

# What guides a search for food that has disappeared? Experiments on cotton-top tamarins

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**RUNNING HEAD: HAUSER ET AL.: Searching for food that has disappeared**

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# 1 Abstract

2 For many species, survival depends upon the capacity to track objects that either move or have been  
3 placed out of sight; for example, prey must attend to the momentary disappearance of a predator behind  
4 a bush, and species that cache their food must recall their location. What expectations do animals form  
5 when objects disappear out of sight, and if they are moving, where do they expect them to appear? The  
6 experiments reported on here with cotton-top tamarins (Saguinus oedipus) were designed to address this  
7 general problem, and to build on previously published work with the same species. Specifically, when  
8 food is launched down a vertically positioned S-shaped opaque tube, tamarins search for the food in the  
9 position directly beneath the release point, even though over several trials, it never appears in this  
10 position. Thus, not only do tamarins generate an incorrect expectation, and search in the incorrect  
11 location, they persevere with this bias. Experiment 1 shows that when the trajectory of the food shifts  
12 from the vertical to the horizontal plane, while keeping everything else constant, tamarins no longer show  
13 systematic perseverative errors, and in general, perform better on this invisible displacement task.  
14 Experiment 2 shows that subjects with experience on the horizontal task show less of a bias when tested  
15 immediately on the vertical task, but nonetheless fail overall to solve this invisible displacement problem;  
16 their performance is substantially worse than it was on the horizontal task. Experiment 3 explores the  
17 possibility that in addition to having problems with invisible displacement, tamarins also have difficulty  
18 with tubes, because they are unfamiliar with objects that contain and constrain the movement of other  
19 objects. Specifically, we presented a vertically oriented apparatus where an occluded ramp replaced the  
20 tube from Experiment 1. When a piece of food was dropped onto the occluded ramp, most subjects  
21 searched in the compartment below the release point, and did so repeatedly even though most subjects  
22 had experience in Experiments 1 and 2. Overall, results indicate that tamarins have a significant gravity  
23 bias when searching for food that has disappeared along the vertical plane, but also have more general  
24 problems tracking the hidden location of objects that have moved out of sight.

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## 29 Introduction

30 Most, if not all animals are confronted with the problem of tracking the location of objects  
31 that are no longer visible. This tracking problem is of exceptional adaptive significance, especially  
32 when one considers the variety of problems that arise in the natural world: prey attending to a  
33 predator that has disappeared behind a bush (Cheney & Seyfarth, 1985), males keeping track of  
34 their allies in cases where coalition support is necessary (Connor, Smolker, & Richards, 1992;  
35 Harcourt & de Waal, 1992), and foragers recalling where they cached food or a tool required to  
36 extract food (Balda & Kamil, 1989; Boesch & Boesch, 1984; Kamil & Jones, 1997). Although  
37 animals engaged in such behaviors clearly have the requisite mechanisms for tracking objects that  
38 have disappeared from view, and may use more than one sensory modality to do so, a challenge  
39 for those interested in the details of such mechanisms is to determine how animals represent such  
40 events in memory, and the kinds of expectations they form regarding where occluded objects  
41 might reappear (Dore & Dumas, 1987; Gagnon & Dore, 1992; Hauser, 2000). Said differently,  
42 when an object moves out of view, what information do animals extract from this event, and how  
43 do they use such information to keep track of the object? Here we address this question by looking  
44 at how a New World monkey – the cotton-top tamarin (*Saguinus oedipus*) -- searches for food  
45 that has moved out of view.

46 Plowright and colleagues (1998) recently explored this problem by testing pigeons in three  
47 different experimental paradigms, and pigeons and mynahs in a fourth. In each of the experiments,  
48 subjects were required to find food that was concealed, either statically or following movement to a new,  
49 occluded location. In general, the pigeons required training in order to solve each of these problems. For  
50 example, when a cart carrying food disappeared inside an opaque tunnel, most of the pigeons failed to  
51 follow the cart; in contrast, when the tunnel was transparent, they all successfully followed the cart. In the  
52 experiment comparing pigeons and mynahs, subjects were required to track a visibly rolling piece of food  
53 down a ramp and into an opaque compartment. There were four adjacent ramps, and thus the subject's  
54 task was to watch the food roll into one box, and then search in this box. In general, the pigeons failed to  
55 reach criterion over 75 trials, whereas the mynahs succeeded; for both species, there were individual

56 differences, with one pigeon succeeding, and one mynah requiring a block of trials before passing the  
57 test.

58           In an invisible displacement experiment by Hood (1995), children between the ages of 2.5-4.0  
59 years were presented with an open frame consisting of three short opaque pipes ("chimneys") on top, and  
60 lined up below each one, three boxes or compartments. On a given trial, an opaque tube was attached  
61 from one chimney to one compartment, and then a ball released into the tube. The child's task was to  
62 search for the ball in one of the three compartments. Young children consistently looked in the  
63 compartment directly below the release point, although in no case was the tube connected in a straight  
64 line down from the chimney to the compartment; older children searched in the correct compartment,  
65 using the configuration of the tube to find the ball. Young children appeared to be guided by the  
66 expectation that falling objects fall in a straight line. This error persisted even though the child was shown  
67 the correct location on each trial, and even though they were able to find the ball when a transparent tube  
68 replaced the opaque one; having solved the transparent tube problem, however, they were incapable of  
69 generalizing to the opaque condition. Hood interpreted this finding as evidence that young children make  
70 a gravity error, assuming that all objects falling along a vertical plane will land directly beneath the release  
71 point.

72           Hood, Hauser, Anderson and Santos (1999) ran the same tubes experiment with adult cotton-top  
73 tamarins. Like young children, the tamarins also searched in the compartment directly below the release  
74 point on the first trial, and perseverated with this response even when they failed to obtain the food  
75 reinforcer. And although some individuals were able to solve the transparent tube condition, they were  
76 unable to generalize to the opaque condition. Because both young children and adult cotton-top tamarins  
77 perseverated with their responses, even in the face of training and the failure to obtain food on dozens of  
78 trials, Hood and colleagues argued that for both young children and adult tamarins, searching for falling  
79 objects is guided by a powerful expectation that invisibly displaced objects along a vertical plane will fall  
80 directly below the release point.

81           To explore this bias further, Hood (1998) ran the same experiment on a video monitor.  
82 When the ball was released down the tube, young children pointed to the box below the release  
83 point. In contrast, when the ball was magically sucked up the tube from the bottom, young children  
84 correctly pointed to the correct box on top. Thus, the perseverative error obtained in the original

85 experiment (Hood, 1995) had nothing to do with the potentially obscure nature of tubes and their  
86 capacity to contain a moving object. At present, we don't know if the tamarins' pattern of search is  
87 due to a bias that is restricted to the vertical plane, a more general problem with invisible  
88 displacements, or some combination of these factors and others. Experiments 1-3 have been  
89 designed to explore these issues.

90

## 91 Experiment 1

92 Experiment 1 was designed to assess whether the tamarins' difficulty with the vertical  
93 tubes task was due to problems with invisible displacement in general, or to tracking occluded  
94 objects displaced along the vertical plane more specifically (Hood et al., 1999). That is, if tamarins  
95 perseverate with an incorrect search response because they are guided by the expectation that  
96 falling objects fall straight down, then by removing the influence of gravity, the tamarin's bias  
97 should go away. In contrast, if the straight-line bias persists in the horizontal plane, then other  
98 factors may account for their poor performance, such as a general problem with invisible  
99 displacements.

100

## 101 Methods

### 102 *Subjects*

103 Subjects were 10 adult (4 males, 6 females; Table 1) cotton-top tamarins. This species is  
104 native to the rainforests of Colombia, and is a member of the New World monkey family. All  
105 subjects were born in captivity at the New England Regional Primate Research Center,  
106 Southborough, MA, and subsequently transported to the Primate Cognitive Neuroscience  
107 Laboratory at Harvard University where they are housed in social groups. Some subjects had  
108 experience with the vertically positioned tube apparatus used in the original experiment conducted  
109 by Hood and colleagues (1999), whereas the other subjects were naïve. All subjects, however,  
110 had a history of experience with experimental tasks of cognitive ability (Hauser, 1997, 1998;

111 Hauser et al., 1995; Hauser, Kralik, & Botto-Mahan, 1999; Santos, Ericson, & Hauser, 1999). The  
112 present experiments therefore represent a continuation of our studies of object knowledge in the  
113 cotton-top tamarin.

