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Means-means-end tool choice in cotton-top tamarins (*Saguinus oedipus*): finding the limits on primates' knowledge of tools

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Abstract Most studies of animal tool use require subjects to use one object to gain access to a food reward. In many real world situations, however, animals perform more than one action in sequence to achieve their goals. Of theoretical interest is whether animals have the cognitive capacity to recognize the relationship between consecutive action sequences in which there may be one overall goal and several subgoals. Here we ask if cotton-top tamarins, a species that in captivity uses tools to solve means-end problems, can go one step further and use a sequence of tools (means) to obtain food (end). We first trained subjects to use a pulling tool to obtain a food reward. After this initial training, subjects were presented with problems in which one tool had to be used in combination with a second in order to obtain food. Subjects showed great difficulty when two tools were required to obtain the food reward. Although subjects attended to the connection between the tool and food reward, they ignored the physical connection between the two tools. After training on a two-tool problem, we presented subjects with a series of transfer tests to explore if they would generalize to new types of connections between the tools. Subjects readily transferred to new connections. Our results therefore provide the first evidence to date that tamarins can learn to solve problems involving two tools, but that they do so only with sufficient training.

Introduction

One feature of human tool use is the capacity to use functional objects in sequence to achieve a particular goal. Much

of our daily life consists of elaborate sequences of means (hereafter, means-means-end sequences) used together to reach a distant goal. For example, a person could use a key to open a locked closet in order to get a stepladder needed to open the door to an out-of reach cabinet where there is a cookie jar that can be opened to obtain some cookies. As this hypothetical problem solving sequence indicates, the individual steps within a sequence are often displaced from the final goal both in time and space; in order to successfully complete the sequence, problem solvers must initially disregard the main goal (e.g., reaching the cookie) in order to focus on first successfully completing the individual subgoals (e.g., opening the closet). Moreover, sequenced tool use often requires a rich knowledge of the causal relations between objects, understanding both the connection between the individual steps of the sequence (a key can open a locked door, a stepladder can be used to gain access to things vertically out-of-reach, etc.) and how they relate (finding the key to the closet is necessary for eventually eating the cookie).

Human tool use regularly involves lengthy sequences of means-means-end actions, but such sequences are actually quite rare in the natural tool use of non-human primates. Although some species demonstrate complex hierarchically-organized action sequences during manual food processing (*Gorilla g. beringei*: Byrne 1999; Byrne et al. 2001; *Pan troglodytes schweinfurthii*: Corp and Byrne 2002), such complex sequencing is far less common in primates' natural tool-using behavior. For example, wild chimpanzees that regularly use a variety of individual tools (see Tomasello and Call 1997; Whiten et al. 1999) have demonstrated little evidence for sequenced tool use. Brewer and McGrew (1990) observed one chimpanzee sequentially using a variety of different tools (e.g., a "fishing tool," a "chisel," etc.) to obtain honey from a bees' nest. Similarly, Boesch and Boesch (1990) reported that chimpanzees in the Tai forest occasionally use two different tools to open shelled nuts (*Detarium senegalense*): one to hammer the shell and the other to extract the embedded kernel. Nevertheless, both of these examples of sequential tool use differ from those of humans in that each individual action involves

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a means directed immediately towards the final goal. At no point in these examples does the chimpanzee use one object as a means to act on an object other than the final goal. Though there are some reports of sequential tool use in non-human primates, the only systematic evidence of primates using tool sequences comes from Matsuzawa's (1991, 1994, 1996) observations of wild chimpanzees. Specifically, chimpanzees in Bossou occasionally use an additional stone to reposition poorly angled stone anvils; the additional stone thus provides a leveler for the anvil (see Matsuzawa 2001 for review). These observations suggest that, at least in one context, chimpanzees are able to use a means (i.e., the additional stone) to act on another means (i.e., the stone anvil) in the absence of an immediate reward.

The relative infrequency of means-means-end tool use among wild primates is mirrored in the spontaneous behavior of captive primates (e.g., Anderson and Henneman 1994; Hihara et al. 2003; Köhler 1925/1959; Parker and Poti 1990; Yerkes and Yerkes 1929; see Tomasello and Call 1997). In one of the first studies of captive chimpanzee tool use, Köhler 1925/1959 presented chimpanzees with a problem in which an out-of-reach food reward could be obtained only by stacking boxes. Although a number of individuals learned to use a single box to obtain the reward, his subjects had great difficulty using two stacked boxes to reach an even higher cluster of bananas (see Povinelli 2000 for a discussion). Similarly, Köhler found that chimpanzees failed to use a smaller stick to obtain a longer stick that could then be used to obtain an out-of-reach food reward (see Hihara et al. 2003 for a similar task with Japanese macaques). As in the box means-means-end task, chimpanzees had great difficulty with this problem (for related failures on a pushing task in brown capuchins, *Cebus apella*, see Visalberghi and Trinca 1989). In a more recent set of studies, Povinelli (2000) presented chimpanzees with a problem in which a hook-shaped tool could be used to pull an out-of-reach post that was carrying a banana. Povinelli found that chimpanzees performed poorly on this problem, failing to distinguish between situations in which the hook and the post were actually connected and those situations in which the hook and post were touching but not fully connected. More recent work on a different group of chimpanzees (Furlong et al. 2004) suggests that the results presented by Povinelli (2000) may not generalize to all individuals. In particular, Boysen and colleagues' chimpanzee subjects succeeded on at least some of the conditions in which Povinelli's chimpanzees fail. Such initial data suggest that non-human tool users have, at the very best, a rather limited ability to use two means in combination to achieve a goal and that means-means-end proficiency might be highly variable across individuals.

