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# Constructive and Deconstructive Tool Modification by Chimpanzees (*Pan troglodytes*)

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KEYWORDS

tool use, chimpanzees, causality, cognition, primate

ABSTRACT

*Nine chimpanzees (Pan troglodytes) were tested for their ability to assemble or disassemble the appropriate tool to obtain a food reward from two different apparatus. In its deconstructed form, the tool functioned as a probe for one apparatus. In its constructed form, the tool functioned as a hook, appropriate for a second apparatus. Each subject completed four test trials with each apparatus type. Tool types were randomized and counter-balanced between the two forms. Results demonstrated that adult and juvenile chimpanzees (N = 7) were successful with both tool types, while two infant chimpanzees performed near chance. Off-line video analyses revealed that tool modifications followed by attempted solutions by the adults and juveniles were typically correct on the first attempt. Neither infant was successful in modifying tools correctly on the first attempt over all eight trials. The older chimpanzees' ability to modify the appropriate tool consistently prior to use indicates an immediate recognition of the functional attributes necessary for the successful use of tool types on each apparatus, and represents a non-replication of a previously reported study by Povinelli.*

## Introduction

Wild chimpanzees have been observed using and making tools proficiently since the pioneering observations of termite fishing and ant dipping by Goodall (1968). Subsequent studies have identified a wide range of tool use behaviors including ant dipping, dentistry, termite fishing, nut cracking, leaf sponging, pestle pounding, and spears for hunting, among others now among the reported repertoire (e.g., Biro et al. 2003; Boesch-Achermann and Boesch 1993; Boesch and Boesch 1990; Hernández-Aguilar et al. 2007; Inoue-Nakamura and Matsuzawa 1997; Matsusaka et al. 2006; Pruetz and Bertolani 2007; Santos et al. 2005; Sanz and Morgan 2006; Tonooka et al. 1997; Whiten et al. 1999, 2001; Yamakoshi and Sugiyama 1995; also see McGrew 1992, for an extensive review). Of these behaviors, use of probes is one of the most prevalent forms of tool use by wild chimpanzees (DeBlauwe et al. 2006; Goodall 1968; Humle and Matsuzawa 2002; McGrew 1974). A probe is used to gain access to items out of reach, usually food, by extending the chimpanzee's reach. Hook tools, although observed less often, can also be used to extend reach (Whiten et al. 1999). Tools may require modification to be suitable for their intended use or an appropriate tool could be selected, if available, such as a long, thick stick for termite fishing, rather than requiring modification. For example, insect or honey probing requires a long, thick stick, while extracting bone marrow or removing kernels from nutshells requires a shorter, finer tool (Boesch and Boesch 1990). Tool modification has been observed in other primates including captive baboons (e.g., Westergaard 1989, 1992, 1993), wild orangutans (Fox and bin'Muhammad 2002; Galdikas 1989; van Schaik et al. 2003; van Schaik and Knott 2001), captive orangutans (Nakamichi 2004; O'Malley and McGrew 2000), captive gorillas (Pouydebat et al. 2005), captive bonobos (Visalberghi et al. 1995), and has been studied extensively with capuchins under captive conditions (e.g., Fragaszy and Visalberghi 1989; Visalberghi et al. 1995; Visalberghi and Limongelli 1994; Westergaard et al. 1995, 1998). Tool use, modification, and manufacture have also been reported for non-primate species such as elephants (Hart et al. 2001), crows (Chappell and Kacelnik 2002, 2004; Weir et al. 2002; Hunt and Gray 2004), and woodpecker finches (Tebbich and Bshary 2004).

While it is possible that appropriate tool modification prior to use could theoretically indicate foresight in tool-using species, it remains highly contentious whether such foresight could be attributed to varying levels of causal understanding (Evans and Westergaard 2004; Fujita et al. 2003; Hauser 1997; Santos et al. 2005), or simpler associative learning (Povinelli 2000; Visalberghi and Limongelli 1994; Visalberghi et al. 1995). Povinelli et al. (2000) proposed that chimpanzees were able to learn to modify available raw materials (e.g., vines, twigs, grasses) quickly, without a definitive understanding how the modified tools are causally related to their proposed function. To explore this hypothesis, Povinelli et al. (2000) conducted a series of experiments requiring tool use and modification, including the tool-construction problem. In this task, chimpanzees were required to modify a tool so that it could be used on two different types of apparatus. In its deconstructed form, the tool functioned as a probe, while in its constructed form, it functioned as a hook. Their results revealed that the chimpanzees had limited success modifying the tool before using it successfully ($X$ = 32.9%). Most of the modifications they made were not directly related to the causal structure of the problem at hand. When compared with the extensive archival literature on tool use in wild chimpanzees, and observations of spontaneous and acquired tool use by our chimpanzees, such poor performance on the tool construction task, the last of an extensive series of tool tasks with captive chimpanzees reported by Povinelli (2000), was inconsistent. Consequently, a replication of the tool construction task was important for identifying possible parameters that might account for task performance differences among groups of captive chimpanzees.