114 All subjects were fed on a diet of marmoset monkey chow, crickets, mealworms, sunflower  
115 seeds, peanuts, fruit, and yogurt. To make sure that our subjects were motivated to search for  
116 food in the experimental task, the above food items were provided at the end of the day, after  
117 subjects had run in these and other experiments; further, the food reward used in the search task  
118 (see below) was never provided as part of the daily diet, and was a highly desirable type of food  
119 for the tamarins. Ad libitum access to water was provided throughout the day. Subjects lived in  
120 their home room except when they were removed to run in an experiment. Subjects were  
121 removed from the home room by luring them into a transport box with a raisin. If the target subject  
122 failed to leave the home cage within 5-10 minutes, we attempted to lure a different subject.

123

## 124 *Apparatus*

125 The apparatus was similar to that used in the vertical version of this experiment (Hood et  
126 al., 1999). In this case, the apparatus rested horizontally on a table, rather than vertically (Figure  
127 1, top).

128 Subjects were placed in a transparent Plexiglas testing chamber; the front panel was solid  
129 except for a tiny rectangular opening at the bottom. This test chamber has been used in a number  
130 of experiments on cotton-top tamarins in our lab (Hauser, 1997, 1998; Santos et al., 1999), and is  
131 thus highly familiar to them. The opening in the front panel was covered by a transparent  
132 Plexiglas shield which could be raised or lowered by the experimenter, providing control over the  
133 subject's access to the apparatus. When the shield was raised, the subject had access to each of  
134 the three doors covering the compartments.

135 The food rewards given to the subjects were round pieces of breakfast cereal, either  
136 "Cocoa Puffs" ® or "Kix" ®, depending on the preference of the individual monkey. These foods  
137 were chosen because their size and round shape allowed them to roll easily through the tubes that  
138 attached to the apparatus, and because the tamarins were motivated to search for them. Because

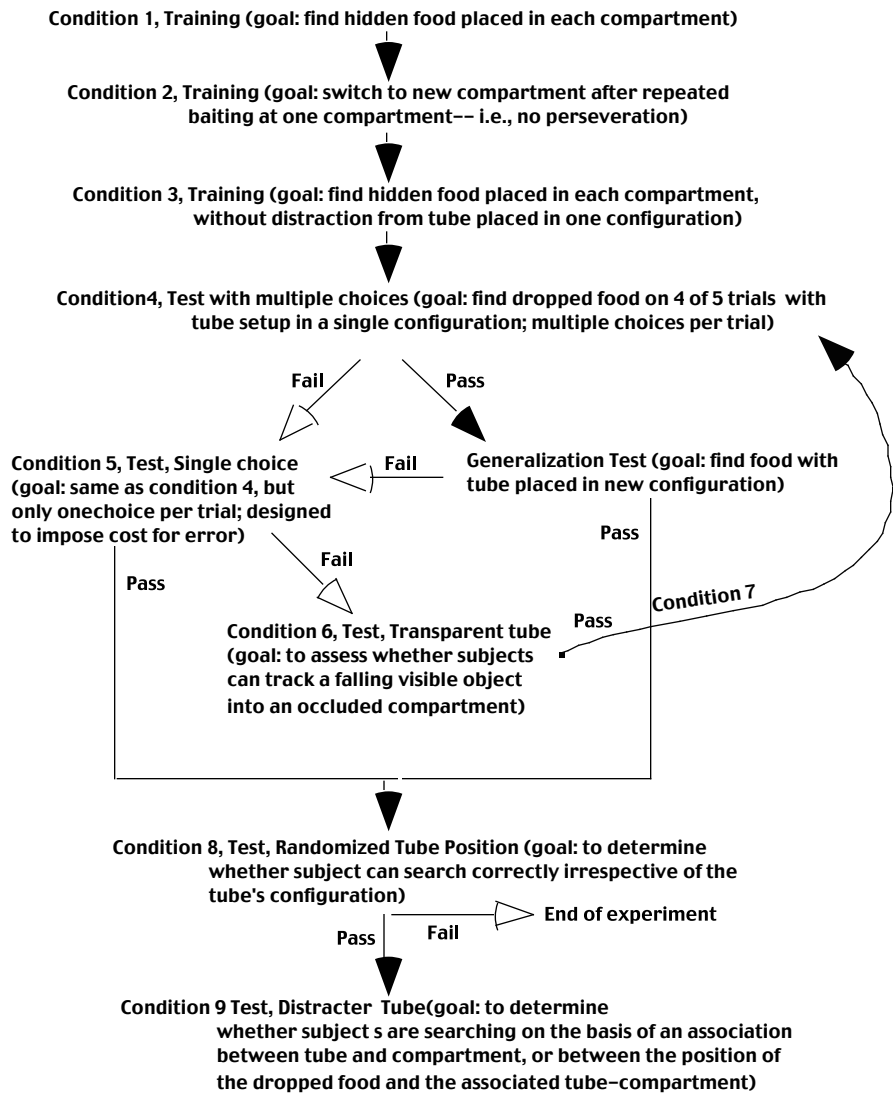
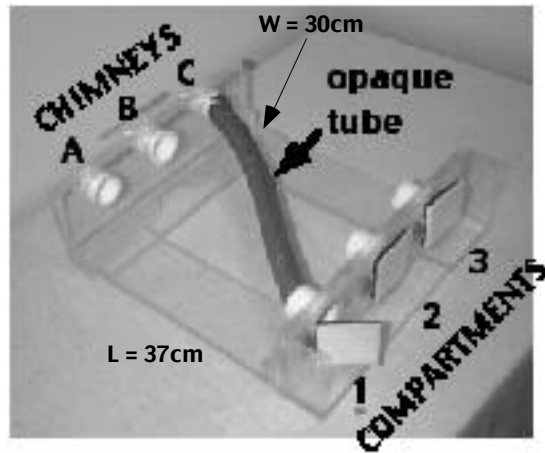
139 these food rewards were substantially larger than those given during the vertical task, we ran only  
140 10 trials per session in the horizontal task, as opposed to 20 trials per session on the vertical task  
141 (Hood et al., 1999); thus, comparisons between tasks are represented in terms of the proportion  
142 of trials in which subjects find the food reward.

143 During all trials, white noise was played through a loud speaker located next to the test  
144 chamber. This eliminated the possibility that subjects could use auditory cues to determine the  
145 location of the food reward after it traveled down the tube.

146

### 147 *Procedural synopsis*

148 The procedure used in this experiment closely matched that used in the original vertical  
149 tubes experiment (Hood et al., 1999); a flow chart of the chronology of the experiment, divided into  
150 conditions, is presented at the bottom of Figure 1. To familiarize subjects with the apparatus, we  
151 started with a series of training conditions (1-3) involving experience opening doors, retrieving food  
152 rewards, and avoiding perseverative biases. Subjects then moved on to one test and one  
153 generalization condition in which they were allowed multiple choices in searching for the invisibly  
154 displaced food reward (Condition 4); if they failed to reach criterion on the multiple choice  
155 condition, they were rerun using only a single choice procedure, thereby increasing the costs of  
156 making an error (Condition 5). Subjects who failed the test or generalization condition were  
157 moved onto a training condition involving a transparent tube (Condition 6). Given that they could  
158 now see the object displaced, we anticipated that they would solve this task and then, potentially,  
159 use this experience to generalize to the original opaque tube condition (Condition 7). Subjects  
160 who passed (i.e., reached criterion) the test and generalization sessions of either the multiple- or  
161 single-choice condition were run on two more test conditions; these final conditions were designed  
162 to provide more detailed information on the factors guiding success in the search task. More  
163 precisely, we wished to establish whether subjects had solved the problem of invisible  
164 displacement along a horizontal plane, or had simply picked up on a set of associations that would  
165 predict the rewarded compartment. Thus, individuals who passed all of the previous conditions  
166 were given sessions where the single tube changed configuration on each trial (Condition 8), and



168

169 Figure 1. Top: Apparatus for testing cotton-top tamarins on an invisible  
170 displacement along a horizontal plane. Chimneys, compartments, and tube were  
171 opaque, whereas the frame was transparent. Tamarins sat in a test box opposite  
172 compartments. Bottom: A flow chart of the chronology of experimental conditions  
173 for Experiment 1.  
174

175 sessions where two tubes were set up, one carrying the food reward and one acting as a distracter  
176 (Condition 9).