In this paper, we examine whether another primate, the cotton-top tamarin (*Saguinus oedipus*), is capable of solving means-means-end problems like the ones used with captive chimpanzees. Unlike chimpanzees, cotton-top tamarins are not renowned for their flexible tool use; tamarins evidence little spontaneous tool use in either the wild or captivity (but see Stoinski and Beck 2001 for a

report of spontaneous tool use in another tamarin species). Nevertheless, cotton-top tamarins provide an ideal species for this type of investigation because much is known about this species' capacity for using single tools to solve simple means-end problems. In a series of studies, Hauser and his colleagues have demonstrated that both adult and infant tamarins can easily be trained to choose between two simple pulling tools in order to obtain a food reward, and based on this experience, properly generalize with little or no training to a suite of related, but novel problems involving different tools and tool connections (Hauser 1997; Hauser et al. 1999; Hauser et al. 2002a, 2000b; Santos et al. unpublished data; Spaulding and Hauser, unpublished data). In these studies, tamarins are presented with a choice between two possible tools (e.g., two cane-shaped tools), each of which is placed on a tray near an out-of-reach food reward by the experimenter. The experimenter positions one food reward inside the hook of the tool and places the other food reward outside of the hook. As a result, if the subject pulls the cane straight back—the simplest motor response—it will retrieve the reward located inside the hook but not the reward located outside the hook. Hauser and colleagues have shown that both adult and infant tamarins quickly distinguish between functional and non-functional pulling tools, choosing only those tools that, based on shape and orientation, can be used to obtain the marshmallow. In addition, once tamarins learn the distinction between functional and non-functional orientations, they can generalize to other pulling canes of different shapes, sizes, colors, and textures (Hauser 1997; Hauser et al. 2002a). Similarly, tamarins can use a cloth tool positioned on a tray by an experimenter to access an out-of-reach food reward and quickly learn that the key distinction is between foods positioned on top of the cloth versus those positioned off of the cloth or touching but to the side of the cloth (Hauser et al. 1999). Taken together, these results suggest that tamarins recognize the functionally relevant features of a single pulling tool acting on a solid substrate.

In the present experiments, we used a similar tool choice study to explore how tamarins perform on a means-means-end problem. As in previous studies, our goal was to explore the skills that tamarins bring to bear on novel tool choice problems using a paradigm adapted for a tamarin's relatively poor dexterity; our assessment of dexterity is subjective, relative to studies of the primary tool users such as chimpanzees, and based in part on observations of their behavior in captivity and in the wild, revealing infrequent spontaneous object manipulation. To date, tamarins have never been tested in situations involving multiple tools, and thus we had no guarantee at the outset that our subjects would even perform a means-means-end task. However, given tamarins' performance on problems involving single tools, we had no convincing evidence to think that they would fail. Thus, in order to collect the relevant comparative data, we ran the following experiments.

We presented tamarins with problems in which they were required to pull one tool to gain access to another tool that could then be used to obtain a food reward. However, because of the tamarins' level of dexterity, we

Table 1 Individual subjects' age, sex, and group information

ID	Sex	Age	Group	Previous testing
DD	M	Adult	H-P First	Hauser et al. 2002a, 2002b
EN	F	Adult	H-C First	Santos et al. (unpublished data); Hauser et al. 2002a, 2002b
JK	F	Juvenile	H-P First	Hauser et al. 2002a, 2002b
KW	F	Adult	H-P First	Santos et al. (unpublished data); Hauser et al. 2002a, 2002b
RW	M	Adult	H-C First	Santos et al. (unpublished data); Hauser et al. 2002a, 2002b
SH	F	Adult	H-C First	Santos et al. (unpublished data); Hauser et al. 2002a, 2002b
SP	M	Adult	H-C First	Hauser 1997; Hauser et al. 1999; Santos et al. (unpublished data)
TF	F	Juvenile	H-P First	Hauser et al. 2002a, 2002b

were constrained in the type of means-means-end task we could present. As such, we were not able to use many of the situations previously presented to more dexterous primate species (e.g., Köhler's (1925/1959) out-of-reach food task or Visalberghi and Trinca's (1989) pushing task). Instead, we adapted the tool choice task previously used with tamarins to explore how tamarins would perform on a pulling problem that required the use of two tools hooked together, a means-means-end problem conceptually similar to those presented to chimpanzees.

We predicted three possible outcomes. First, tamarins could fail to solve a problem involving two tools, despite their successful performance on simple means-end problems. If so, we would expect tamarins to perform poorly on all problems involving the use of one tool to obtain another tool. A second outcome would be that tamarins spontaneously solve means-means-end problems; if this outcome is obtained, then we would expect tamarins to perform well on their first and all subsequent sessions with two-tool combinations. A final possibility is that tamarins exhibit poor performance on means-means-end problems initially, but then improve following some experience with the problem.

To distinguish between these alternatives, we first trained tamarins on single pulling tools and then presented them with problems involving multiple tools that, when pulled successively, provided access to the food. After training on the means-means-end problem, we modified the task by manipulating different features associated with the tools, and their connection to each other and the food. With this design, we were able to explore not only if tamarins could use two tools to obtain an out-of-reach food reward, but also identify which features are spontaneously used to solve this task.

