A potent effect of observational learning on chimpanzee tool construction

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Although tool use occurs in diverse species, its complexity may mark an important distinction between humans and other animals. Chimpanzee tool use has many similarities to that seen in humans, yet evidence of the cumulatively complex and constructive technologies common in human populations remains absent in free-ranging chimpanzees. Here we provide the first evidence that chimpanzees have a latent capacity to socially learn to construct a composite tool. Fifty chimpanzees were assigned to one of five demonstration conditions that varied in the amount and type of information available in video footage of a conspecific. Chimpanzees exposed to complete footage of a chimpanzee combining the two components to retrieve a reward learned to combine the tools significantly more than those exposed to more restricted information. In a follow-up test, chimpanzees that constructed tools after watching the complete demonstration tended to do so even when the reward was within reach of the unmodified components, whereas those that spontaneously solved the task (without seeing the modification process) combined only when necessary. Social learning, therefore, had a powerful effect in instilling a marked persistence in the use of a complex technique at the cost of efficiency, inhibiting insightful tool use.

Keywords: social learning; tool use; tool manufacture; video demonstration; chimpanzees

1. INTRODUCTION

Complex tool use is a distinctive feature of humans, characterized by multiple sequential steps, understanding of causal relationships and rapid expansion of increasingly complex technological additions, or cumulative culture. However, many other species display a range of tool-using abilities, and recent discoveries in the field include examples of tool use in non-human species previously thought to be restricted to humans (Hunt & Gray 2003; Pruetz & Bertolani 2007). Chimpanzee tool use, in particular, has many similarities to behaviours found in humans; it is widespread (Whiten *et al.* 1999), it requires years of practice to master (Matsuzawa *et al.* 2001; Biro *et al.* 2003) and recent archaeological evidence suggests that some forms have a history of centuries at least (Mercader *et al.* 2007). Free-ranging chimpanzees also use tool sets, or more than one tool used sequentially for a single task (Brewer & McGrew 1990; Sanz *et al.* 2004; Deblauwe *et al.* 2006). Furthermore, distinct patterns of tool use in chimpanzee groups have recently been described as ‘cultural’ behaviours, maintained by social learning with no apparent ecological or environmental explanation (McGrew 1992; Boesch & Tomasello 1998; Whiten *et al.* 1999; Schöning *et al.* 2008).

Despite this complexity, there is minimal evidence of modification to tool technology over time (Sanz *et al.*

2009)—the ‘ratcheting effect’ so evident in human cumulative culture (Tomasello *et al.* 1993; Boesch & Tomasello 1998). Chimpanzee tool ‘manufacture’ in the wild mostly involves removal of materials (Beck 1980), and tool construction involving more than one raw component is lacking. There is some evidence of wild chimpanzees using one tool (a ‘metatool’) to render another tool more effective, but such behaviour is rare and has not spread as simpler tool-using behaviour has (Matsuzawa 1994, 2001; Sugiyama 1997). Combinatorial technology is likely to be more cognitively demanding than other forms because the second tool acts as an intermediary step between the main tool and a goal. The spread of such technology in the wild requires the cognitive ability for innovation, the capacity for social transmission and an ecological niche affording technological fixes (van Schaik *et al.* 1999; van Schaik & Pradhan 2003). It may be that developments of this nature are not seen in wild chimpanzees because their ecological niche does not call for them. Alternatively, the limit may lie in physical cognition (e.g. understanding causality), or the behaviour may be too complex for chimpanzee social learning abilities (Boesch & Tomasello 1998).

Controlled experiments in captivity can help determine whether the lack of such tool manufacture is the result of cognitive constraints. Many species display a greater range of tool-using behaviours in captivity, and chimpanzees have spontaneously combined objects to produce tools in a captive environment (Köhler 1957; Schiller 1957). However, it remains unclear what aspects of this process are understood by the inventor

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(Povinelli 2000), and overall performance tends to be marked by vast individual differences.