## Method

### *Subjects*

Nine chimpanzees (*Pan troglodytes*) housed at the Ohio State University Chimpanzee Center, including five adults (Sarah, 44 years; Darrell, 24 years; Kermit, 23 years; Sheba, 22 years; and Bobby, 17 years), two juveniles (Keeli and Ivy, both age 7), and two infants (Harper and Emma, both age 4) participated in the experiment. The chimpanzees were maintained in a highly enriched environment, including daily access to indoor and outdoor enclosures, structural and object enrichment, and ongoing research of advanced cognitive skills. The group was housed under stable social conditions, and developed strong relationships with their human caretakers and teacher/experimenters. Most of the animals had extensive experience with a variety of cognitive tasks (e.g., Kuhlmeier and Boysen 2001, 2002; Boysen 2006), including one that required tool use (Limongelli et al. 1995). In the present study, all subjects had previous experience with the testing apparatus, but had no prior training with the specific tools used.

### *Apparatus*

The apparatus used in the tool insertion (TI) portion of the experiment consisted of a black metal case (101 cm × 63 cm × 71 cm) with a clear Lexan™ front (50 cm × 66 cm) that left an opening (50 cm × 9 cm) at the bottom of the case (Fig. 1). In the center of the clear front, a hole (9 cm diameter) was cut 17 cm from the top. Behind the Lexan™ front, a wooden shelf (7 cm × 49 cm) was placed, approximately 20 cm behind the hole. A plywood section (25 cm × 18 cm) was positioned at an angle from the upper back to the lower front of the box, and there was a door in the back that allowed the experimenter to place a food reward on the shelf before each trial. The apparatus used in the hook retrieval (HR) task consisted of a flat wooden base (44 cm × 13 cm × 2 cm) that was placed perpendicular to an attached dowel (13 cm × 2 cm diameter) (see Fig. 2).

**Fig. 1.** Apparatus used for tool insertion task

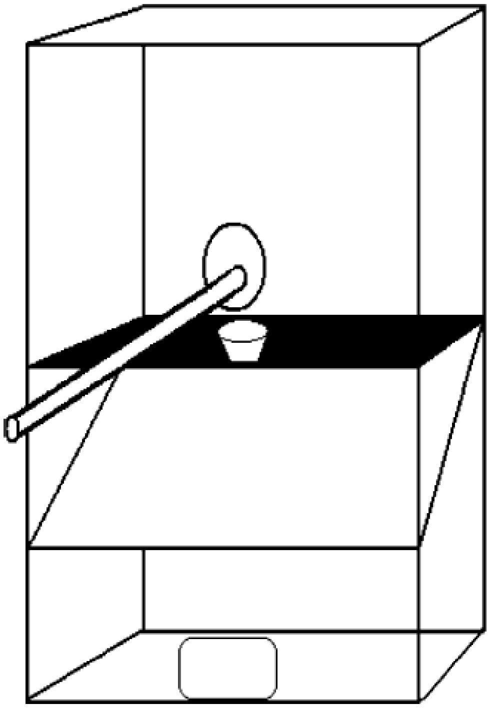


**Fig. 2.** Apparatus used in hook retrieval task.

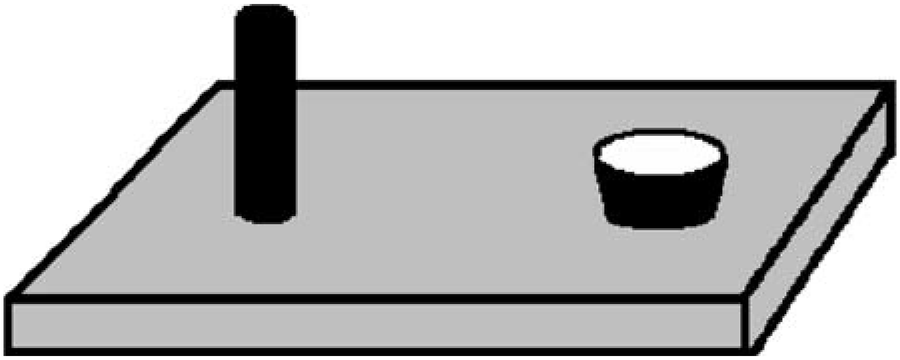
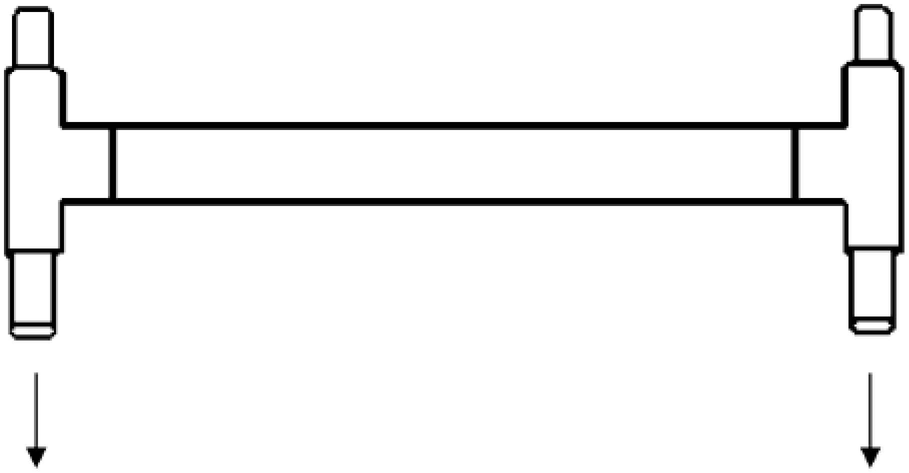