We note here that creating an ideal set of conditions to tap means-means understanding in tamarins is limited by this species' manual dexterity, which is much poorer than that of many other primates, especially most Old World monkeys and apes. Thus, although we would have liked to place different kinds of tools in spatially distinctive locations (see for example Hihara et al. 2003), requiring subjects to position the first tool themselves in order to retrieve the second tool, and then to position this second tool to reach the target goal, this was simply not possible. Thus, in the following experiments our goal was to use a simplified set of means-means relationships, some of which conceptually parallel those initially designed by Povinelli (2000) for the significantly more dexterous chimpanzee.

Methods

Subjects

We tested eight cotton-top tamarins (see Table 1 for details on individual subjects). The subjects tested in these experiments were born in captivity; three females were born at the Primate Cognitive Neuroscience Laboratory at Harvard University, Mass., USA, whereas the rest were born at the New England Regional Primate Center, Southborough, Mass., USA. All are currently housed at the Primate Cognitive Neuroscience Laboratory; subjects inhabit homecages (1.2 × 1.2 × 1.8 m) in small pair-bonded family groups. Subjects are fed a diet of monkey chow, crickets, sunflower seeds, mealworms, yogurt, and fruit. They have continuous access to water.

Each of the subjects tested in this study have had previous experience with tools (see Table 1 for details). Although their experiences with tools varied, all subjects had learned to pull a small blue cane to obtain food. In addition, no subject had yet had the opportunity to use multiple tools to gain access to a reward.

Testing apparatus

We used the same general testing set-up as in previous experiments on tool use in tamarins (see Hauser 1997; Hauser et al. 1999, 2002a; Santos et al. unpublished data; see also Fig. 1). Tools were constructed from Sculpey, a non-toxic clay that hardens when baked. During testing, subjects left the cages in their homeroom in a wire transport cage and were moved into the testing room. Subjects were tested in their transport box (approximately 20 cm³). The experimenter exchanged the front panel of the transport box for a Plexiglas front panel; this panel had two centered openings separated by a piece of Plexiglas. The openings were designed to be wide enough for manipulation of the selected objects on one side, but too narrow for subjects to access objects on both sides simultaneously; thus the subjects could select only one tool or tool-combination during each trial (see Fig. 1). We positioned a two-tiered stand in front of the transport box and used this stand to present the stimuli. As in previous experiments, all stimuli were presented on a tray divided down the middle by a 1-inch barrier.



Fig. 1 Depiction of the experimental set-up. Subjects sat inside a transport box and were presented with the stimuli on a tray

Procedure

The general procedure also followed that of previous experiments (see Fig. 2 for a flowchart of the procedure). Subjects had to manipulate tools presented to them on a tray by the experimenter in order to access a 45-mg food reward (a marshmallow). During each trial, subjects were required to choose between two configurations of tools: one side of the tray had a food pellet that was accessible by pulling the tool(s), and the other side had a food pellet that was not accessible by pulling the tool(s).

The experimenter began each session by setting up the tool configurations out of view of the subject. The experimenter then presented the tray on the lower level of the stand for 3 s. Because the subject could not reach the tray at this level, it could use this period to observe both tool configurations. After the subject had seen both configurations, the experimenter placed the tray on the upper tier and allowed the subject to reach and select one tool. As described above, the structure of the Plexiglas barrier prevented the subject from making more than one choice. The experimenter allowed the subject 10 s to select one of the tools. If the subject did not select either tool upon the first presentation, the tray was presented again in the same manner after a 3-s delay. Once the subject touched either tool, whether they pulled or not, the trial was terminated.

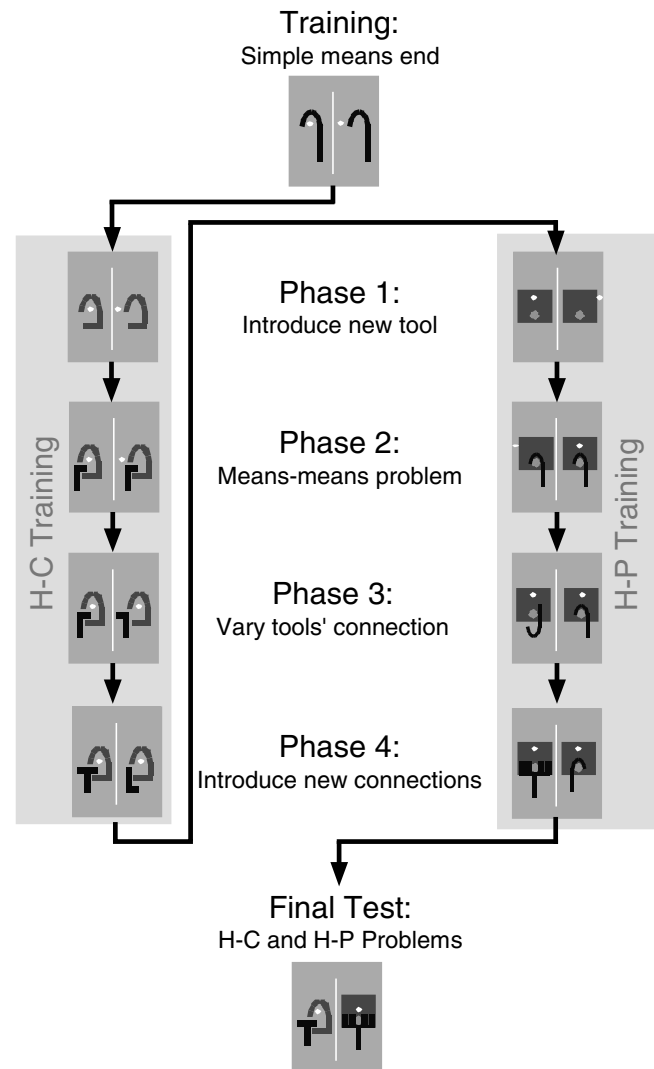


Fig. 2 Flowchart of the experimental procedure

Each session consisted of 20 randomized trials. Subjects received no more than one session each day. All subjects were required to complete two consecutive sessions with a score of 90% correct or higher on a single condition in order to advance to the next condition.