Studies of social learning in captive chimpanzees suggest that tool use can be facilitated by the observation of skilled demonstrators (Tomasello *et al.* 1987; Myowa-Yamakoshi & Matsuzawa 2000; Whiten *et al.* 2005; Hopper *et al.* 2007). However, the type and amount of information chimpanzees are gleaning and replicating from an observation are still open to debate (Byrne & Russon 1998; Zentall 2006). In addition, although several studies have used increasingly complex tasks involving hierarchical steps (Whiten 2002; Whiten *et al.* 2007; Marshall-Pescini & Whiten 2008), the complexity of the foraging task itself is typically manipulated, while the required tool remains relatively simple (e.g. a rake). Observational learning of complex tool modification has yet to be investigated in any detail. An individual chimpanzee in the wild will probably not face increasingly complex food defences in her lifetime, but might benefit from constructing a complex tool with which to more efficiently extract food. This being the case, the complexity of the tool itself, or the ways in which an individual can modify the tool, might be better variables to manipulate.

In the current study, we assessed not only whether captive chimpanzees can socially learn how to construct a composite tool from two components, but also how much information they require to do so and how well they understand the tool's function. We also explored whether such complex information could be transmitted via video footage of a conspecific model. Video demonstrations have been used to successfully influence behaviour in several species (e.g. Burmese red junglefowl, McQuoid & Galef 1993; budgerigars, Mottley & Heyes 2003; apes, Poss & Rochat 2003; black-and-white colobus monkeys, Price & Caldwell 2007; for a review, see D'eath 1998), controlling demonstration discrepancies across subjects and allowing precise manipulation of the amount of information available in a demonstration.

2. MATERIAL AND METHODS

(a) *Participants*

Fifty chimpanzees (25 males and 25 females) housed at the University of Texas M.D. Anderson Cancer Center (Bastrop, TX, USA) participated in the study (see appendix 1 in the electronic supplementary material for demographic data). One additional male chimpanzee from the centre acted as the demonstrator for all conditions. Participants reside in social groups of 5 to 14 individuals with access to four inner housing compartments and were tested in one-half of their inside enclosure, measuring $2.4 \times 2.4 \times 1.8$ m³. Chimpanzees were not food-deprived and had constant access to water.

(b) *Apparatus*

The tool composite consisted of two elements. The first was a 39-cm-long hollow polycarbonate tube containing an internal nylon rod that protruded 3 cm out of one end. The second element, a 28 cm rod, could be inserted into an 8 cm hollow opening on one end of the polycarbonate tube, creating a 59-cm-long stick. Alternatively, the tool could be elongated to 59 cm by twisting on the protruding end of the internal rod and extending it.

Figure 1. Experimental set-up. At the start of the experimental session, the food retrieval platform was placed flush to the edge of the enclosure as depicted. The monitor was directly attached to the laptop seen pictured, so that all video demonstration clips could be watched simultaneously by the experimenter.

The raking platform consisted of a 50×55 cm acrylonitrile-butadiene-styrene tray placed atop a wheeled cart measuring 1.22 m long by 74 cm wide and 31 cm high. Grapes were placed 55 cm back from the edge of the platform against a 13-cm-high wall. Video footage was played on a laptop connected to an external LCD monitor, so that the experimenter had visual access to what the chimpanzees were seeing at all times. The monitor was enclosed in a viewing box measuring 48 cm wide by 45 cm high and 67 cm long, so that the screen was placed 23 cm back from the edge and visible through a viewing window measuring 13 cm by 7.6 cm. The entire monitor/viewing box was placed on the top of a wheeled cart 61 cm wide by 91 cm long. When fully assembled on the cart, the base of the viewing window measured 83 cm from the ground (figure 1).

(c) *Procedure*

(i) *Baseline*

All participants were first provided with baseline raking sessions to ascertain individual raking abilities. Participants were provided with a grape placed approximately 30 cm out of reach on the platform and with sticks of adequate length. Once two grapes were successfully retrieved, the session ended.