177

### 178 *Conditions 1-3, Training Phase*

179 Subjects were run on three training conditions to insure that they were free from any  
180 biases to select one of the three doors preferentially (Condition 1), that they could switch to a new  
181 door following repeated selection of one door (Condition 2), and that they were not influenced in  
182 their search behavior by the addition of a tube to the apparatus (Condition 3). In every session,  
183 during both training and testing, the experimenter began by opening each of the three doors to  
184 show that the compartments were empty, then closing them again. The Plexiglas shield was then  
185 raised, allowing the subject to open more than one door and search the compartments (i.e.,  
186 spontaneous searches). Once the subject had ceased spontaneous searching (pre-trial phase),  
187 the Plexiglas shield was lowered, and any doors that the subject had opened were closed. The  
188 subject then watched as a piece of food was moved back and forth above the compartments. This  
189 step was implemented to insure that the subject was visually tracking the food item. We never  
190 released the food item if the subject looked away. Although in the early portion of training, some  
191 subjects failed to track the moving food item, by the end of the second training phase, all subjects  
192 readily attended to the experimenters' actions, tracking the food until it was released.

193 During the training phase, the experimenter opened one of the doors, checked to make  
194 sure the subject was watching the hand holding the food, placed the food inside the compartment,  
195 and closed the door again. The Plexiglas shield was raised and the subject was allowed to search  
196 for the food; a search was terminated once the subject successfully retrieved the food. In order to  
197 advance to the next condition, however, subjects were required to retrieve the food on the first try  
198 on 9 out of 10 trials.

199 In Condition 1, the placement of food into one of the three compartments was determined  
200 by a random number generator. In Condition 2, we started with 10 trials of random placement of  
201 the food reward behind one of the doors (i.e., the same set-up as in the first training phase) and  
202 then followed with 5 consecutive trials in which the food was placed in the same compartment.  
203 Then, on the sixteenth trial, the location of the food was switched to a new compartment, and the  
204 subject had to choose correctly on this “switch” trial. This phase was designed to test whether the  
205 tamarins could switch to a newly reinforced compartment following a sequence of 5 trials in which  
206 the same compartment was reinforced; we expected the tamarins to have some problems with this  
207 phase given their tendency in other experiments to perseverate with the same response when  
208 they have previously been rewarded for their actions (Hauser, 1999; Hauser et al., 1999; Hood et  
209 al., 1999). In Condition 3, the experimenter attached an opaque plastic tube from either the  
210 extreme left or right chimney to the diagonally corresponding compartment at the opposite end of  
211 the apparatus. Once the tube was in place, the subject was allowed to search behind the doors  
212 and check to see that the containers were empty. The trial then proceeded as in Condition 2, with  
213 food placement determined by a random number generator for 10 trials, followed by 5 trials of  
214 placing the food in the same compartment, and a sixteenth trial involving a switch. In order for a  
215 subject to move from one training condition to the next, we required 90% accuracy.

216

#### 217 *Condition 4, Test and Generalization with a single tube: Multiple* 218 *choices*

219 In view of the test subject, the experimenter attached an opaque tube in the same  
220 orientation as in Condition 3. A small section of the upper portion of the tube (i.e., the part furthest  
221 from the subject) was transparent and inclined at roughly 30 degrees, allowing the subject to see  
222 the piece of food placed and then launched into the rest of the tube which was opaque and  
223 positioned horizontally with respect to the table. This piece of clear tubing was added so that the  
224 amount of time the tamarins saw the food before it disappeared inside the opaque tube was  
225 equivalent to the vertical condition where the food was dropped from above; thus, the release  
226 distance from the experimenter's hand to the opaque portion of the tube was the same in the

227 vertical and horizontal conditions. By plucking the piece of food with sufficient force, we were able  
228 to insure that the food traveled all the way down the tube on each trial. Again, the experimenter did  
229 not displace the food into the tube until the subject was attending to this location; if the subject  
230 looked away during the food's release, the trial was aborted and a new trial started. Half of the  
231 subjects were first presented with a tube running from the extreme left to the extreme right,  
232 whereas the other subjects were given the opposite configuration; each subject received the same  
233 configuration as in Condition 3.

234         Subjects were given a pre-trial phase, allowing them to view the empty compartments and  
235 then open either one or all doors to each compartment. When spontaneous searching ended, all  
236 of the doors were closed if they had been opened, and a piece of food was moved back and forth  
237 across the upper portion of the apparatus to insure visual tracking. Once the subject tracked, the  
238 food was released into the tube nearest the experimenter. The shield was then raised and the  
239 subject allowed to search until it found the food; thus, if a subject picked the incorrect  
240 compartment first, it was allowed to search the remaining two compartments. All trials were  
241 recorded onto video tape, and the order of door-opening noted by the experimenter onto a  
242 checksheet.

243         If the subject found the food correctly (i.e., first door opened) on at least 4 out of 5  
244 consecutive trials, they proceeded to the generalization condition. The session was terminated if  
245 the subject failed to reach this criterion after 10 trials.

246         Following success on the test condition, subjects were run on a generalization condition  
247 to assess whether they had solved the invisible displacement problem, or simply learned to search  
248 in the previously reinforced compartment. The tube was removed from its previous configuration  
249 and reconnected. The new configuration consisted of a connection from the middle chimney to  
250 the compartment opposite to where it had terminated before; for example, if the tube originally  
251 terminated in the extreme right compartment, it was switched to the extreme left compartment for  
252 the first generalization test. Once connected, the same pre-trial and search procedures were  
253 implemented and the subject's door opening pattern recorded.

254         Subjects that failed any of the above test conditions were run on a series of conditions  
255 designed to facilitate comprehension of the task. Thus, to increase the costs of making an

256 incorrect choice, subjects were given only one choice per trial (Condition 5); to determine whether  
257 they could track a visible displacement into an occluded compartment, subjects were run with a  
258 transparent tube (Condition 6); subjects succeeding on the transparent tube condition were moved  
259 back to opaque to assess whether they could generalize from their success (Condition 7). Finally,  
260 subject passing the opaque condition were tested on two advanced conditions involving a set of  
261 trials where the position of the tube varied from trial to trial (Condition 8), and where a distracter  
262 tube was put in place along with the correct tube (Condition 9).

263           Subjects were tested only once each day, and typically, were tested five days per week.  
264 Consequently, Experiment 1 was run over a period of approximately 1-2 months.

265

## 266 *Statistics*

267           Non-parametric, two-tailed tests were used throughout, with significance set at  $p < 0.05$ .  
268 Given that we presented subjects with a 3-choice option on each condition, all search patterns  
269 were evaluated with a 3-choice binomial test (Siegel & Castellan, 1988); this is the statistical  
270 procedure used by Hood (1995) and by Hood et al. (1999) in the original tubes experiments. The  
271 equation for a 3-choice binomial is the following:

272

$$273 \quad p(X_1 = n_1 \text{ and } X_2 = n_2 \text{ and } X_3 = n_3) = (n! / (n_1! n_2! n_3!)) * (p_1)^{n_1} * (p_2)^{n_2} * (p_3)^{n_3}$$

274

275            $p$ : the probability that  $X_1 = n_1$  and  $X_2 = n_2$  and  $X_3 = n_3$

276            $X_1$ : the random variable representing location 1

277            $n_1$  : the number of trials in which location 1 was chosen

278            $p_1$  : the probability of choosing location 1 at random ( $p_1 = p_2 = p_3 = 0.33$ )

279

280

## 281 Results

### 282 *Conditions 1-3, Training*

283 All 10 subjects reached criterion for each of the three training phases. Subjects reached  
284 criterion in 2.3 sessions (SD = 1.5) for Condition 1, in 1.4 sessions (SD = 0.8) for Condition 2,  
285 and in 2.0 sessions (SD = 1.7) for Condition 3. Subjects with experience on the vertical tube  
286 apparatus moved through each of the training conditions at a faster pace than did naïve subjects,  
287 but in none of these conditions was this difference statistically significant (Mann Whitney tests:  $p >$   
288 0.05).