**Fig. 3.** Initial wood tool designed for tool insertion and hook retrieval tasks

**Fig. 4.** Re-designed tool constructed from PVC for TI and HR tasks



*Procedures*

The tool used in the first eight sessions consisted of a wooden dowel (62 cm × 3 cm diameter) with 1-cm holes drilled through each end. Two wooden cross-pieces (20 cm × 1 cm diameter) could be inserted or removed to achieve different forms of the same tool (Fig. 3). Because the materials used for the original tool could not withstand strenuous use by the chimpanzees during the HR task, the tool was redesigned from PVC tubing (56 cm × 1.5 cm diameter) with a plastic "T" shape affixed to each end, and used during Sessions 9–12. Four smaller pieces of PVC tubing (12 cm × 1.5 cm diameter) could be inserted into either end of the T-shaped section for testing on the HR task (Fig. 4).

In the TI task that we replicated in the present study, the tool used for "standard trials"[1] consisted of a straight piece of PVC tubing (51 cm × 1.5 cm in diameter). For the second study replicated here, the HR task, the tool provided during "standard trials" consisted of a piece of PVC tubing (51 cm × 1.5 cm in diameter) with a curved J- shaped hook at both ends. As in Povinelli et al.'s procedures, during experimental testing with our chimpanzees, we used the same apparatus for standard trials, and always provided the correct form of the tool so that it required no modification. Each chimpanzee completed four standard trials that were randomized among the experimental trials, and included two such TI and two HR trials.

Prior to the experiment, all subjects were evaluated to assess their ability to assemble and disassemble the tools. Two sessions were completed, consisting of four trials each, during which the chimpanzees were presented with the tool twice in assembled form, and twice in disassembled form. The order in which tools were presented was randomized for each subject within each session. Once the animals were presented with a tool, they were given 2 min to manipulate the tool in any way they chose. A "success" was defined as either assembling a disassembled form, or disassembling an assembled form during this preliminary phase. When they were successful, subjects received social praise and a small food reward. If initially successful, the chimpanzees were allowed to continue manipulating the tool for the remainder of the 2-min period. Criterion performance in this phase of the experiment required that the chimpanzees succeed on 7/8 trials, or 88% CR, before they could move on to the test phase. All animals met the criterion within two sessions.

Each chimpanzee initially completed eight test sessions that were comprised of either a single test trial, or a test trial followed by a standard trial. Trials were arranged so that the type of apparatus and necessary tool alternated every session (e.g., a TI session was followed by a HR session, and so on). Subjects were randomly assigned to receive either the assembled tool or the disassembled version for the first two trials, and then received the two tools in the reverse order for the next two trials. This procedure insured that each subject received every possible trial combination during the first half of the trials, and then again during the second half. Before each trial, the test apparatus was pushed to the front of the animal's enclosure, just out of its direct reach. Depending upon which tool type (assembled or disassembled) was to be presented to the subject, the experimenter either assembled the tool from its component parts, or disassembled the tool into separate pieces, following methods outlined in Povinelli et al. (2000). When this demonstration was complete, the chimpanzee was offered the tool. The animals had 2 min to complete the task, and retrieve the food reward.

Hook retrieval sessions were completed using the reconstructed tools that were made from more durable PVC. A trial was considered correct when the chimpanzee obtained the reward within the 2-min period, using the most suitable form of the tool. This meant using the disassembled tool for the TI task or the assembled tool for the HR task. If the subjects were able to obtain the reward using the inappropriate tool form, their response was considered incorrect for purpose of analyses. Similarly, if the subject was unable to retrieve the food reward in the allotted time, despite attempting with the appropriate tool, the trial was considered a failure. All trials were recorded on data sheets and also videotaped for subsequent off-line coding by a research assistant naive to the experimental hypotheses. Inter-rater reliability between coders was 98% ($K = 0.9319$, $P < 0.0001$) across all trials.

## Results

The chimpanzees were highly successful on both the TI and HR tasks. Overall, the chimpanzees were 91.5% successful on the TI tasks, and 89% successful on the HR tasks. These results were in direct contrast to the data for the same tasks reported by Povinelli et al. (2000). These investigators found that their chimpanzees performed at 78.5% CR on the TI tasks, and 55.8% CR on the HR tasks. Table 1 represents an overall comparison of the differences in performance between the Povinelli subjects and our chimpanzees in the present study.

One-tailed binomial tests were conducted to determine our animals' success on both tasks. Binomials were completed assuming three possible values for chance. First, values based on chance = 50% were calculated, representing a conservative estimate, with chance representing either success or failure. Second, chance was set at 12.5%, and defined by modification of the tool (yes or no); correct use of the tool (yes or no), and success or failure when using the tool, resulted in chance = $1/2^3 = 1/8 = 0.125$.