(ii) *Video demonstrations*

One adult male chimpanzee (not a member of the group of any other participant) acted as the model for all demonstration conditions and was trained using positive reward shaping. Video footage was captured on a Sony Handycam and then digitized and edited using Adobe PREMIER Pro 2.0. All demonstration clips consisted of a combination of alternating close-up and far-away shots captured from the same angle. Each clip lasted approximately 25 s and clips were looped continuously with a 1 s pause between close-up and far-away shots.

(iii) *Experimental sessions*

Participants were assigned to one of the five demonstration conditions: combine-and-retrieve, retrieve-only, video control, no-video control and alternative method. In all but the no-video control, video footage was presented. Participants in the combine-and-retrieve condition had access to video footage of an unfamiliar chimpanzee slotting the nylon rod into the hollow

Figure 2. Demonstration stills taken from (a–c) the combine method and (d–f) the alternative method. Stills show the sequence of actions for combining: (a) picking up and positioning both components, (b) slotting the two components together and (c) retrieving the reward; and for the alternative method: (d) twisting the black end of the complex component, (e) extending the internal rod and (f) retrieving the reward.

end of the complex tool, thereby creating a longer tool and retrieving a food reward off the platform. The retrieve-only condition involved the chimpanzee model retrieving the reward with a combined tool, but the modification process was omitted. In the video control condition, the model was eating the food reward in the absence of tools or platform. Chimpanzees in the no-video control condition received no prior video demonstration. We added an alternative method of lengthening the tool, which did not require combining two components. In this condition, chimpanzees saw the model twisting the end of the complex tool, extending an internal rod, and then retrieving a reward (figure 2).

Participants were isolated from their social group in one-half of their inside housing area. Video footage of the appropriate demonstration was shown for 5.5 min, or 16 demonstrations. During this time, the raking platform was visible but not accessible. After the pre-session, the platform was pushed flush with the cage with a food reward placed 49 cm out of reach, and the tool set handed to the participant. An additional 48 demonstrations were played simultaneously for the entire 20 min test session. Participants were given access to the platform, and the tool set for up to a total of three 20 min sessions or until they solved the task. As soon as a subject had successfully modified the tool and retrieved a reward, the session ended, giving each subject only one opportunity to obtain a reward.

(iv) Post-session

Successful participants (that had successfully modified the tool and retrieved a reward) were tested away from their group two weeks after their final session. Each trial started with the presentation of the tool components immediately following the placement of a grape at one of four different locations on the platform: close (13 cm), mid-close (22 cm), mid-far (36 cm) and far (49 cm; figure 3). Close and mid-close rewards could be retrieved easily with the unmodified components; mid-far rewards required the longer, polycarbonate tube; and far rewards could only be retrieved by combining. Rewards were placed in each location four times, for a total of 16 presentations. Presentation order was

Figure 3. Post-session reward distances. The reward distance positions for the post-session, accompanied by the uncombined components and a combined tool. A reward was placed in each position four times: F, far distant; MF, mid-far; MC, mid-close; C, close.

randomized across subjects. All chimpanzees had previously been trained to return objects in response to a 'give' hand gesture (open hand, palm up) and returned the tools prior to the next grape presentation.

(d) Coding and reliability

In coding videotapes, participants were assigned a score on a scale of interaction for both combining and using the alternative method (0, no interaction; 14, complete modification and retrieval; table 1). Ten randomly selected trials were coded independently by an additional rater and overall scores assigned on both the combining and alternative method indices. Inter-rater reliability was assessed using Spearman's rank order coefficient, yielding 0.90 for the combining index and 1.00 for the alternative method index.