289

### 290 *Condition 4, Test and generalization with a single tube: Multiple* 291 *choices per trial*

292 Data on first trial and session performance for Experiment 1 are presented in Table 2.  
293 Subjects did not show systematic biases in their responses on the first trial ( $p > 0.05$ ). Three  
294 subjects passed the test condition within 5 trials, while the remaining subjects failed to reach  
295 criterion; of those that passed, one had prior experience on the vertical tubes, whereas the other  
296 two were naïve. Of the 7 that failed, there were no systematic biases in their patterns of search.  
297 Of the three subjects that reached criterion on the test condition, none succeeded on the  
298 subsequent generalization. Two searched in the straight compartment, while the third searched at  
299 the previously correct (i.e., reinforced) location.

300 Performance on the second test session was comparable to the first. On the first trial,  
301 there was an overall preference for the middle container ( $p = 0.014$ ). One subject passed the test,  
302 but then failed on the generalization test, searching at the previously correct location. Those that  
303 failed to reach criterion showed no biases in their responses. Overall, subjects did not show  
304 systematic biases with respect to their search patterns, and most subjects failed to show high  
305 levels of accuracy in searching for the invisibly displaced food. This either suggests that they had  
306 difficulty with invisible displacement along the horizontal axis or that the costs of searching multiple

307 compartments was insufficient, thereby resulting in somewhat random patterns of search. The  
308 single-choice condition (5) was designed to rule out this alternative explanation.

309

310 *Condition 5, Test and generalization with a single tube: Single-Choice*  
311 *per trial*

312           Nine subjects were given the same task as described above, but this time were allowed  
313 only one search response per trial; one subject from the multiple-choice condition could not be run  
314 due to health problems. On the first trial of session 1, there were no biases with respect to the  
315 pattern of search ( $p > 0.05$ ). This time, four subjects passed the test in less than 10 trials, and  
316 these were the same subjects who passed one session of the multiple-choice condition. Of those  
317 who failed, there were no systematic search biases ( $p > 0.05$ ).

318           On the subsequent generalization, one subject chose correctly; this subject moved on to  
319 the advanced conditions. The remaining three subjects searched at the previously correct  
320 location. These subjects, together with the four who failed to pass the test, moved on to a second  
321 session of the one-choice condition; one subject developed behavioral difficulties and was no  
322 longer run.

323           On the second, one-choice session, a significant number of subjects selected the correct  
324 compartment ( $p < 0.05$ ). Again, prior experimental history was not a factor in the pattern of  
325 successes and failures in this condition. Three of the seven subjects passed the test in four trials,  
326 but on the following generalization, all of them searched at the previously correct location. The four  
327 subjects that failed to pass showed no significant search biases ( $p > 0.05$ ).

328           Overall, even though the search costs increased, subjects had difficulty locating the  
329 invisibly displaced food reward. In parallel with the multiple-choice condition, however, subjects  
330 generally showed no systematic search biases. This pattern of search stands in contrast with the  
331 findings for the vertical tubes task (Hood et al., 1999), but also shows that tamarins have some  
332 difficulty with invisible displacements, irrespective of orientation. To determine whether some  
333 experiences might facilitate their performance on the invisible displacement task, we next tested  
334 subjects with a transparent tube oriented along the horizontal axis.

335

336 *Condition 6, Test with a single transparent tube*

337           Eight subjects were tested using a transparent tube. On the first trial, a significant  
338 proportion of subjects were correct on the first trial ( $p = 0.004$ ). Seven of the eight subjects  
339 reached criterion in two sessions or less. Four subjects were successful on the first generalization  
340 condition with a new tube configuration, and were also successful when the position of the  
341 transparent tube was randomized across trials. Three subjects failed on this condition, and were  
342 thus were dropped from the experiment.

343

344 *Condition 7, Retest with a single opaque tube: single choice*

345           On the first trial of the single-choice opaque tube, a significant proportion of subjects  
346 picked the correct compartment ( $p=0.05$ ). All four subjects reached criteria in 2 sessions or less.  
347 Three subjects then chose correctly in the generalization condition. The other subject continued to  
348 search at the previously correct location, and was dropped from the experiment.

349

350 *Conditions 8 & 9, Randomized tube position and distracter tube*

351           All three subjects who succeeded in the test and generalization conditions with opaque  
352 tubes searched in the correct compartment on the first trial of the randomized tube position. Two  
353 individuals continued to succeed at this task, each showing 70% correct responses ( $p < 0.01$ ). The  
354 third subject did not perform well in this condition, showing a bias for the straight container ( $p =$   
355  $0.05$ ).

356           The two subjects who were successful on the randomization test moved on to the two-  
357 tube distracter condition. Both subjects chose correctly on the first trial. One subject reached  
358 criterion in eight trials, succeeded on the second generalization session when the tubes were  
359 placed in a novel configuration, and only searched in the compartment associated with the  
360 distracter tube on 11% of trials. The other subject passed the test condition in five trials, failed to  
361 generalize to a new tube configuration, and never searched in the compartment associated with

362 the distracter tube. Although our sample size is admittedly small, these results suggest that in  
363 solving the invisible displacement, neither subject was strictly using the association between the  
364 location of the food in the compartment and the end of the opaque tube.

365

## 366 Discussion

367           When young children and adult cotton-top tamarins are presented with an invisible  
368 displacement along a vertical trajectory, they perseverate with a highly non-random response. As  
369 Hood and colleagues (Hood, 1995, 1998; Hood et al., 1999) have argued, these organisms  
370 appear to be guided by a bias, one that causes them to search for a fallen object in a location  
371 directly beneath the release point – a gravity bias. Experiment 1, together with the ones that  
372 follow, were designed to explain why the tamarins fail to search in the correct location for objects  
373 that are invisibly displaced along a vertical trajectory. Specifically, do they have a general problem  
374 with invisible displacements or do they have a specific problem with vertically displaced objects  
375 that move out of sight?

376           In contrast to their search patterns on the original vertical tube set-up (Hood et al. 1999),  
377 tamarins implemented different search behavior on the horizontal version of this task, and in  
378 general, performed better than they did on the vertical set-up. Perhaps the most revealing  
379 difference between the two tasks emerged from the first trial performance results. In the original  
380 vertical task (Hood et al. 1999), most subjects searched in the compartment directly beneath the  
381 release point, and then perseverated with this response over the course of the experiment. In the  
382 horizontal task, however, there was no bias on the first trial, and although some subjects failed to  
383 advance to subsequent conditions, they did not develop extreme response biases to particular  
384 compartments or tube configurations. By the fourth session of the horizontal task, there was a  
385 significant first-trial effect with the majority of subjects searching correctly on the first trial.

386           To understand better the differences between the vertical and horizontal search tasks, it is  
387 useful to examine the tamarins' performance in each condition. In particular, 5 out of 9 (55%)  
388 subjects reached criteria on the original vertical task, but only 2 were able to generalize. On the  
389 comparable horizontal task, 7 out of 10 (70%) reached criteria, and 3 subjects generalized

390 successfully. In the vertical task, no subject generalized from the transparent tubes back to the  
391 opaque tubes, whereas all 4 subjects tested on the horizontal task chose correctly on the first trial  
392 of opaque, and reached criteria as well. Critically, subjects tested on the vertical task failed to  
393 reach the advanced conditions that a small sample of subjects tested on horizontal attained.  
394 Thus, two subjects successfully located the food on the horizontal task when it was randomly  
395 moved to novel configurations, and when a distracter tube was inserted into the apparatus. Thus,  
396 unlike the tamarins tested on the vertical condition, and children tested by Hood (1999) with the  
397 video monitor representation of the vertical apparatus and the dropping condition, two tamarins  
398 tested on the two-tube horizontal task were generally able to locate the food by means of tracking  
399 the invisible displacement. Although the number of subjects represented here is admittedly small,  
400 it suggests that the capacity is present in the species, at least under some testing conditions.