A third value also was determined to take into account trials during which the chimpanzees were successful (in obtaining the food), but did not use the tool correctly ($1/2^2 = 1/4 = 0.25$) (Table 2)

**Table 1. Overall performance comparison between OSU chimpanzees and Povinelli et al. (2000) subjects**

| Subjects | Tool insertion assembled (%) | Tool insertion disassembled (%) | Hook retrieval assembled (%) | Hook retrieval disassembled (%) |
|---|---|---|---|---|
| OSU chimpanzees | 89 | 94 | 100 | 78 |
| POV chimpanzees | 52 | 100 | 83 | 29 |

**Table 2. Overall performance on both tool insertion and both hook retrieval tasks, under conditions of successful retrieval with either tool version (assuming chance at 50 or 12.5%), or reward retrieval only (assuming chance 50 or 25%)**

| Condition | Successful retrieval with either tool version | | Successful retrieval of reward only | |
|---|---|---|---|---|
| | Chance = 50% | Chance = 12.5%$^{+}$ | Chance = 50% | Chance = 25%** |
| Tool insertion disassembled (%) | 94$^{+}$**<br>$P = 0.039$ | 94$^{+}$**<br>$P < 0.001$ | 94$^{+}$**<br>$P = 0.039$ | 94$^{+}$**<br>$P < 0.001$ |
| Tool insertion assembled (%) | 100<br>$P = 0.004$ | 100<br>$P < 0.001$ | 89<br>$P = 0.039$ | 89<br>$P < 0.001$ |
| Hook retrieval disassembled (%) | 100<br>$P = 0.004$ | 100<br>$P < 0.001$ | 78<br>$P = 0.18$ | 78<br>$P = 0.001$ |
| Hook retrieval assembled | 100<br>$P = 0.004$ | 100<br>$P < 0.001$ | 100<br>$P = 0.004$ | 100<br>$P < 0.001$ |

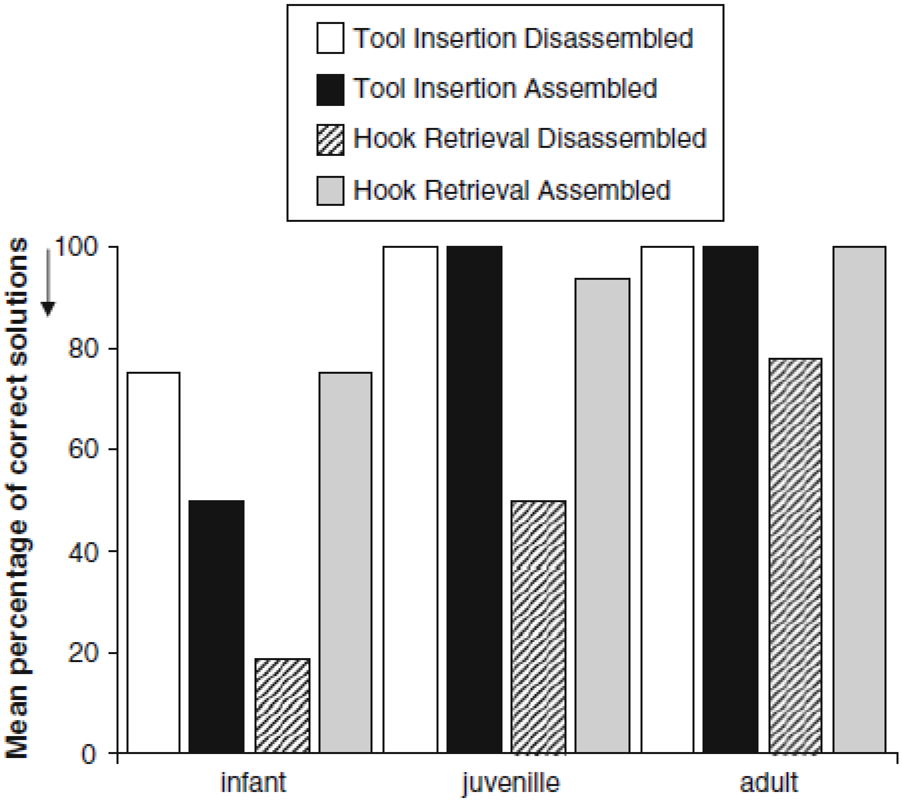
**Table 3. Trial 1 performance across subjects for all tasks**

| Tool task | Correct trials | Binomial assuming chance = 50% | Binomial assuming chance = 12.5% |
|---|---|---|---|
| Tool insertion disassembled | 8 | $P = 0.02$ | $P < 0.001$ |
| Tool insertion assembled | 8 | $P = 0.02$ | $P < 0.001$ |
| Hook retrieval assembled | 9 | $P = 0.002$ | $P < 0.001$ |
| Hook retrieval disassembled | 8 | $P = 0.02$ | $P < 0.001$ |

In addition, we characterized performance in two different ways. We defined “success” as successfully retrieving the food reward, regardless of tool choice. A “correct” response was defined as the correct modification of a tool, and retrieving the food reward. The chimpanzees were successful (and correct) on all trials of the TI trials across all three levels of chance, as described above. Similarly, they were successful (and correct) with most HR trials, with the exception of the disassembled condition, where they were not correct with chance at 50%. This was despite the fact that their Trial 1 performance was quite good (Table 3).