Initial training condition.

All subjects began with the training condition used in Hauser (1997; see Fig. 3a); each subject received all of the comparisons in a randomized order. We presented subjects with a choice between two identical blue canes that were differently positioned with respect to the food reward: the reward was either outside or inside the hook of the cane. Subjects could obtain the food by choosing the cane with the reward inside the hook and pulling this tool straight back. Pulling straight back on the cane with the reward outside the hook would not move the pellet. Based on prior performance on this task, we expected the tamarins to pick the tool requiring the fewest manipulative steps.

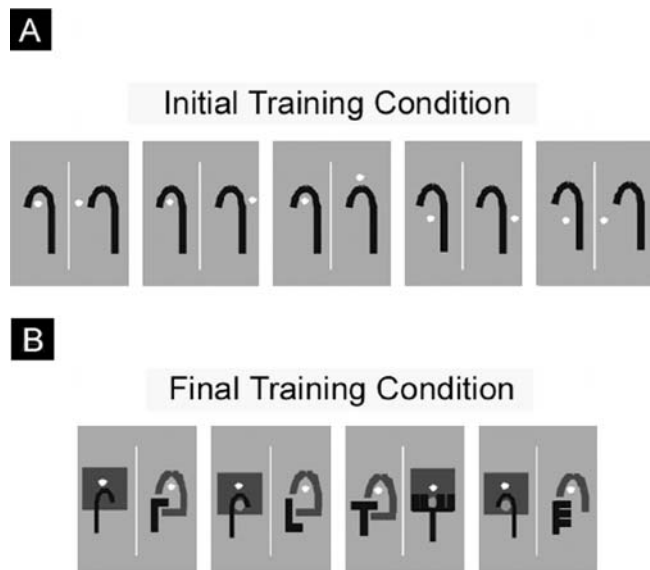


Fig. 3 **a** The initial training condition, and **b** the final training condition

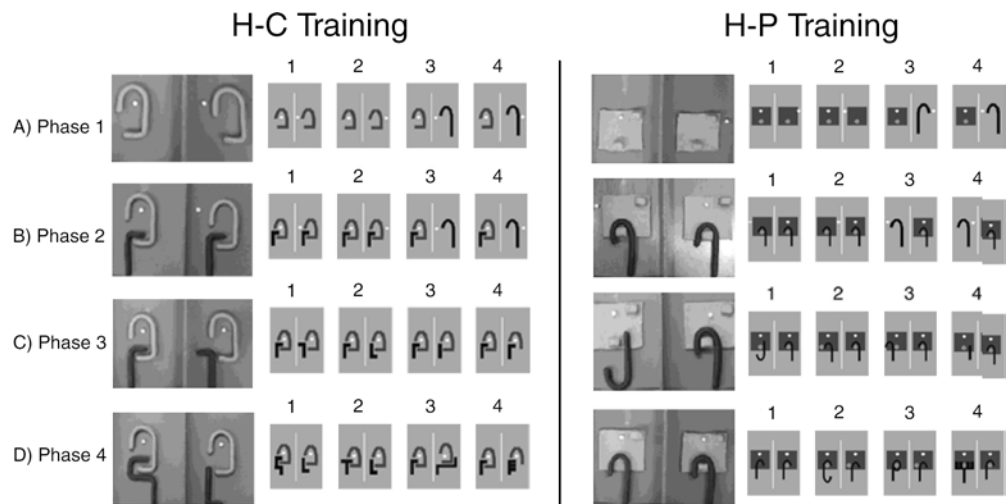
Means-means-end testing

After reaching criterion on the initial training condition, subjects moved onto the means-means-end testing (see Fig. 2 for a flowchart of the means-means-end testing). We designed two different means-means-end problems for subjects to solve: a hook-to-cane problem (H-C) and a hook-to-post problem (H-P). In the H-C problem, subjects had to use an L-shaped hook tool to pull another cane-shaped hook tool that was located around the food reward. In the H-P problem, subjects had to use a cane-shaped hook tool to pull a square flat post tool that carried the food reward (see Povinelli 2000, chapter 9 for a conceptually similar test with chimpanzees). All subjects received both H-C and H-P problems, the order of which was counterbalanced across subjects. Each testing session included 20 trials (see specific conditions described below) counterbalanced across subjects. Throughout testing, a

subject's choice was defined as the first tool touched; "correct" choices were those in which a subject first touched the correctly positioned cane. If subjects made a correct choice, they were allowed to manipulate the tool until they successfully retrieved the marshmallow. If subjects made an incorrect choice, subjects were allowed to pull the incorrect tool (with which they would be unable to access the marshmallow) before the experimenter removed the tray.

