacement tasks. This is clearly NOT the case. There were significant effects found between accuracies between single visible and invisible displacement (Tasks 3 and 8) and marginally significant differences between double hidings visibly and invisibly displaced (Tasks 4 and 9). While subjects could respond above chance levels to all the tasks mentioned above, they remained more accurate in those tasks in which the item was visibly displaced. Clearly the invisible movement of the object in the displacer caused a heavier cognitive load in representing the object and its final location, and this cognitive work was not erased by a “peek” to remind subjects or to inform them of the demise of the object.

Finally, the difference between exposing monkeys to 9 as opposed to 6 trials in each task could have made a difference in their understanding of the game, and thus brought success where other NW monkeys in other tasks failed. It is clear that individuals of the species squirrel monkey failed in tests of invisible displacement in the prior study, but their actual strategy during the 5 trials in which they were tested in single invisible displacement across both a single location and an A not B switch is not at all clear, especially since they responded at **below** chance level, or worse than one would do by selecting randomly across the 3 sites in the tasks. The squirrel monkeys were not tested on double invisible displacement at all in the prior study, so a direct comparison was not possible at any rate.

This study capitalized on the development of well-designed tasks from prior studies of primates and on in-depth analyses to test for simpler strategies for response. By tracking the subjects' success and any systematic tendencies uncovered by their failures, a clearer picture of tamarins' representational capacity emerged. In this case, cotton top tamarins showed many of the same tendencies for object search as do chimpanzees, orangutans, and children after 12 months of age, including a greater facility with visible displacements, accurate performance with invisible displacements, a lack of perseverance of a previously reinforced response, and cognitive limits within invisible displacement tasks. By their accurate performance, and by many aspects of their performance tendencies, tamarins demonstrate an ability to represent absent objects and to extrapolate their locations when they are visibly or invisibly moved, as have all tested great apes.

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Table 1a. Description of Procedure for Visible Displacement Tasks 1 - 5.




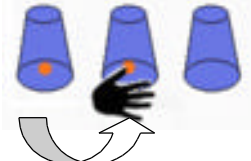
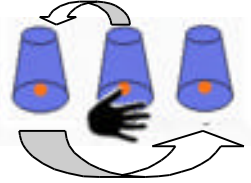
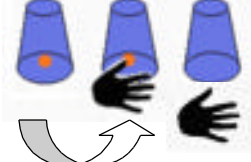
| | | | |
|-----------------|--|---|---|
| Task 1 | Single Visible Displacement |  | 9 trials, same location |
| Task 2 | A not B test: Visible Displacement |  | 9 trials, new location, repeated for all trials |
| Task 3 | Random Single Displacement |  | 9 trials, each location visited 3 times, random pattern |
| Task 4 | Double Visible Displacements |  | 9 trials, final location randomly selected. |
| Task 5 | Triple Visible Displacements |  | 5 trials. Final location randomly selected. All 3 cups used in hiding process. |
| Task 5 CATCH | Double Visible Displacement with a Final Touch |  | 4 trials. Final location randomly selected. 2 cups used in hiding, with third cup touched at the end of the trial. |

Table 1b. Description of Invisible Displacement Tasks 6 – 9.

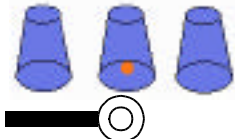
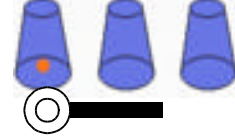
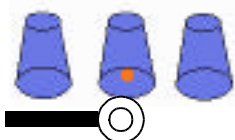
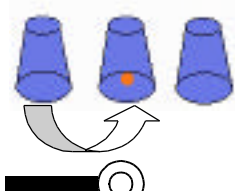
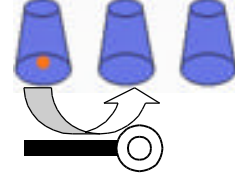
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|--------------|---------------------------------------|--|---|
| Task 6 | Single Invisible Displacement |  | 9 trials. Item is placed in the displacer, and the displacer travels to the same location every trial. |
| Task 7 | A not B Error: Invisible Displacement |  | 9 trials. Same as Task 6 except a new location is repeated for all 9 trials. |
| Task 8 | Random Single Invisible Displacement |  | 9 trials. Same as Task 6 except each location is visited 3 times, randomly dispersed. |
| Task 9 | Double Invisible Displacement |  | 9 trials. Item is placed in displacer and displacer placed successively in two locations. |
| Task 9 CATCH | Double Invisible CATCH |  | 4 trials, intermixed in the 9 trials of Task 9. Exactly as Task 9, except item is hidden during the first of two visits to two locations. |