In order to explore possible differences in performance among the different conditions (TI assembled; TI disassembled; HR assembled; HR disassembled), a Friedman’s test was performed. No differences in performance were found, indicating that our chimpanzees performed equally well across all conditions. This included comparing both successful ($\chi^2 = 0.2$, $df = 3$, $P = 0.977$) and correct tool usage ($\chi^2 = 2.1$, $df = 3$, $P = 0.551$). Similarly, there were no differences across these conditions on Trial 1 performance alone, either when considering successful ($\chi^2 = 3$, $df = 3$, $P = 0.392$), or correct tool use ($\chi^2 = 1.061$, $df = 3$, $P = 0.787$). However, the dissembled condition was clearly more difficult for all the subjects, and required the re-creation of the tool form, rather than the more simple approach of removing one or more components to render a tool useable. It is noteworthy that wild chimpanzees typically modify, or deconstruct, natural materials from their habitat in order to use them effectively as tools for extractive foraging. Thus, modification of raw materials or an intact tool, as a motor skill or process, is likely to be inherently easier and more suited for chimpanzees than the assembly of a functional tool from optional parts.

**Fig. 5. Mean percentage of correct solutions across age categories; infants (*N* = 2), juveniles (*N* = 2), and adults (*N* = 5), for each task type**



In addition, the average score for each group of chimpanzees (infants, juveniles, and adults) was calculated to investigate possible developmental differences (Fig. 5). Overall, the infant subjects performed at chance at the more conservative value (50%), and responded successfully on 62.5% of the trials (one-tailed binomial test, chance = 50%, *P* = 0.727). However, if chance was set at 25%, that is, the infants were successful at retrieving the reward, but did not use the tool properly (i.e., “successfully”), a one-tailed binomial test revealed significant performance (chance = 25%, *P* = 0.027). The juvenile and adult chimpanzees, however, performed significantly above chance when they used the tool correctly and were successful at retrieving the reward. The juveniles performed at 94% (one-tailed binomial test, if chance = 25%, *P* < 0.001), and the adults were 100% (one-tailed binomial test, chance = 25%, *P* < 0.001). When considering only “correctness” (correct modification of the tool and retrieval of the reward), however, the developmental differences disappeared. The infant chimpanzees were correct 94% of the time (one-tailed binomial test, chance = 12.5%, *P* < 0.001), and juveniles and adults were both 100% correct (one-tailed binomial test, chance = 12.5%, *P* < 0.001).

To examine developmental differences further, a Kruskal–Wallis test was used to explore differences in performance among the three age groups. No significant differences were found when looking at “correctness” ($\chi^2$ = 3.5, $df$ = 2, $P$ = 0.174). However, when looking at “success when defined as successful retrieval of the reward, developmental differences emerged ($\chi^2$ = 11.202, $df$ = 2, $P$ = 0.004). Post hoc Mann–Whitney $U$ tests examined possible differences in performance between the different cohorts. A comparison between infants and juveniles revealed that the overall scores between the two groups did not reach significance, which would have suggested that juveniles were better at retrieving the reward [$U$ ($N_1$ = 2 and $N_2$ = 2) = 1 and $P$ = 0.057]. Between the infants and adult subjects, the adult chimpanzees also performed better [$U$ ($N_1$ = 2 and $N_2$ = 5) = 1 and $P$ = 0.004]. However, no differences were found between the juveniles and adults success at retrieving the reward [$U$ ($N_1$ = 2 and $N_2$ = 5) = 17, $P$ = 0.733]. A final comparison between the infants and the combined older group was also not significant [$U$ ($N_1$ = 2 and $N_2$ = 7) = 0.00, $P$ = 0.056].

With respect to tool modification, the adults and juveniles were successful at modifying the tool and using it correctly on 79% of the trials that required modification (i.e., Tl assembled trials and HR disassembled trials; $N$ = 22). It is noteworthy that for all 22 trials requiring modification, both older groups modified the tool before they attempted to use it. However, they were still able to retrieve the reward successfully on 21% of the trials ($N$ = 6) without modifying the tool. The infants’ data for tool modification were more variable, and appeared to reflect a trial-and-error strategy. The male infant, Harper, did not attempt to modify the tool on three of four trials where tool modification was necessary. However, on his first TI assembled task, which required that he disassemble the tool for it to be used effectively, he exhibited the following pattern of manipulation: modify → incorrect attempt → modify → incorrect attempt → modify → correct attempt. In contrast, the female infant, Emma, modified the tool three of the four trials where necessary, using a highly dissimilar strategy from Harper’s. Her strategies differed from his for the TI assembled task (requiring disassembly for use), and the HR disassemble (requiring assembly for use), as follows: modify → no attempt → modify → no attempt → modify → correct attempt. As noted, both strategies by the infants were in direct contrast to the adults’ performance of modifying the tool on all necessary trials, prior to any attempt at use.