3. RESULTS

(a) Experimental sessions

Overall, there were significant differences in the level of combining across groups (Kruskal–Wallis test,

Table 1. Combine and alternative method indices, with corresponding scores.

combine index	score	alternative method index
successful retrieval with the combined tool	14	successful retrieval with alternative method
combine tools successfully, retrieval attempt with combined tool	13	successful modification (twist and extend), retrieval attempt with modified tool
combine tools successfully, retrieval attempt with either or both unmodified components	12	successful modification, retrieval attempt with either or both unmodified components
combine tools successfully, no retrieval attempt	11	successful modification, no retrieval attempt
combine attempt with hollow (correct) end, retrieval attempt with either or both unmodified components	10	twist and pull attempt (unsuccessful modification), retrieval attempt with either or both unmodified components
combine attempt with hollow end, no retrieval attempt	9	twist and pull attempt, no retrieval attempt
combine attempt with black (incorrect) end, retrieval attempt with either or both unmodified components	8	twist attempt, retrieval attempt with either or both unmodified components
combine attempt with black end, no retrieval attempt	7	twist attempt, no retrieval attempt
insert finger into hollow end, retrieval attempt with either or both unmodified components	6	pull attempt, retrieval attempt with either or both unmodified components
insert finger into hollow end, no retrieval attempt	5	pull attempt, no retrieval attempt
look into or mouth hollow end, retrieval attempt with either or both unmodified components	4	bite or hand touch to black end, retrieval attempt with either or both unmodified components
look into or mouth hollow end, no retrieval attempt	3	bite or hand touch to black end, no retrieval attempt
retrieval attempt with either or both unmodified components	2	retrieval attempt with either or both unmodified components
contact, but not retrieval attempt	1	contact, but no retrieval attempt
no contact	0	no contact

$\chi^2(4) = 13.07$, $p = 0.01$). Participants that saw the combine-and-retrieve demonstration scored significantly higher on the combine scale than those in the video control (following Siegel & Castellan 1988, critical value = 18.2; significant at $p = 0.05$), no-video control ($p = 0.05$) or alternative method ($p = 0.05$) conditions (figure 4). There was no significant difference between the retrieve-only condition and any other condition ($p > 0.05$), with the level of combining in this condition (four combiners) lying between that in the combine-and-retrieve (eight combiners) and the control conditions (one combiner in each condition). We ran the same analyses on the scores for the alternative method and found no significant differences (Kruskal–Wallis test, $\chi^2(4) = 3.61$, $p = 0.46$). Two subjects from the no-video control condition and one from the retrieve-only condition did manage to extend the tool using the alternative method, but only one of these (from the no-video control condition) successfully retrieved a reward. The other two individuals successfully made and used a combined tool to retrieve a grape.

Intriguingly, three of the eight chimpanzees that learned to combine in the combine-and-retrieve condition, and one of the four chimpanzees in the retrieve-only condition, nevertheless failed to retrieve a reward. In the case of one combine-and-retrieve condition individual, her combined tool fell apart during the retrieval process and she did not attempt to retrieve again. The other three individuals combined the tool, in some cases several times, but then pulled them apart and attempted to retrieve the reward using the separated components. This suggests that while they had learned to combine the components, they did not understand the utility of doing so.

(b) *Post-session*

In order to ascertain whether or not chimpanzees understood the function of combining, those individuals that solved the task (combined and retrieved the reward) were

given a follow-up test two weeks after their final session. The one individual that had successfully extended the tool and retrieved a reward using the alternative method did not make any attempts during the post-session using either method and was subsequently excluded from the analysis. Those who solved the test after seeing video footage of the combining process (combine-and-retrieve, $n = 5$) combined significantly more in the close, mid-close and mid-far reward positions (when the unmodified tools could be used) than those who had solved the test without first seeing the combination process (retrieve-only $n = 3$; video control $n = 1$; no-video control $n = 1$; Mann–Whitney $U = 1$, $p = 0.02$). Those who had not seen the combining demonstration switched between using the unmodified tools and the combined tool depending on the distance of the reward (close versus far positions, Wilcoxon test, $z = -2.12$, $p = 0.034$), whereas those in the combine-and-retrieve condition did not switch significantly between the two techniques (Wilcoxon test, $z = -1.63$, $p = 0.102$; figure 5).

4. DISCUSSION

Chimpanzees that saw a conspecific combining two tool elements and retrieving a reward fared significantly better than those under all conditions aside from the retrieve-only condition. This result provides the first experimental evidence of chimpanzees socially learning how to manufacture a tool by combining separate elements. Such a result suggests that the spread of similarly complex tool manufacture in free-ranging chimpanzees is unlikely to be blocked by cognitive deficits in social transmission.