401         Subjects in both the vertical and horizontal tasks developed a slight preference to search  
402 at the middle compartment. This preference was most pronounced in the horizontal task,  
403 especially following failure on a generalization trial. This search pattern may reflect an  
404 intermediate strategy to approximate the position of the unseen food; at present, however, we do  
405 not have a clear understanding of why this pattern emerged.

406         The results presented in Experiment 1 suggest that the systematic and repeated search  
407 error exhibited in the vertical tubes task may be guided by a strong bias, rather than an inability to  
408 solve invisible displacements in general. The fact that at least some tamarins can solve an  
409 invisible displacement when the trajectory is horizontal, rules out the hypothesis that errors on the  
410 vertical condition are due to subjects' difficulties with tubes. Nonetheless, some tamarins had  
411 problems with the horizontal task, suggesting that invisible displacements, together with other  
412 factors, may contribute to their problems in searching for the occluded food. Experiments 2 and 3  
413 were designed to address some of these factors.

414

## 415 Experiment 2

416 In the original invisible displacement experiment with tamarins tested on vertical tubes  
417 (Hood et al., 1999), most of the tamarins searched in the compartment beneath the release point  
418 on the first trial, and then perseverated with this response for several trials. All subjects were  
419 naïve with regard to tubes, as well as experimental tasks involving invisible displacement. It is  
420 therefore important to determine whether certain kinds of experiences might influence the patterns  
421 of search. Although subjects with prior experience on the vertical apparatus fared no better than  
422 naïve subjects on the horizontal task, it is possible that those subjects tested first on horizontal  
423 would do better on vertical search. To explore this possibility, we used the original vertical tubes  
424 apparatus and design (Hood et al. 1999) to test subjects within one week of their experience with  
425 the horizontal search task. If experience with tubes and invisible displacement plays a significant  
426 role in performance, then we would expect such experienced subjects to search in the correct  
427 compartment on the first trial, and to be able to generalize to novel configurations of the tube.

428

429

## 430 Methods

### 431 *Subjects*

432 Five cotton-top tamarins previously tested on the horizontal search task (ID, RB, ES, EM,  
433 MR) were run on the vertical tubes search task. Subjects started this task within one week of  
434 finishing the horizontal search.

435

### 436 *Apparatus*

437 We used the same apparatus as in Experiment 1 and in the original report by Hood and  
438 colleagues (1999). The only procedural difference from the Hood et al. experiment was that we  
439 used Kix® or Cocoa Puffs® as food rewards, as opposed to raisins, and ran 10 trials per session

440 as opposed to 20 trials. We considered these differences to be minimal when contrasted with the  
441 potential costs of running subjects on longer sessions and with relatively novel food.

442

## 443 *Procedure*

444 The procedure for this experiment was identical to Experiment 1 as well as the experiment  
445 run by Hood et al. (1999); see also Figure 1. In brief, all subjects received three training  
446 conditions and then moved on to the test conditions. Three subjects were tested with a tube  
447 running from the far upper left to the far lower right, whereas the other two were tested with the  
448 opposite configuration. If subjects searched in the correct compartment on 4 out of 5 trials, the  
449 configuration of the tube was changed; the tube was attached from the middle chimney to either  
450 the far lower right or far lower left. If subjects failed this initial condition, involving multiple  
451 opportunities within a trial to find the food, they were moved to a condition where only one search  
452 was permitted per trial. If subjects failed this condition, they were transferred to the transparent  
453 tube condition. If they succeeded with the tube in one configuration, they were transferred to a  
454 condition where the tube's configuration changed on each trial. Finally, if they passed the random  
455 transparent tube condition, they were put back on the opaque test condition.

456 Subjects were tested only once each day, and typically, were tested five days per week.  
457 Consequently, Experiment 2 was run over a period of approximately one month.

458

## 459 **Results**

### 460 *Conditions 1-3, Training*

461 The mean number of sessions to pass Condition 1 ( $X = 7.9$ ;  $SD = 6.1$ ) was greater than in  
462 the horizontal task of Experiment 1 ( $X = 2.3$ ;  $SD = 1.5$ ), but this difference can be accounted for  
463 by two animals that performed poorly; the mode for this phase was 1.0 session. All animals  
464 passed Condition 2 in one session. The mean number of sessions to pass Condition 3 was 3.4  
465 ( $SD = 2.1$ ) with a mode of 1.0 session.

466

467 *Condition 4, Test and generalization with a single tube: Multiple*  
468 *choices per trial*

469 Data on first trial and session performance for Experiment 2 are presented in Table 3. On  
470 the first trial of the first session, there was no significant bias to pick one compartment over the  
471 others ( $p > 0.05$ ). Only two of the five subjects reached criterion on the first test condition, and  
472 both subjects failed on the generalization, picking either the straight compartment or the previously  
473 reinforced compartment. There was no significant bias in terms of the distribution of searches  
474 across the session

475 On the first trial of the second session, there was no significant bias to pick one  
476 compartment over the others ( $p > 0.05$ ). None of the subjects reached criteria, and there were no  
477 search biases.

478

479 *Condition 5, Test and generalization with a single tube: Single choice*  
480 *per trial*

481 On the first trial of the first session, there was no significant bias to pick one compartment  
482 over the others ( $p > 0.05$ ). Only one subject reached criterion, and then failed to generalize.  
483 There was no significant search bias across the session ( $p > 0.05$ ).

484 On the first trial of the second session, there was no significant bias to pick one  
485 compartment over the others ( $p > 0.05$ ). Two subjects reached criterion. Neither subject passed  
486 the generalization test.

487

488 *Condition 6, Test with a single transparent tube*

489 On their first trial, there was no significant bias to pick one compartment over the others ( $p$   
490  $> 0.05$ ). On the first session, only two subjects reached criterion, and both were correct on the  
491 generalization test. On the second session, there was no significant bias to pick one compartment

492 over the others ( $p > 0.05$ ). Four subjects reached criterion, but only one subject passed the  
493 generalization condition.

494 All subjects were transferred to the random transparent tube condition. Overall,  
495 performance declined, with no significant search bias over two sessions ( $p > 0.05$ ).

496 Although none of the subjects reliably passed the randomized transparent tube condition,  
497 one subject came close. We thus tested her on the original opaque tube condition. She failed to  
498 reach criterion on two consecutive sessions.

499

## 500 Discussion

501 Results from Experiment 2 allow us to make two points. First, subjects performed poorly  
502 on the vertical task, even though all subjects had prior experience with an invisible displacement  
503 along a horizontal trajectory. In other words, although some of our subjects successfully reached  
504 criterion on the horizontal trajectory, they were not able to use the information gained from this  
505 experience in a different invisible displacement problem. Furthermore, even though subjects  
506 tested on the horizontal transparent condition were able to solve this problem, and to some extent,  
507 generalize to a horizontal opaque condition, few subjects were able to pass the transparent  
508 vertical condition, and none generalized to the opaque vertical condition. Second, although  
509 experience with the horizontal task failed to improve the tamarins' overall success on the vertical  
510 task, it appeared to have some effect on their initial and subsequent search behavior.

511 Specifically, although naïve subjects tested on the vertical task appeared to expect the food to  
512 land in the compartment below the release point (Hood et al. 1999), subjects with experience on  
513 the horizontal task did not. None of the subjects tested in Experiment 2 exhibited a search bias in  
514 either the first trial, or across the sessions of the conditions run.

515 Results from Experiment 2 further support the claim that tamarins have greater difficulty  
516 with invisible displacements when the trajectory is vertical as opposed to horizontal. These results  
517 also suggest that certain kinds of experience may alter an individual's specific patterns of search.  
518 The tamarins tested on the vertical apparatus for the first time appeared to expect the food to land  
519 in the compartment below the release point. In contrast, subjects with prior experience on the

520 horizontal apparatus did not generate such specific expectations; nonetheless, they failed to learn  
521 from their experience on the horizontal task.