## Discussion

These results demonstrate that enculturated chimpanzees were able to apply their knowledge of tool properties when tool types were either assembled or disassembled, and also understood the physical structure and functional requirements of two different test apparatus. Using their understanding of these causal relationships, the juvenile and adult chimpanzees were successful in using the appropriate tools, either through modification of the tool, or through immediate use of the tool form available, to accomplish the task at hand. That the chimpanzees were typically successful on the first attempt further indicated that they were able to recognize the functional requirements of the task, and respond according by using or modifying the available tool. Such understanding of the requisite functional properties of a tool may reflect a level of causal understanding that emerged experientially. This understanding may have been emerged via implicit folk knowledge, derived in part through prior experiences, particularly with the mechanical and functional properties of artifacts, natural materials, and substrates that the chimps encountered within their daily environment. However, the two infants were not consistent in selecting the correct tool for a particular test apparatus on a given trial. Thus, different from the juveniles and adults, the youngest animals’ performance revealed a seemingly less sophisticated level of understanding of the functional properties of the tools in relation to the apparatus type presented, and/or potential difficulties with the motor requirements of the task. Although the infants were able to retrieve the food reward 98% of the time, they often did so using an inappropriate form of the tool. They also generally took longer to complete a trial, and were more likely to exhibit play with the tool. During the course of such play, however, they were acquiring information through exploration of a novel object that may have included how the specific tool might function. Although they were no less motivated than the older animals, the infants' overall behaviors were generally less focused on completing the task. It is interesting to note that all of the above behavioral descriptions are highly reminiscent of the characterization of young chimpanzees in the wild as they begin developing expertise with tools while observing their mothers (e.g., Goodall 1968; Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2006; McGrew 1992).

Indeed, over the past four decades, observations of chimpanzees in the wild have shown complex use of tools that requires a sophisticated level of causal understanding of the tool requirements necessary for extractive foraging (Goodall 1968; McGrew 1992; Whiten et al. 1999). In many instances, the nature of tool selection, modification, or transporting of a tool to a food site suggests prior planning or foresight (Boesch-Achermann and Boesch 1993). For example, prior to ant dipping, chimpanzees modify twigs to an appropriate length, and remove bark and leaves before using the newly formed probe (Goodall 1968; also see McGrew 1992). For those chimpanzees that use stone tools, when they need to open a particularly hard species of nuts, they will select a stone hammer rather than a wooden log, since the latter would not be an effective tool (Boesch and Boesch 1990). Similar instances suggestive of foresight also have been demonstrated by captive chimpanzees during studies of tool use and tool modification (Furlong et al. 2008; Visalberghi et al. 1995).

In light of previous reports from the Weld and the laboratory (see Fredman and Whiten 2008; Martin-Ordas et al. 2008; Mulcahy and Call 2006), and the positive results reported in the present paper, what variables may have contributed to difficulties when Povinelli's (2000) chimpanzee subjects were tested with the same tasks? Recall that his animals were unable to demonstrate or acquire an understanding of the relationship between the necessary version of a tool and the requirements of specific apparatus in almost all of the 27 tool tasks reported (Povinelli 2000). Several explanations for the observed differences in performance between the two groups of chimpanzees were suggested by our findings. One hypothesis is that the disparity in performance may be the dramatic result of differences in developmental experiences, that is, the contributions and impact of enculturation. Indeed, Povinelli et al. (2000) themselves reiterated that tool-using ability in chimpanzees was learned through a slow trial-and-error process that took place throughout infancy and the juvenile years (Biro et al. 2003; Goodall 1968; Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2006; McGrew 1992).

In addition, documentation of tool use in wild chimpanzees has been available in the archival literature for over three decades. At the time the tool construction experiment was conducted with his animals, Povinelli's subjects were all between 9.5 and 10.5 years old, and had participated in several years of tool-related studies. From his described methods and procedures, however, his chimpanzees did not have ready access to materials (e.g., sticks, foliage) or manipulanda during their early development (i.e., birth 3 years.). In addition, Povinelli's subjects were given only 15 min of exposure to a novel tool or material immediately prior to initiation of the task, for some experiments (e.g., Povinelli et al. 2000). Consequently, though development and acquisition of tool-use expertise in chimpanzees has been well-documented, the investigators undertook a tool task with chimpanzees who were destined to fail, having been brought to the experimental situation highly unprepared to meet the task demands (Povinelli et al. 2000) Without opportunities for play, exploration, and interaction with a variety of objects and materials throughout infancy for a species that has been documented historically and experimentally to be highly prepared for complex motor manipulation of objects and materials in their environment, Povinelli et al.'s (2000) subjects' pre-potent, behavioral predispositions were likely blunted. Chimpanzees in the wild typically display adult-like competence in tool use between 6 and 7 years of age, after years of observation of tool use by their mothers and other adults in the community (Biro et al. 2003; Goodall 1968; Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2006; McGrew 1992). Young chimpanzees in the wild also experience continual opportunities for exploration and play with natural materials and other objects found throughout their habitat. Thus, it is not surprising that, in contrast to the poor performance of Povinelli's older subjects, even the juvenile subjects in our study performed at comparable levels as our adult chimpanzees. As these results indicated, a developmental difference was shown among our subjects. The infant chimpanzees exhibited a more limited understanding of the task demands, and sometimes performed at levels similar to Povinelli's adult subjects.