Additional inferences can be made about the types of social learning involved. Chimpanzees in the retrieve-only condition did not differ significantly from those in the control conditions, suggesting that the chimpanzees in our study were attending to the combination process

Figure 4. The median scores and interquartile ranges on both the combine index and the alternative method index for the combine-and-retrieve (CR), retrieve-only (RO), alternative method (AM), video control (VC) and no-video control (NVC) conditions ($n = 10$ in each group). Boxes represent the interquartile ranges, and whiskers the maximum and minimum values that are not outliers (values between 1.5 and 3 times the interquartile range, marked by circles) or extreme cases (values over three times the interquartile range, marked by asterisks). Grey bar, combine; striped bar, alternative; black section of bar, median.

itself, rather than the product of that process. However, the level of combining in this condition did not differ significantly from the combine-and-retrieve condition either, indicating that seeing a conspecific using a completed tool, but not seeing the process itself, was enough to facilitate some chimpanzees to solve the task on their own, but this was not so for the majority.

None of the chimpanzees in the alternative method condition learned how to retrieve a grape. Although this task did not involve combining two tool components together, it is arguably more perceptually opaque. Twisting and extending an internal rod might be beyond the capabilities of chimpanzee physical cognition and, additionally, may be too subtle to learn socially. Although many individuals across the conditions tried to pull on the end of the stick, only 3 out of the 50 succeeded in twisting the end to elongate the tool, and only one was successful at using the tool to retrieve a reward. It may be that for the majority, chimpanzee understanding of 'folk physics' does not extend to such mechanisms. If chimpanzees are relying heavily on their own individual problem-solving skills in addition to information gleaned through observation, a task outside of chimpanzee physical cognition abilities may be less easily facilitated by a demonstration.

Understanding of the function of the combining process was limited in several chimpanzees. Although they learned how to combine the two components together, three participants in the combine-and-retrieve condition failed to grasp the function of combining. In addition, in the post-session, those individuals that saw the combination process tended to combine even when the reward was within reach of the unmodified

Figure 5. The overall proportion of combining in the post-session across the reward distance positions. Those subjects who solved the task after seeing a model combining the two components ('combine': combine-and-retrieve, $n = 5$) tended to combine more, even when unnecessary compared with those who had not seen a model combining ('control': retrieve-only, $n = 3$; video control, $n = 1$; no-video control, $n = 1$). Grey diamond, combine; black square, control.

components. This is especially intriguing, given that the combining process was more time-consuming and the elongated tool more awkward to use with a reward in the close position. Nevertheless, although combining is less effective in the two close positions, it always works and thus does not require a re-evaluation of distance at the start of each trial. In two recent studies, chimpanzees have been found to persist in an acquired method, even when presented with a demonstration of a more effective technique (Hrubesch *et al.* 2008; Marshall-Pescini & Whiten 2008).

However, if chimpanzees are merely employing a conservative strategy, then both groups tested in the post-session should use the combine method equally. All subjects entered the post-session having retrieved a reward using the combine method once; the only difference between the two groups was whether they saw a conspecific model combining the two components. The five individuals who did not see the combination process constructed tools selectively, only combining when the reward was out of reach of the unmodified components. They therefore demonstrated the capacity to develop an efficient solution through individual problem-solving skills and seemed to have a causal understanding of the task. It may be that those who socially learned to combine the tools did not understand the function of combining and were blindly copying what they had seen. Alternatively, seeing a conspecific combine the tools may have had an inhibiting effect on insightful behaviour, such that chimpanzees were adopting a conformist strategy. Either way, our results suggest that socially learning a task, rather than learning through individual exploration, can have a potent effect on maintaining a particular method among chimpanzees, even at the cost of efficiency.