We introduced subjects to each of the two means-means-end problems (H-C and H-P) in three phases. Once subjects reached criterion in each phase (90% correct choices) for two consecutive sessions, they moved onto the following phase. Subjects who did not reach criterion after 30 sessions in one phase were dropped from training. In phase 1, we presented subjects with the individual tools they would see in the final means-means-end condition with food reward positioned as accessible or inaccessible (see Fig. 4a). This simple means-end condition was done first to ensure that subjects would generalize their success with blue canes to novel individual tools. In phase 2, we presented subjects with their first means-means-end problems. Subjects had to choose between a well-connected means-means-end configuration with an accessible food reward and one with an inaccessible food reward (see Fig. 4b). To succeed in phase 2, subjects had to use the first tool to retrieve the second tool. However, because both tool configurations had functional means-means connections, subjects did not have to reason about the connection between the two tools; they merely had to attend to the location of the reward relative to the second tool. In phase 3, in contrast, subjects had to pay attention to the functional connection between the two tools. Here, subjects had a choice between two well-connected tools and two poorly connected tools (i.e., the position of the first tool did not allow the second tool to be pulled), both with an accessible food reward (see Fig. 4c). Since both options presented appropriately located food rewards, subjects had to focus on the connection between the two tools in order to succeed on the task. The final phase, phase 4 (see Fig. 4d), explored what subjects learned about the functional connections by presenting them with

Fig. 4 Phases 1–4 of the H-C training and H-P training



novel between-tool connections. If subjects learned to attend to the functional aspects of the connection in phase 3, as opposed to some specific perceptual feature of the task (unconnected with the functionality of the problem), then they should succeed on the novel connections presented in phase 4.

We included four trials from the initial training condition in all test sessions (not pictured). These initial training trials served two purposes. First, they served as an indicator of the motivational state of the subject. Second, they ensured that each subject had access to some food on each session and thus would not lose motivation during the means-means-end training which we assumed would be harder, and thus lead to less frequent food rewards.

H–C training

Phase 1 of the H–C training introduced a small pink cane tool with a bent bottom edge (Fig. 4a). Subjects had to choose between (1) the pink cane with an accessibly placed reward (i.e., inside the cane's hook) and one with an inaccessibly placed reward (i.e., placed to the side) or (2) the small pink cane with an accessibly placed reward and a blue cane from the initial training with an inaccessibly placed reward.

Phase 2 of the H–C training (Fig. 4b) introduced an L-shaped blue tool that could be functionally connected to the pink cane. In half of the trials, subjects had to choose between a pink cane/blue hook configuration in which the marshmallow was accessible and a pink cane/blue hook configuration in which the marshmallow was inaccessible; in the other half of trials, subjects had to choose between a pink cane/blue hook configuration with an accessible marshmallow and a blue cane from the initial training condition with an inaccessible marshmallow.

Phase 3 of the H–C training (Fig. 4c) presented subjects with a choice between two pink cane/blue hook configurations. In both configurations, the marshmallow was placed inside the hook of the pink cane. The two configurations differed only in the nature of the connection between the pink cane and blue hook. Half of the connections between the pink cane and the blue hook were functional. The other half of the connections were non-functional. In some of these non-functional configurations, the blue hook was broken and thus did not connect to the pink cane. In others, the pink cane was broken and thus did not connect to the blue hook. Subjects had to attend specifically to the nature of the connection between the two tools in order to succeed on phase 3.

Subjects reaching criterion on phase 3 moved onto phase 4. Phase 4 presented subjects with novel types of connections between the hook and the cane (see Fig. 4d). If subjects learned to succeed in phase 3 by memorizing specific configurations of each tool, then they should perform poorly on the novel configurations of phase 4 trials.

H–P training

Like the H–C training, the H–P training began with an initial phase 1 condition in which we introduced subjects to a novel tool: a flat pink square with a vertical post (Fig. 4a). Subjects in this phase had to choose between the pink square with an accessibly placed reward (i.e., on the tool) and one with an inaccessibly placed reward (i.e., placed to the side of the square).

Phase 2 of the H–P training introduced a small blue hook that could be functionally connected to the pink square (Fig. 4b). In half of the trials, subjects had to choose between a pink square/blue hook configuration in which the marshmallow was accessible and one in which the marshmallow was inaccessible; in the other half of trials, subjects had to choose between a pink square/blue hook configuration with an accessible marshmallow and a blue cane from the initial training condition with an inaccessible marshmallow.

In phase 3 of the H–P training (Fig. 4c), subjects had to choose between two pink square/blue hook configurations. In both configurations, the marshmallow was placed accessibly on the pink square tool. The two configurations differed only in the nature of the connection between the pink square tool and blue hook. Again, if subjects attended to the nature of the connection between the two objects, then they should perform well on phase 3. However, if subjects focused instead on the position of the food reward and not the connection between the two tools, then they should perform poorly when presented with phase 3 trials.

Subjects who completed phase 3 moved onto phase 4. In phase 4, subjects were presented with novel types of connections (see Fig. 4d). If subjects succeeded in phase 3 because they learned to attend to the connections between canes, then they should show similar success in phase 4. Alternatively, if subjects succeeded in phase 3 by memorizing specific configurations, then they should perform poorly on the novel configurations of phase 4 trials.

Final testing condition

After completing phases 1–4 for the H–C and H–P problems, subjects were tested on two sessions of a final training condition (see Fig. 3b). This condition pitted the configurations presented in the final H–P training condition against the configurations presented in the final H–C training. The novel combinations of this final condition allowed us to explore if subjects had developed set-specific strategies within each training condition or if they had acquired a more general capacity to recognize functional connections.