Table 2. Individual Performances on Tasks 1 – 9. Chance Level is 33%.

| Name | Task 1 | Task 2 | Task 3 | Task 4 | Task 5 | Catch: Task 5 | Task 6 | Task 7 | Task 8 | Task 9 | Catch: Task 9 |
|---------|--------|--------|--------|--------|--------|------------------|--------|--------|--------|--------|------------------|
| Caitlin | 88 | 77 | 66 | 77 | 80 | 75 | 100 | 88 | 77 | 55 | 0 |
| Dante | 88 | 88 | 77 | 55 | 40 | 75 | 100 | 77 | 55 | 44 | 50 |
| Ophelia | 77 | 77 | 77 | 66 | 100 | 50 | 44 | 33 | 66 | 44 | 50 |
| Olympia | 66 | 55 | 55 | 66 | 60 | 75 | 66 | 88 | 55 | 66 | 25 |
| Fozzie | 77 | 100 | 88 | 88 | 75 | 40 | 88 | 66 | 66 | 44 | 0 |
| Zhivago | 77 | 55 | 66 | 44 | 40 | 50 | 44 | 44 | 44 | 55 | 75 |
| Mac | 88 | 66 | 77 | 88 | 50 | 40 | 55 | 55 | 55 | 33 | 25 |
| Oprah | 77 | 66 | 66 | 66 | 75 | 40 | N/A | N/A | N/A | N/A | N/A |

Table 3. Linear Trend Analyses of Tasks 1 – 9.

| <i>Task</i> | <i>Equation</i> | <i>R²</i> | <i>Significance</i> |
|-------------|--------------------|----------------------|---------------------------|
| Task 1 | $y=1.67x + 72.22$ | 0.059 | F(1,7)= 0.43, p=0.53 |
| Task 2 | $y=2.38x + 61.11$ | 0.129 | F (1,7)=2.24, p=0.18 |
| Task 3 | $y=5.62x + 44.10$ | 0.78 | F(1,7)=24.97, p=0.002** |
| Task 4 | $y=-0.83x + 73.61$ | 0.06 | F(1,7)=0.47, p=0.51 |
| Task 5 | $y=1x + 63.00$ | 0.018 | F(1,3)=0.05, p=0.83 |
| Task 6 | $y=5.42x + 40.97$ | 0.56 | F(1,7) = 8.81, p = 0.02** |
| Task 7 | $y=2.38x + 53.17$ | 0.103 | F(1,7) = 0.80, p=0.40 |
| Task 8 | $y=-0.24x + 61.52$ | 0.001 | F(1,7)= 0.007, p=0.93 |
| Task 9 | $y=-1.19x + 55.16$ | 0.03 | F(1,7) = 0.21, p=0.66 |

Figure Captions

Figure 1. Mean percent correct scores for all subjects for each task in visible displacement testing (left) and invisible displacement testing (right). Error bars show standard deviations. Dashed line indicates chance-level responding in the task.

Figure 2. Averaged accuracy across all subjects per trial throughout the experiment. Trials graphed include all standard consecutive trials in Tasks 1 – 9. Task 5 includes 5 consecutive standard trials (with the 4 catch trials not included). Task 9 includes 9 consecutive standard trials (with the 4 catch trials not included).