The question remains as to why combinatorial tool behaviours like these, although observed on rare occasions in the wild, do not spread. The number of available demonstrators or quality of available demonstrations may be a crucial limiting factor. The rare instances of combinatorial tool construction in the wild

typically involve low-ranking individuals (Sugiyama 1997). These individuals might be more likely to perform such tasks because they have more restricted access to prime foods and, as low-ranking group members, they are then less likely to act as salient models for other group members (Laland 2004).

The number of available demonstrators may also be limited by a disparity between the development of advanced physical cognition and the social tolerance of potential demonstrators. Social tolerance can play an important role in the spread of new behaviours (Matsuzawa 1999; van Schaik *et al.* 1999). Adults are highly tolerant of infants, allowing young chimpanzees to observe their mother and other adults in close proximity (Inoue-Nakamura & Matsuzawa 1997; Hirata & Celli 2003; Lonsdorf 2006). Free-ranging chimpanzees typically become proficient at extractive tool use between the ages of 4 and 7 years (McGrew 1977; Biro *et al.* 2003; Hirata & Celli 2003; Lonsdorf 2006), and there is evidence for a critical age in the development of more advanced tool use, such as nutcracking, between the ages of 3 and 5 (Matsuzawa *et al.* 2001). Individuals who do not learn during these years do not become proficient later. The few instances of metatool use (e.g. an anvil prop used to level a surface on which to pound nuts) have been observed solely in individuals over the age of 6.5 years (Matsuzawa 2001). Such tasks involve not only manual dexterity and motor control, but also demand sophisticated physical cognition. It is possible that when chimpanzees reach an age at which they are physically and cognitively capable of performing these higher level techniques, they are too old to have access to sufficiently tolerant demonstrators.

The video demonstrations we developed allow adult chimpanzees to observe a skilled conspecific perform a task without fear of repercussion. They witness repetitions and precise details of the actions involved. In addition, observers can explore use of their own set of tools while watching the demonstration. Video demonstrations afford the opportunity to test the effect of demonstrator type, varying the rank, age, sex, familiarity or even species of the model. In the current study, we have shown chimpanzees can not only learn from a video image of a conspecific, but that male and female chimpanzees alike can learn from an unfamiliar male. In the retrieve-only condition, when subjects were able to see the final result of the combination process, but not the process itself, the level of combining was roughly midway between the combine-and-retrieve and control conditions. This might be more akin to the amount of information they would be able to see as adults in the wild, given the presence of skilled users. Without access to precise details, observers may gain a global idea of the task, but may experiment with their own methods to solve it. As a consequence, it might be difficult for new technological additions to spread through the group owing to an information 'slippage effect' (Boesch & Tomasello 1998). If these innovated additions are particularly subtle or complex, they might not spread at all.

5. CONCLUSION

Chimpanzees are the most proficient tool users in the wild and use an array of tools for diverse purposes. Yet there is

still little evidence that tool technology builds much over time, with new additions leading to greater technology, as happens in humans. We have shown that captive chimpanzees are cognitively capable of socially learning a technological addition to an existing tool behaviour. Those that saw the complete process, rather than just the end result or products of the process, performed the best. Furthermore, chimpanzees who socially learned the task, rather than spontaneously inventing it, continued to use the new method more faithfully. The capacity for cumulative culture in humans may be the result of a combination of other mechanisms such as language, cooperation, teaching or niche construction rather than a difference in enhanced social learning abilities.

The chimpanzees used in this study are housed in facilities that have been accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care International and in accordance with current United States Department of Agriculture, Department of Health and Human Services and National Institutes of Health Regulations and Standards. All testing has been approved by the University of Texas Institutional Animal Care and Use Committee. We thank Andrew Burnley for construction of the tools, Lydia Hopper and Erica Thiele for logistical support and Jason Zampol for figure rendering. We also thank Thomas Bugnyar, Christine Caldwell and William Hoppitt for their comments on the manuscript. E.E.P. was supported by the Overseas Research Student Award Scheme and by a School of Psychology Studentship. A.W. was supported by a Royal Society Leverhulme Trust Senior Research Fellowship.

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