Results

Initial training condition

All subjects completed the initial training condition in only a few sessions (mean=7.00 sessions). This performance did

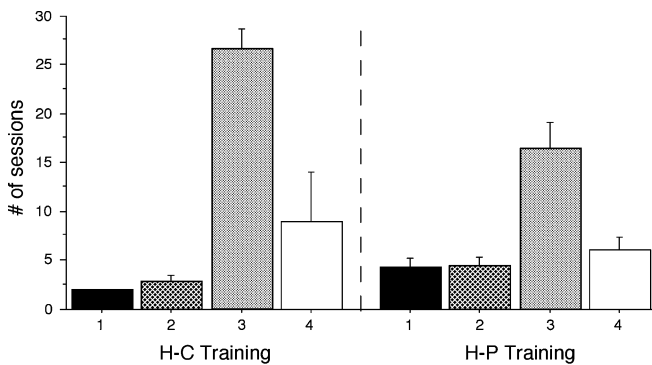


Fig. 5 Mean number of sessions required to reach criterion in each phase across the two training conditions

not differ from that of previous experiments (e.g., Hauser (1997): mean=7.89 sessions).

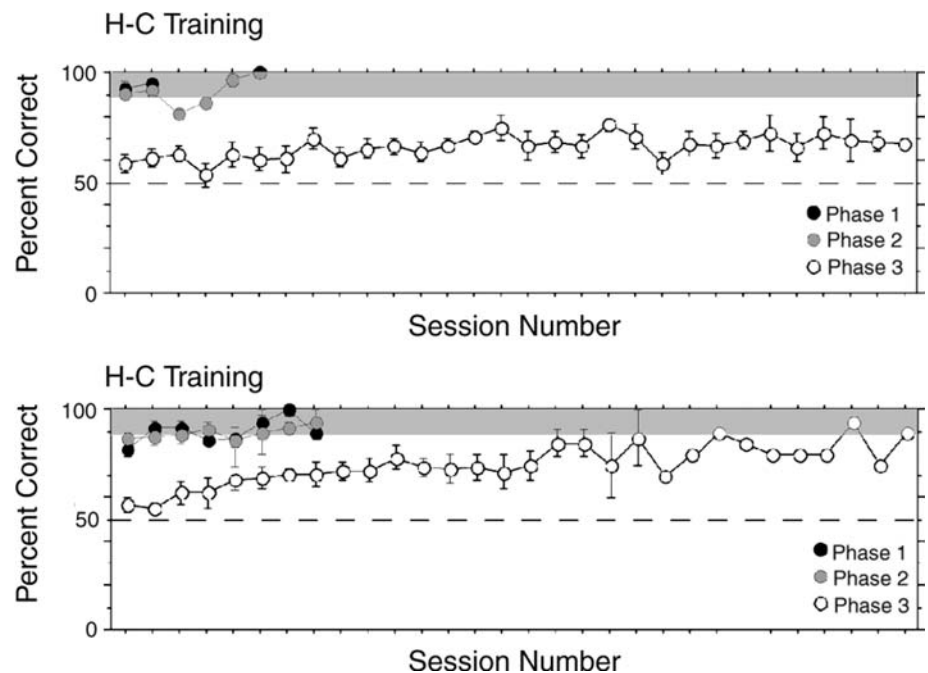
H-C and H-P training

Figure 5 depicts the mean number of sessions needed to reach criterion across the two training conditions. Across both H-P and H-C training conditions, all subjects completed phases 1 (introducing new tool) and 2 (introducing first means-means problem) in approximately the same number of sessions as in the initial training condition. However, subjects required more sessions to reach criterion in phase 3 (varying tools' connection). Five of the eight subjects failed to reach criterion after 30 sessions in phase 3 of the H-C training and one of the eight subjects failed to reach criterion in the H-P training. Those subjects that did reach criterion ($n = 3$ in H-C training, $n = 7$ in H-P training) took four times as long to com-

plete this phase of the training (mean=16.5 sessions) than they did to complete either phase 1 (mean=3.2 sessions) or phase 2 (mean=3.7 sessions). To explore this pattern more systematically, we entered all of the training data into an analysis of variance with condition (H-C training or H-P training) and phase (1, 2, or 3) as factors. We found no main effect of condition ($F_{(1, 7)}=3.17, P=0.12$). Subjects showed no difference in performance across the H-P and H-C training. We did however find a main effect of phase (ANOVA: $F_{(2, 14)}=139.06, P < 0.0001$). To further explore this omnibus effect, we performed three Bonferroni-adjusted contrast t -tests ($\alpha=0.02$). Collapsing across condition, subjects took reliably longer to complete phase 3 than to complete either phase 1 ($t_{(15)}=8.37, P < 0.0001$) or phase 2 ($t_{(15)}=7.66, P < 0.0001$, see Fig. 6). Subjects completed phases 1 and 2 at the same rate ($t_{(15)}=0.89, P=0.39$).

A similar pattern emerged in subjects' performance on their first session of each phase. In the H-P training, subjects performed above chance on their first sessions of phase 1 (mean=82.5%, one-sample t -test: $t_{(7)}=7.96, P < 0.0001$) and phase 2 (mean=87.5%, $t_{(7)}=9.93, P < 0.0001$), but performed at chance on their first session of phase 3 (mean=56.9%, $t_{(7)}=2.20, P=0.06$). Similarly, in the H-C training, subjects performed above chance on their first sessions of phase 1 (mean=93.0%, $t_{(7)}=14.5, P < 0.0001$) and phase 2 (mean=90.5%, $t_{(7)}=17.7, P < 0.0001$), but performed at chance on their first session of phase 3 (mean=58.6%, $t_{(7)}=1.96, P=0.09$). We directly compared these first session data using a repeated-measures ANOVA with training condition (H-P or H-C) and phase (1, 2, or 3) as factors. We found no main effect of training condition ($F_{(1,7)}=1.61, P=0.24$). We did however find a significant main effect of phase ($F_{(2,14)}=127.36, P < 0.0001$). Bonferroni adjusted P values for the t -tests

Fig. 6 Performance to criterion across phase 1, 2, and 3 in H-P and H-C training conditions



($\alpha=0.02$) revealed that subjects performed worse on their first session of phase 3 than either their first session of phase 1 ($t_{(15)}=12.17, P<0.0001$) or their first session of phase 2 ($t_{(15)}=13.04, P<0.0001$). There was no difference in first session performance between phases 1 and 2 ($t_{(15)}=0.56, P=0.58$).