Given these comparisons, it seems unlikely that age was a critical factor in determining the tool-using skills exhibited by both groups of chimpanzees, with the exception of the two infants tested. However, the infants were able to complete the standard trials effectively, and also were able to assemble and disassemble potential tools, including dissembling a tool prior to use, but not when a tool required assembling prior to use. Were it not for the fact that, as noted, tool use by wild chimpanzees is always a modification process from an intact natural object such that they must "disassemble" the object in order to render it functional, the performance of the youngest subjects might seem unusual. It is also the case the wild chimpanzees learn to use tools through observation of skilled adults, a process that can take up to 7 years to achieve expertise, as in using stone tools as hammers and anvils (Boesch and Boesch 1990; Lonsdorf 2006). In addition, in young captive chimpanzees, Bard and Gardner (1996) found that 3- and 4-year-olds showed enhanced performance after observing demonstrations of a tool task, but that younger subjects (age 2) did not benefit from such demonstrations, and ultimately failed the task. In a similar task with captive capuchins monkeys, Fredman and Whiten (2008) tested human-reared monkeys and mother-reared subjects with a foraging task that required a tool to open. The box could be opened either by using the tool as a lever or with a poking technique. The human-reared animals saw a familiar human model use the tool, either by the poke method or using the lever. The mother-reared subjects saw the tool used by a monkey model. The human-reared group showed the greatest fidelity with respect to the specific tool used by the models. In contrast, the mother-reared monkeys used either the lever or the poke action. The investigators reported that the mother-reared subjects were more focused on the goal of the task and in retrieving the food reward than on the specific technique used by the monkey model. The results indicated that social learning through observation of a model enhanced performance for the mother-reared monkeys when compared to controls, although a similar effect was not seen between the human-reared animals and their control group. The authors concluded that observations of a model resulted in a socially shaped response that was more reminiscent of the model's behavioral approach than responses seen in the control groups (Fredman and Whiten 2008).

Based on the present findings, we propose that given the enculturated conditions under which our chimpanzees were raised, the processes of enculturation had a significant impact on their behavior, as well as expression of subsequent, long-term cognitive competence. Similarly, we would propose that such differences would be anticipated with any great ape species that was raised under comparable conditions. In several studies of captive chimpanzees, there were convincing evidence that enculturation had a greater effect on chimpanzee tool-using abilities than contributions from experience alone (Brent et al. 1995; Menzel et al. 1970). In both latter reports, wild-born, captive subjects performed better than nursery-reared conspecifics. In another experiment, Tomasello et al. (1993) studied imitative learning and its relationship to tool use in enculturated and mother-reared captive chimpanzees. They found that the enculturated animals consistently performed better on all tasks than mother-reared subjects. Enculturated chimpanzees exposed to a wide array of tools and other objects early in their development also had a greater propensity to manipulate the objects during both free play and experimental testing (Tomasello et al. 1993). A subsequent study addressing the explicit way that a tool had to be used, and its impact on great apes' performance was devised by Mulcahy and Call (2006). In their first experiment, all four species of great apes had to use a rake to reach food that had been placed in the middle of a trap-table, a modified apparatus that was redesigned based on the original trap-tube experiments reported by

Visalberghi and Trinca (1989). The results suggested that chimpanzees may have an understanding of specific causal relationships that can be expressed behaviorally if they are allowed to choose between alternative actions with the tool (Mulcahy and Call 2006). Their findings also indicated that some specific actions or apparatus used to test apes can require particularly difficult or awkward hand or body movements for success, and minimal changes in task demands may possibly result in greater success. In a extension of the trap-table studies, another modified version of the apparatus and the task requirements that were used by Mulcahy and Call (2006) was implemented by Martin-Ordas et al. (2008), using a newly designed trap-platform. The trap-platform was presented to all four species of great apes, and required the subjects to decide where to insert the tool, and also which direction the reward should be pushed. The modified trap-tube task (Mulcahy and Call 2006) was also completed with the same subjects for comparison across the two tasks. Overall results revealed that the animals performed better with the trap-platform than the trap-tube, and also showed a preference to rake toward themselves, rather than using a push-away action. The authors concluded that their findings were consistent with the conclusions drawn by Mulcahy and Call (2006) in that apes likely possess specific causal understanding and knowledge about the traps. However, they suggested that since there was no correlation between any species' performance on both tasks, apes may have lacked the ability for utilizing analogical relationships across the two tasks (Martin-Ordas et al. 2008).

Further, in their discussion of the potential impact of enculturation, Call and Tomasello (1996) outlined four mechanisms that could affect cognitive development in apes. The first was simple exposure, through which apes could learn about objects and their associated properties. Apes in captivity, whether enculturated or not, are exposed to a greater number of objects and artifacts in general than those who grow up in the wild. Second, the authors proposed that apes learn about objects through another type of social learning called emulation. Emulation refers to the process whereby a captive ape observes an object being used, and could learn about the object's properties or relation to another object that might not have been discovered on their own (Call and Tomasello 1996). However, observation alone would provide limited contributions to the functional understanding of a tool that could have multiple uses. Rather, the observer must have the opportunity to interact with the tool, as a novel object, for complete understanding and competence to be established. Without question, chimpanzees have remarkable behavioral and cognitive plasticity that reflect a significant cognitive capacity. Apes can learn specific skills through training by humans, such as those in the US entertainment business who may be taught to perform quite complex, specific behaviors, on command. Apes are also able to acquire an understanding of the task demands for a wide range of cognitive tasks under experimental conditions (e.g., Boysen and Berntson 1989; Matsuzawa 1985; Savage-Rumbaugh 1986; Rumbaugh and Washburn 2003).