522

## 523 Experiment 3

524 In the natural world, there are few containers. Tubes are artifacts —human creations. Given  
525 their lack of experience with tubes, it is possible that the tamarins' difficulties with both vertical and  
526 horizontal search tasks were due to their lack of experience with containers and containment, especially  
527 with respect to the propagation of food from one location to another. To explore the possibility that the  
528 physical properties of a tube contribute to the difficulty of the invisible displacement task, in Experiment 3  
529 we presented the tamarins with an apparatus that was virtually identical to the vertical tube apparatus  
530 except that an occluded ramp replaced the tube. Consequently, we asked whether the tamarins'  
531 performance would both improve, and shift away from the systematic and perseverative search bias,  
532 when the invisible displacement was no longer strictly associated with a container. This experiment also  
533 sought converging evidence on a second vertical task.

534

## 535 Methods

### 536 *Subjects*

537 We tested 12 adult cotton-top tamarins, five males and seven females. Most, but not all  
538 subjects had been run on the search task with vertically- and horizontally-oriented tubes (Table 4).  
539 Subjects were tested approximately 6-8 weeks after Experiment 2 was completed.

540

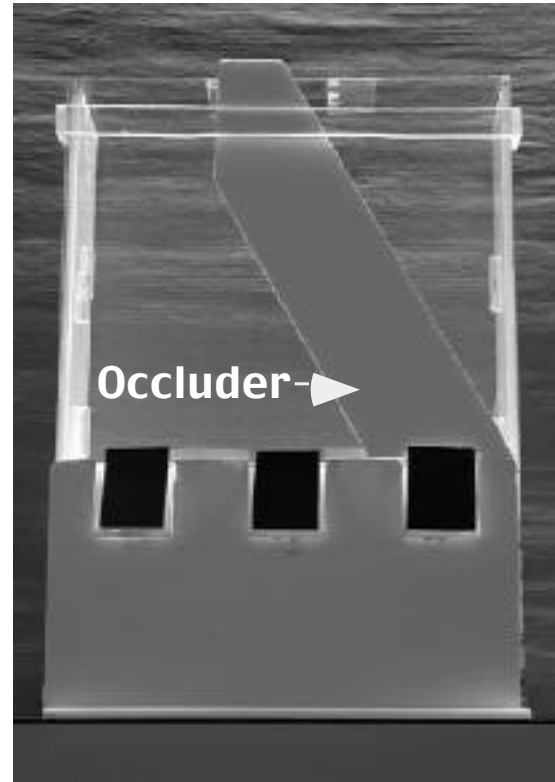
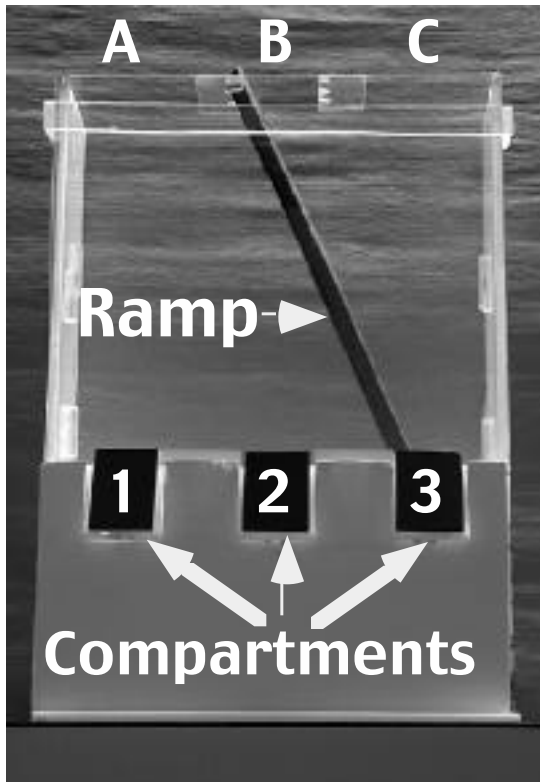
### 541 *Apparatus*

542 The apparatus was similar to the vertical tube apparatus used in the original Hood et al.  
543 (1999) experiment, as well as in Experiment 2. It consisted of a Plexiglas box (31cm L x 14cm W  
544 x 45cm H) with an open top and back, opaque sides, a front whose upper part was transparent,  
545 and a bottom part that was opaque (Figure 2). Attached to the top of the front panel were notches

546 in which we could place the upper ends of the ramps; these notches were functionally like the  
547 chimneys in the tube apparatus. At the bottom of the front panel were three compartments; each  
548 one had a black, hinged door (6cm L x 5cm W) that could be opened to gain access to the  
549 compartment behind it. Black Plexiglas ramps could be connected from the notches to the  
550 compartments at the bottom of the apparatus. White foamcore occluders (37cm L x 8cm W or  
551 33cm L x 8cm W) could then be placed against the front panel in the same configurations as the  
552 ramps, thereby concealing the ramps from the subject's view.

553

## Release positions



554

555

556 Figure 2. Apparatus for testing cotton-top tamarins on an invisible displacement  
557 using ramps and a vertical trajectory. Ramp, occluder, compartments, and lower  
558 part of the frame were opaque, whereas the upper part of the frame was  
559 transparent. Tamarins sat in a test box opposite the compartments.  
560

561

## 562 *Procedure*

563           The procedure used in this experiment was essentially the same as in Experiments 1 and  
564 2 (see Figure 1). To familiarize subjects with the apparatus, we started with a training phase  
565 (Conditions 1-3). Subjects then moved on to test and generalization conditions (Condition 4 and  
566 5). If they failed these conditions, they were moved to an unoccluded ramp (Condition 6),  
567 paralleling the transparent tube conditions of Experiments 1 and 2; the unoccluded ramp was  
568 designed to help subjects understand how falling objects move across the ramp, and thereby  
569 potentially facilitate their ability to pass the occluded ramp task. If subjects passed the unoccluded  
570 ramp condition, they moved back to the original occluded ramp condition (Condition 7). Finally, if  
571 subjects passed Condition 7, they were run on two more test conditions, designed to provide  
572 more detailed information on the factors guiding success in the search task. More precisely, we  
573 wished to establish whether subjects had acquired an understanding of invisible displacement, or  
574 had simply picked up on a set of associations that would predict the rewarded compartment. Thus,  
575 each subject was tested on Condition 8 where the position of the occluded ramp changed from  
576 trial to trial, and Condition 9 involving two occluded ramps (i.e., one distracter ramp).

577           Subjects were tested only once each day, and typically, were tested five days per week.  
578 Consequently, Experiment 3 was run over a period of approximately 1-2 months.

579

## 580 **Results**

### 581 *Conditions 1-3, Training*

582           All 12 subjects reached criterion for each of the three training phases. Subjects reached  
583 criterion, on average, in 2 sessions (SD = 0.43) for Condition 1, and in 1 session (SD = 0) for  
584 Conditions 2 and 3.

585

586 *Condition 4, Test and generalization with a single tube: Multiple*

587 *choices per trial*

588

589           Results for Experiment 3 are presented in Table 5. On the first trial of session 1, a  
590 statistically significant number of subjects searched in the straight compartment ( $p = 0.001$ ).  
591 None of the twelve subjects chose the correct location on the first trial. One subject passed the  
592 test condition in the first session, but then failed the generalization. Across the entire session,  
593 there was a statistically significant bias to search in the straight box ( $p = 0.0001$ ).

594           Eleven subjects were tested again (session 2) on the first test condition; one subject gave  
595 birth to twins and was dropped from the experiment. On the first trial, a significant number of  
596 subjects searched in the straight compartment ( $p = 0.01$ ). Across the session, subjects failed to  
597 show a significant search bias ( $p > 0.05$ ). Five subjects reached criteria, but only one passed the  
598 generalization trial; this subject was moved on to Conditions 8 and 9. All four subjects that failed  
599 the generalization trial tended to search in the previously correct location throughout the session.  
600 In neither session 1 nor 2 were there differences in the patterns of search for subjects with prior  
601 experience on tubes and those without.