Subjects who reached criterion on phase 3 moved onto phase 4 (introducing new connections between tools). Collapsed across both training conditions, all subjects performed above chance on their first session of phase 4 (mean=80.4%, $t_{(9)}=8.97, P<0.0001$). In addition, all subjects tested on phase 4 reached criterion in both the H-P (mean=6.1 sessions) and H-C training conditions (mean=9.0 sessions). Moreover, subjects that reached phase 4 met criterion more quickly than they had in phase 3 ($t_{(9)}=3.97, P=0.003$).

Final testing condition

Subjects performed above chance on the two final testing conditions. On their first session, subjects averaged 90.0% correct ($t_{(7)}=14.11, P<0.0001$) and performed similarly well on their second session (mean=88.1%, $t_{(7)}=10.44, P<0.0001$).

Discussion

The experiments presented in this report were designed to test if cotton-top tamarins can use two tools to obtain an out-of-reach food reward. Accordingly, we presented tamarins with novel tool combinations in four distinct phases, each designed to reveal different aspects of their performance. Phase 1 presented subjects with individual versions of the novel tools they would see later in succession. Subjects performed perfectly with these individual tools in both H-P and H-C training conditions; on their first session, tamarins reliably chose the most functional single tool. The results of this first condition replicate those of previous experiments (Hauser 1997; Hauser et al. 1999; 2002a; 2002b; Santos et al. unpublished data) suggesting that tamarins trained on a blue cane-shaped pulling tool can generalize to other functional pulling tools of different shapes, sizes, and colors.

In phase 2, subjects had to choose to pull one tool (a hook) to gain access to another tool (a cane or a post) in order to access the marshmallow. The tool combinations differed only with respect to the marshmallow's accessibility; both combinations were configured such that the first tool readily accessed the second. Subjects could therefore succeed on this phase simply by attending to the connection of the second tool and the marshmallow, ignoring the connection between the two tools. All subjects performed above chance on their first session in phase 2. Tamarins who had previously experienced only single tools immediately used two tools in combination to obtain the marshmallow.

How did subjects solve the problem presented in phase 2? One possibility is that tamarins succeeded in the phase not

by seeing the tools as distinctive objects that were physically connected, but instead through a more straightforward perceptual analysis. Specifically, subjects could have succeeded in phase 2 simply by attending to the connection between the second tool and the food, ignoring the nature of the connection between the first and second tools. Therefore, although phase 2 performance indicates that tamarins spontaneously use two tools in conjunction to obtain a food reward, they are silent on whether tamarins recognize which means-means relationships can yield a target end.

For this reason, phase 3 explored tamarins' capacity to recognize effective means-means relationships by modifying critical features of the tools and their physical connections. Subjects had a choice between two well-connected tools with an accessible food reward and two poorly connected tools with an accessible food reward. Note that both options had accessibly located food rewards (i.e., both rewards were physically connected to the second tool or positioned in line with a straight pull of the second tool). Therefore, in order to successfully obtain the marshmallow, subjects could not merely examine the relationship between food and tool. Rather, subjects had to focus on the connection between the two tools in order to succeed in this task. Did tamarins' attention to the physical connection between the tool and food spontaneously generalize to the physical connection between the first and second tool? Results from phase 3 suggest that it did not. Subjects dropped to chance performance on the first session of phase 3. Many subjects failed to reach criterion in at least one of the training conditions and those subjects who did reach criterion took four times as long to complete this phase than they did to complete previous phases.

The results of phase 3 are important, suggesting that tamarins trained on single tool pulling problems initially fail to generalize to multiple tool pulling problems, even though the causal aspects of these problems are identical. These failures are striking in light of the ease with which tamarins generalize to perceptually novel single tool problems (e.g., feature and orientation changes) in other studies (see Hauser 1997; Hauser et al. 1999). Like chimpanzees, tamarins seem unable to spontaneously apply their knowledge of single tool problems to tasks involving combinations of tools.

Despite their initially poor performance, some tamarins did learn to attend to the connection between the two pulling tools. All but one tamarin completed phase 3 in at least one of the training conditions. This result suggests that tamarins can learn to solve problems involving connections between two tools, but that they require a substantial amount of training to do so; in fact, these subjects required twice as much training to attend to two means in combination as they did to initially master the tool-to-marshmallow single tool problem. The extent of training required for tamarins to succeed in this task suggests that attending to the connection between the two tools is a difficult aspect of the tool choice task for tamarins to learn, perhaps even more difficult than

originally learning the functional properties of a single pulling tool.

Phase 4 explored the nature of tamarins' capacity to use two tools in combination to attain a reward. Did tamarins succeed on prior conditions because they learned to attend to functionally relevant aspects of the task, or did they instead memorize the specific patterns associated with successful choices (e.g., successful tools show more perceptual contact, etc.; see chapter 9 of Povinelli 2000). Phase 4 presented subjects with novel connections between the two tools: some were physically functional and thus allowed subjects to obtain the second tool, others were non-functional connections. If tamarins memorized the pattern associated with functional connections (more contact, specific cane position, etc.), as opposed to learning something more general about the nature of a functionally relevant connection, then their performance should have plummeted in phase 4. Subjects performed well on the novel phase 4 tool connections even on their first session, suggesting that although tamarins have some difficulty initially learning to attend to the connection between the two tools, once they master this distinction, they seem to generalize to perceptually different but functionally similar connections between the tools.