Call and Tomasello (1996) also hypothesized that the process of human enculturation may lead to more highly developed social cognition that permits apes to view others as intentional agents. Thus, unenculturated, nursery-reared or laboratory chimpanzees, growing up in an abnormal social unit (i.e., a group of conspecifics that are all the same young age), as described for Povinelli's research subjects (e.g., Povinelli and Eddy 1996), would likely be at a decided disadvantage, in terms of cognitive development via such mechanisms. Under these conditions, no other juvenile, adolescent, or adult chimpanzees would be part of the social group that could serve as possible models. Though animals raised under these conditions might be exposed to more novel experiences than wild chimpanzees, they would be denied the important benefits from older, more experienced group members from whom they could learn by emulation, including species-typical social and behavioral norms. In contrast, enculturated chimpanzees in an enriched environment, with multi-age conspecifics, frequently would have the opportunity to learn through emulation, readily imitating the actions of other chimpanzees and their human caregivers. Thus, while training can be attempted with any chimpanzee for some types of skills, regardless of background and rearing history, enculturated animals, as proposed by Call and Tomasello

(1996), may be more aware of the intentional behavior of others. Such understanding would facilitate the acquisition and comprehension of some specific types of concepts and/or tasks that unenculturated animals might not easily grasp, particularly for those tasks that required sustained attention (Bulloch et al. 2008). Herrmann et al. (2007) have expanded the hypotheses put forth by Call and Tomasello (1996) into the “cultural intelligence hypothesis”, providing a framework to account for the differences in cognitive skills between humans and other apes. They argued that humans possess a species-specific set of social/cognitive skills that allow for effective and efficient exchanges of knowledge, and that facilitate participation in social interactions within a culture (Herrmann et al. 2007). The authors proposed that such emergent skills appear early in development, and are the cornerstone for specialized skills for social cognition that humans possess. This hypothesis was derived from a set of cognitive tests given to 2½-year-old children, captive chimpanzees and orangutans. Herrmann et al.’s (2007) Findings indicated that children and chimpanzees had similar cognitive skills related to the physical environment, but children excelled in social cognition over either of the ape species tested (Herrmann et al. 2007).

In our own study reported here, although all of our chimpanzee subjects came from varying backgrounds, from home-reared, nursery-reared, and including one wild-born subject; they have all spent most of their lives living under conditions of continuous human enculturation. All subjects either joined the project from another enculturated environment, or were brought to the project at a very young age (e.g. 3 years. or younger). Thus, during a major portion of their physical and cognitive development, all of our subjects were immersed in a highly enculturated setting. The findings from the tool construction and deconstruction tasks reported here, in sharp contrast to those of Povinelli et al. (2000), demonstrate that a lack of experiences inherent in an enculturated context can have a dramatic impact on later problem solving, among other capacities. Such significant experiences would include the following: (1) highly social, long-term, and stable engagement with a cohort of humans as well as mixed-age conspecifics, (2) opportunities to explore and manipulate a wide range of objects and activities throughout their environment, (3) acquisition and subsequent use of human gestural performatives and other communicative social rules, including pointing, orienting, turn-taking, and joint attention, and (4) a host of additional sequelae that could emerge as a consequence of the features of their rearing and living conditions. Many of these phenomena that emerge from living within an enculturated environment remain to be investigated and quantified in humans, as well as in apes (see Bulloch et al. 2008; Furlong et al. 2008)

The impact of enculturation was, indeed, a critical question we intended to address in the present study. Among the many features of enculturation process, we were aware that this included prior experience, that is, those that had occurred over the many years of our chimpanzees’ participation in the project, and well before the demonstration of the tool types for this experiment. Important experience for the animals also included their opportunity to use the tools prior to experimental testing, as part of the creation of an active teaching context. Consequently, we speculate that our subjects, unlike Povinelli’s chimpanzees, had a long, stable history of trust with their teacher and experimenters, from whom they expect to learn and succeed. These phenomena, akin to the impact on cognitive style and learning observed in young children whose teachers encourage them to instill confidence, are likely significant components of the enculturation environment. Among these variables, the specific features and the relative contributions of each, however, have yet to be measured empirically with apes. Future studies, where long-term standardized testing, measures of social referencing, and a systematic video record can be completed, may provide new directions for further microanalytic analyses of the dynamic, emergent processes of enculturation and the mechanisms that subserve them. Taken together, these features represent but one portion of a constellation of critical factors responsible for marked developmental differences from the tool use abilities in chimpanzees reared under more impoverished conditions (e.g., Brent et al. 1995; Menzel et al. 1970; Povinelli 2000; Schiller 1952). Thus, we propose that the impact of human enculturation on the cognitive development and subsequent capacities of our chimpanzee subjects are strongly supported by the current data. These conclusions garner further support from comparison of the limitations for effective tool use and problem-solving reported by Povinelli et al. (2000) across a range of experiments. They also represent a powerful reminder of the significance of human care-giving and enculturation (Bulloch et al. 2008; Furlong et al. 2008), and the more global contributions of our cultural practices, in particular, active and intentional teaching across generations, toward normal social and cognitive development.

[1] In all of their tool use studies, Povinelli et al. (2000) used what they termed “standard trials” that were used for training, and subsequently included during novel probe tests to maintain his chimpanzees’ “motivation”. A standard trial typically represented training trials during which the chimpanzee subject was provided with only one tool choice that was always functional, and thus, the correct version of the tool. Such standard trials usually preceded and followed novel test trials, insuring that his animals were successful with the majority of trials within a session, since they did not have to make a choice as to the correct tool.

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