602

603 *Condition 5, Test and generalization with a single tube: Single choice*

604 *per trial*

605           Nine subjects were run on Condition 5 because one subject from the previous condition  
606 moved on to Conditions 8 and 9, and one subject gave birth. On the first trial of session 1, a  
607 significant number of subjects selected the correct compartment ( $p = 0.01$ ). Seven subjects  
608 reached criteria, but only two passed the generalization trial and thus moved on to Conditions 8  
609 and 9; most subjects selected the previously reinforced compartment ( $p < 0.05$ ). The two subjects

610 that failed to reach criteria searched significantly more often in the straight compartment ( $p =$   
611 .002).

612         Seven subjects were tested on a second session of Condition 5. A significant number of  
613 subjects searched in the correct compartment on trial 1 ( $p = 0.05$ ). Six of the seven subjects  
614 reached criterion within the session, but none of these subjects passed the generalization test,  
615 searching mostly at the previously correct location. In neither session 1 nor 2 were there  
616 differences in the patterns of search for subjects with prior experience on tubes and those without.

617

### 618 *Condition 6, Test with a single unoccluded ramp*

619         The seven subjects that failed the single-choice or generalization conditions were tested  
620 with an unoccluded ramp. On the first trial with the unoccluded ramp, a significant number of  
621 subjects searched in the correct location ( $p = 0.01$ ). All seven subjects reached criterion during  
622 the unoccluded session, but only four passed the generalization test. The remaining three  
623 subjects were tested for a second session on the unoccluded test condition. All three subjects  
624 again passed the unoccluded test, and this time, also passed the generalization test. These  
625 seven subjects then moved to the next two conditions with the unoccluded ramp.

626         On the first session, 6 of the 7 subjects passed the random ramp and distracter ramp  
627 conditions. One subject passed the random ramp condition on the first session, but did not pass  
628 the distracter ramp condition. Overall, subjects' performance on the unoccluded ramp exceeded  
629 their performance on the transparent vertical tube (see Experiment 2). All seven subjects were  
630 then moved back to Condition 5 to see if their experience on the unoccluded ramp would transfer  
631 to the occluded ramp. In none of the sessions with an unoccluded ramp were there differences in  
632 the patterns of search for subjects with prior experience on tubes and those without.

633

### 634 *Condition 7, Retest with a single occluded ramp: Single choice*

635         On the first trial of the first session with an occluded ramp, a significant number of subjects  
636 searched in the correct location ( $p = 0.05$ ). Five subjects reached criterion, but only one subject  
637 passed the generalization condition.

638           The six subjects that failed to reach criteria on session 1 or to pass the generalization  
639 condition, were run on a second session. On the first trial, a significant number of subjects  
640 searched in the correct location ( $p = 0.05$ ). Four subjects reached criterion, but only one subject  
641 passed the subsequent generalization test. In neither session 1 nor 2 were there differences in the  
642 patterns of search for subjects with prior experience on tubes and those without.

643

### 644 *Conditions 8 & 9, Randomized ramp position and distracter ramp*

645           Only two subjects were able to generalize to a new configuration in the previous condition,  
646 showing some comprehension of the invisible displacement problem. Paralleling the vertical tube  
647 task (Hood et al., 1999; Experiment 2), each subject was first tested with an occluded ramp placed  
648 randomly across trials (Condition 8), and if they succeeded, were run on a test involving one  
649 functional ramp and one distracter ramp (Condition 9). Only one subject passed the randomized  
650 ramp condition; this subject was also one of the two subjects to reach criteria and pass the  
651 generalization test on the previous condition. On the randomization test, this subject's first trial  
652 response was correct, and within seven trials she reached criterion. On the first trial of the first  
653 session of the two ramp task, she was incorrect, selecting the compartment associated with the  
654 distracter ramp location; 45% of her remaining responses were also to the distracter ramp  
655 location. In the second session, she selected the correct compartment on the first trial, but failed  
656 to maintain this search pattern over the course of the session; 35% of her search errors were to  
657 the compartment associated with the distracter ramp.

658

## 659 **Discussion**

660           The tamarins had difficulty with both vertical and horizontal versions of the tube task, even  
661 though their performance on horizontal was superior to that on vertical. To determine whether this  
662 difficulty resulted from the potential artificiality of a tube and the problem of containment, we  
663 designed Experiment 3 involving a vertical apparatus with occluded ramps rather than tubes. If  
664 containment contributed to the tamarins' errors, we would expect their performance to improve

665 when containment is removed, or at least reduced as a factor; we note that an occluded ramp is,  
666 in some sense contained in that an object travelling down the ramp is constrained in part by the  
667 occluder. Results indicate that the tamarins had difficulty with the ramps task, showing the same  
668 kinds of response biases and perseverative errors as they did on vertical tubes (Hood et al. 1999;  
669 Experiment 2). Specifically, most of our subjects showed a bias toward the straight compartment  
670 on the first trial, and maintained this error throughout the first session. Only one subject passed  
671 the test, but then failed the generalization. On the second session, a significant proportion of  
672 subjects again showed this bias on the first trial. Although a greater proportion of subjects passed  
673 the test, only one of these passed the generalization. By the third session, involving only a single  
674 choice, a significant proportion of subjects picked the correct compartment on the first trial, and  
675 two subjects passed both the test and the generalization; although most of the subjects receiving a  
676 fourth session passed the test, none of them passed the generalization. Further paralleling the  
677 original vertical tube task, several subjects passed the unoccluded ramp task, but both failed to  
678 generalize when they returned to the occluded ramp, and failed to pass the two-ramp condition.

679         These results allow us to make two points. First, although the results from Experiment 2  
680 suggested that the straight compartment bias could be broken by prior experience on a horizontally-  
681 positioned, invisible displacement task, this effect appears fragile. Specifically, following approximately  
682 six weeks without running on either horizontal or vertical invisible displacement tasks, subjects  
683 approached the ramp task with an initial straight compartment bias, and perseverated with this bias over  
684 the course of several trials; this pattern holds even if one excludes those subjects with no experience on  
685 the tubes tasks. Apparently, whatever information about invisible displacement they acquired on the  
686 tubes tasks, they were incapable of transferring this information to a highly similar problem, the vertical  
687 ramp task. What this suggests, therefore, is that captive cotton-top tamarins approach the problem of  
688 invisible displacement along the vertical plane with an initial straight compartment bias, one that causes  
689 them to search for a fallen object directly below the release point. Over the short run, this bias can be  
690 altered by certain kinds of relevant experience. In the absence of repeated exposure to such problems,  
691 however, subjects resort to their original search bias, guided by the expectation that objects fall straight  
692 down when released in the vertical plane.

693           Second, the vertical trajectory is difficult for tamarins, even when containment (i.e., tubes) is  
694 eliminated or reduced as a factor. This suggests that tamarins, and perhaps many other primates as well,  
695 have difficulty solving invisible displacement tasks, especially along the vertical axis. This hypothesis  
696 requires further investigation.

697

698

## 699   General Discussion

700           The experiments discussed in this report were designed to explore how tamarins search  
701 for objects that have disappeared from view, and why they sometimes perseverate with strong  
702 response biases. Like studies of brain damaged patients (Caramazza, 1986), we find that in-  
703 depth analyses of errors may provide some of the richest material for the study of animal cognition  
704 (Boysen, 1996; Hauser, 1999, in press; Hauser et al., 1999). In answer to the question we pose in  
705 the title of our paper: what guides tamarins to search for food that has been invisibly displaced  
706 along the vertical plane is a bias to look below the release point, even though this represents the  
707 incorrect outcome; a similar search pattern has recently been reported for semi-free-ranging  
708 rhesus monkeys (Hauser, in press). More importantly, tamarins perseverate with this response  
709 even when they fail to obtain the target goal — a piece of food. This suggests that tamarins, and  
710 presumably other animals as well, are guided by a bias, and that this bias is difficult to overcome.  
711 When the displacement occurs along the horizontal plane, however, tamarins do not exhibit any  
712 search biases. Although their performance with horizontal tubes exceeds that obtained with either  
713 vertical tubes or ramps, tamarins nonetheless have a general problem solving invisible  
714 displacement tasks.