These results together allow us to draw two conclusions concerning tamarins' attention toward means-means-end connections. First, although tamarins will spontaneously attempt to use a tool positioned by the experimenter to gain access to another tool, they do not spontaneously attend to the features that are most relevant for this problem, namely the functional connection between the two tools. This finding differs from previous results with these subjects on single tool tasks: tamarins naturally attend to the connection between a single tool and a food, and easily generalize to perceptually different connections. For example, Hauser et al. (1999) showed that tamarins successfully choose between a continuous piece of cloth supporting a piece of food and two discontinuous pieces with food supported as well. It is currently unclear why the significance of the connection is salient in this second case, but not in the present situation. Second, our results demonstrate that although tamarins do not spontaneously attend to the connection between two tools, they are able to learn to do so with some training, and then are able to generalize to other perceptually distinctive but functionally similar connections.

As mentioned previously, the means-means-end choice task we used with our tamarin subjects was somewhat simpler than the means-means-end tasks used with other primate species, raising four significant questions about task demands. First, because tamarins subjectively lack the dexterity of chimpanzees and capuchins—the target subjects for most studies of tool use—we tested them instead on a comprehension task involving a choice between two different means-means-end configurations. Choosing between two means-means-end configurations is undoubtedly much easier than the type of problem presented to other primate subjects, in which subjects were forced to develop an effective means-means-end configuration on their own (see

Hihara et al. 2003; Köhler 1925/1959; Visalberghi and Trinca 1989).

Second, unlike previous tests of means-means-end problem solving in other species, our study presented tamarins with a choice between two combinations of tools, both of which were situated in close spatial and temporal proximity to the goal; in the case of the H–P condition, the food reward was actually on top of the second tool. Such proximity may have allowed subjects to chunk the two objects together and concentrate on them as a single object. Subjects may have, for example, perceived a connected hook-to-post combination of two tools as a single connected tool (see Hauser et al. 1999 for tamarins' performance on single tool connectedness problems). If tamarins were able to chunk tools in this way—seeing them as a single connected or disconnected unit—then tamarins performance may not reflect their attention to means-means connections per se, but instead reveal their understanding of broken versus intact single tools. A better way to explore tamarins' attention to functional means-means connections, then, would be to separate the two tools in time and space, making it more clear that the two means were in fact separate objects that could potentially be used in combination. For example, one could place a few tools within reach and others out of reach. To attain the goal, subjects would have to pick one of the near tools and use it to reach one of the far tools. Having then obtained one of the far tools, subjects would then need to use it to attain the distant goal. This set up requires attention to the physical details of tool one in terms of its capacity to retrieve tool two. It then requires subjects to explore the physical details of tool two in terms of its capacity to retrieve the goal. Unfortunately, it would be difficult to set up such a tool-use problem with tamarin subjects due to their level of dexterity. Future studies could therefore profit from developing other methods to present more difficult means-means-end problems to less-dexterous subjects like tamarins. Such tasks might include perceptually-based looking tasks, like the expectancy violation methodology (see Santos et al. 2003). These tasks, which simply require subjects to watch visual displays, are often able to circumvent the problem of determining competence from performance (see Santos and Hauser 2002; Santos 2004 for a review).

Third, our study focused primarily on subjects' attention to the connection between two means that could be used to obtain a food reward. At no point in our studies did we present tamarins with problems in which they were required to attend to both the connection between the first and second tools and the connection between the second tool and the food reward at the same time. It is possible that attending to two connections at the same time would require even more training than tamarins received in our study.

Fourth, our studies presented tamarins with perceptually salient means-means connections. Povinelli (2000) found that chimpanzees succeed on means-means-end problems primarily in cases in which the effective means-means connection is perceptually different than the ineffective means-means connection. He presented chimpanzees with

a training problem in which subjects were allowed to use an accessible cane to hook a ringed-platform carrying food. After this training, subjects were presented with a choice of two different hook-platform combinations and allowed to pull one of the two hooks to obtain the platform with the food. When faced with perceptually identical yet physically different means-means connections (e.g., an attached post versus one that is touching but not attached), chimpanzees failed to discriminate functional and non-functional connections. Note that all the means-means discriminations presented to tamarins in the present studies used connections that were perceptually salient—at no point were they faced with the perceptually obscure connections presented to chimpanzees in which perceptual contact and simple visual features were not enough to determine whether there was an effective physical connection between the two means. If tamarins were faced with means-means connections like those presented to chimpanzees, it is possible that their performance would have been equally poor.

In conclusion, we have presented the first evidence to date that cotton-top tamarins can be trained to solve at least one simple pulling problem involving the use of two tools. Although they do not spontaneously attend to the correct aspects of this problem, with sufficient experience, they are able to generalize to the relevant aspects of the means-means problem. Our results therefore demonstrate that even a species that does not normally use tools can, with training, efficiently choose between sets of differently connected tools to achieve a goal. This suggests that at least some aspects of an animal's competence with tools may derive from more general problem solving abilities, a theme that we have articulated in several other experiments (reviewed in Hauser and Santos 2005). This perspective provides a direct challenge to those who wish to see the evolution of tool use as a specialized adaptation to the problem of using tools.

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