715           On several levels, the tamarins' perseverative errors on the vertical search task are  
716 striking. First, whereas subjects show strong response biases on the vertical version of the tubes  
717 task, they failed to show such biases on the horizontal version of the task. Consequently, the  
718 perseverative errors recorded are not due to a general difficulty with invisible displacements, but  
719 rather, to problems that arise when an object has disappeared along a vertical trajectory.

720           Second, although some individuals were able to solve the transparent vertical tube  
721 condition, as well as the unoccluded ramp condition, they were incapable of transferring this  
722 particular experience to the opaque and occluded conditions. This result stands in contrast to the  
723 results obtained on the horizontal tube task, where experience gained on the transparent tube was  
724 more successfully transferred to the opaque condition.

725           Third, subjects could solve the vertical search tasks without attending to the food's release  
726 point. In the single-tube or –ramp conditions, the correct compartment is always the one with a  
727 tube or ramp attached. It is surprising, therefore, that the tamarins failed to learn how to find the  
728 food reward by simply forming an association between outcome and configuration. In a variety of  
729 other contexts, animals readily form associations and use these to solve problems (reviewed in  
730 (Gallistel, 1990; Shettleworth, 1998)).

731           Fourth, in the multiple-choice condition of the original vertical tubes, as well as in the  
732 vertical ramp task, the tamarins were provided with an opportunity to search all compartments.  
733 Surprisingly, they often searched in the straight and other compartment, but not in the correct  
734 compartment. Their search patterns were highly non-random. In fact, on several trials, with  
735 several subjects, the doors attached to the straight and other compartments were repeatedly  
736 opened without even trying the door to the correct compartment. Once again, this pattern of  
737 search stands in striking contrast to the patterns obtained with the horizontal tube task, where all  
738 compartments were searched, and some subjects successfully solved the problem.

739           Fifth, although subjects tested first on the horizontal tubes task were less likely to search  
740 in the straight compartment on the vertical task as were subjects exposed to the vertical tubes  
741 first, the impact of this experience was short-lived. After a 6-8 week period with no testing,  
742 tamarins once again searched in the straight compartment when tested on the vertically positioned  
743 ramp task. Although this task greatly reduced the possible effects of containment in solving the  
744 invisible displacement task, subjects nonetheless searched in the straight compartment on the first  
745 trial, and maintained this bias throughout most of the test conditions. In parallel with our  
746 comments on transfer and associative learning mechanisms, one would have expected the  
747 tamarins to learn from their earlier mistakes on the tubes tasks, recognize the similarity between  
748 the tubes and ramp task, and use simple associative cues to solve the problem. The fact that they

749 were unable to solve the vertical ramps task following several trials suggests that they are  
750 relatively immune to negative feedback; needless to say, we are not claiming that the tamarins  
751 would never solve this problem, but rather, that they were unable to solve it even when given  
752 repeated, un-reinforced trials (i.e., the single-choice condition).

753         At present, it is not possible to say how either the tamarins or the human children acquired  
754 such biases because in both species, the experiments were conducted with relatively mature  
755 individuals: adult tamarins and 2.5-3 year old children. In both species, therefore, there has been  
756 time to develop expectations about falling objects on the basis of either direct or indirect  
757 experience. To determine how this search bias is acquired, and how older children override this  
758 bias, other tests will be necessary, perhaps running young infants from both species on  
759 experiments that rely less on reaching and searching. The expectancy violation procedure, used  
760 successfully on human infants and adult primates to explore other aspects of object knowledge  
761 (Baillargeon & DeVos, 1991; Hauser, 1998; Munakata, Santos, O'Reilly, Hauser, & Spelke, in  
762 press; Spelke, 1985; Spelke, Vishton, & von Hofsten, 1995), may provide one possible solution.

763

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765

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771

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**Table 1.** Subjects and prior experimental experience

<u>Subject</u>	<u>Sex</u>	<u>Group</u>	<u>Previous experience with vertical tubes?</u>
JL	m	L2	yes
EM	f	L2	no
SP	m	L3	yes
SC	f	L3	yes
UB	f	L1	yes
RW	m	A1	no
MR	f	A1	no
ID	m	A2	no
ES	f	CS1	no
RB	f	CS1	no

**Table 2.** Chronology of conditions and performance on Experiment 1 – Horizontal Tubes.

Chronology of conditions	First Trial*			Session†			
	% (N) Correct	% (N) Straight	% (N) Other	% (N) Passing	% (N) Correct	% (N) Straight	% (N) Other
Condition 4, Session 1, 1-opaque tube, multip. choice	30 (3)	40 (4)	30 (3)	30 (3)	12.9	41.4	45.7
Condition 4, Session 2, 1-opaque tube, multip. choice	10 (1)	30 (3)	60 (6)	10 (1)	31.1	28.9	40.0
Condition 5, Session 1, 1-opaque tube, single choice	33 (3)	11 (1)	56 (5)	44 (4)	22.7	34.1	43.2
Condition 5, Session 2, 1-opaque tube, single choice	57 (4)	14 (1)	29 (2)	43 (3)	11.8	38.2	50.0
Condition 6, transparent tube	75 (6)	12.5 (1)	12.5 (1)	88 (7)	-	-	-
Condition 7, 1-opaque tube, single choice	75 (3)	-	25 (1)				
Condition 8, Randomized position of 1-opaque tube	100 (3)	-	-	67 (3)	26.0	47.0	26.0

\*: All subjects

†: All subjects that failed to reach criterion

Table 3. Chronology of conditions and performance on Experiment 2 – Vertical Tubes.

Chronology of conditions	First Trial*				Session†		
	% (N) Correct	% (N) Straight	% (N) Other		% (N) Passing	% (N) Correct	% (N) Straight
Condition 4, Session 1, 1-opaque tube, multip. choice	60 (3)	-	40 (2)	40 (2)	34.0	18.0	48.0
Condition 4, Session 2, 1-opaque tube, multip. choice	20 (1)	20 (1)	60 (3)	0	34.0	16.0	50.0
Condition 5, Session 1, 1-opaque tube, single choice	20 (1)	40 (2)	40 (2)	20 (1)	36.0	23.0	41.0
Condition 5, Session 2, 1-opaque tube, single choice	20 (1)	40 (2)	40 (2)	40 (2)	37.0	33.0	30.0
Condition 6, transparent tube	60 (3)	20 (1)	20 (1)	40 (2)	-	-	-

\*: All subjects

†: All subjects that failed to reach criterion

**Table 4.** Subjects and prior experimental experience

<u>Subject</u>	<u>Sex</u>	<u>Previous experience with vertical tubes?</u>	<u>Previous experience with horizontal tubes?</u>
UB	f	yes	yes
RW	m	no	yes
SH	f	yes	no
AC	m	yes	no
JG	f	no	no
SP	m	yes	yes
EN	f	no	no
DD	m	no	no
RB	f	yes	yes
ES	f	yes	yes
EM	f	yes	yes
ID	m	yes	yes

**Table 5.** Chronology of conditions and performance on Experiment 3 – Vertical Ramps.

Chronology of conditions	First Trial*			Session†			
	% (N) Correct	% (N) Straight	% (N) Other	% (N) Passing	% (N) Correct	% (N) Straight	% (N) Other
Condition 4, Session 1, 1-opaque tube, multip. choice	0	67 (8)	33 (4)	8 (1)	9.0	56.0	30.0
Condition 4, Session 2, 1-opaque tube, multip. choice	18 (2)	55 (6)	27 (3)	45 (5)	20.0	28.0	40.0
Condition 5, Session 1, 1-opaque tube, single choice	67 (6)	22 (2)	11 (1)	77 (7)	35.0	55.0	10.0
Condition 5, Session 2, 1-opaque tube, single choice	72 (5)	14 (1)	14 (1)	86 (6)	-	-	-
Condition 6, transparent tube	86 (6)	14 (1)	0	100 (7)	-	-	-
Condition 7, Session 1, 1-opaque tube, single choice	57 (4)	29 (2)	14 (1)	71 (5)	-	-	-
Condition 7, Session 2, 1-opaque tube, single choice	57 (4)	29 (2)	14 (1)	67 (4)	-	-	-

\*: All subjects

†: All subjects that failed to reach criterion