Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes)

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ORIGINAL PAPER

Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*)

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Abstract Geographic variation in socially transmitted skills and signals, similar to human culture, has been well documented for great apes. The rules governing the adoption of novel behaviours, however, are still largely unknown. We conducted an innovation-and-transmission experiment with two groups of chimpanzees living at *hopE* Primate Sanctuary Gänserndorf, Austria, presenting a board on which food had to be manoeuvred around obstacles to be acquired. Most chimpanzees used sticks to acquire the food, but five adults independently invented a novel technique, rattling, which was subsequently tested by almost all group members. However, individuals who had become proficient with sticks were reluctant to switch to rattling, despite it being more efficient. Similarly, after rattling was prevented, rattle specialists kept trying to rattle and made no attempt to use the stick technique, despite their knowledge about its existence. We conclude that innovators stimulate others to experiment with the solutions they display, but that chimpanzees are nevertheless conservative; mastery of a skill inhibits further exploration, and hence adoption of alternative techniques even if these are more efficient. Consequently, conformity among group members should not be expected in great apes when individuals develop proficiency at different techniques. Conservatism thus joins conformity as a mechanism to bring about cultural uniformity and stability.

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Introduction

Experimental studies of great apes have demonstrated the existence of various social learning processes, including imitation and emulation (Byrne 2002; Whiten 1998; Whiten et al. 2004, 2005), which are thought to be conducive to reliable transmission of behavioural variants. These experiments strengthen claims for traditions based on innovations that are spread and maintained by social learning among great apes in the wild (van Schaik et al. 2003; Whiten et al. 1999).

Although experiments have abundantly demonstrated the chimpanzees' capacity to learn through observation of others' behaviour, they have not yet revealed the rules governing individuals' learning from one another. Such rules may affect the rate of spread, spatial and social patterning of novel variants, as well as which alternative variants can enter into a population in which another variant is already predominant (cf. Laland 2004), and the extent to which skill possession inhibits exploration. Recent work that used the two-action approach has suggested that chimpanzees are able to copy the technique that is demonstrated to them by experts in their groups, and that adoption of one technique stops further exploration of the problem, leaving individuals to stick to what they have observed (cf. Whiten et al. 2005; Bonnie et al. 2007). This result was interpreted as an indication of conformity in social learning. An alternative explanation, however, is that having learned a particular solution to a problem inhibits further exploration of that problem, as has been suggested for humans (Boyd and Richerson 1985), regardless of what variants others have adopted.

We attempted to distinguish between these two possibilities, offering a simple foraging task in two different groups of captive chimpanzees. The expected technique to obtain food was raking with sticks as the participants were already familiar with sticks to solve foraging tasks, but in both groups several individuals spontaneously invented a novel technique, rattling. The two techniques were not equally efficient, and we therefore asked whether individuals would (1) show a form of social conformity, (2) simply choose the most efficient technique, or (3) show reluctance to switch to an alternative technique, and instead stick to the technique they knew well.

Animals and methods

Subjects

Subjects were 13 chimpanzees (*Pan troglodytes*) living in 2 social groups at *hopE* Primate Sanctuary Gänserndorf, Austria. Group C consisted of 5 individuals (1 adult male and 4 adult females), group D of 9 individuals (2 adult males, 1 subadult male, 1 juvenile male, 4 adult females and 1 juvenile female). One female of group D never approached the experimental apparatus and was therefore excluded from the analyses. The chimpanzees were former biomedical research subjects with experience in various environmental enrichment and tool use tasks. As a result, the animals were familiar with sticks, but had used different techniques than the one required in this study. The experiments were conducted between April and September 2006, over 3 years after re-socialisation began.

Apparatus

A ‘food board’, of 70 × 38 × 1.8 cm, with barriers and obstacles attached to its surface, was mounted to the wire mesh outside the chimpanzee enclosure (Fig. 1). A rim of 1 cm around the three outward edges prevented food from rolling off. The experimental task was to move food items such as grapes, peanuts and cherries presented on that board closer, in such a way that they became manually accessible through the wire mesh.

Experimental procedure

As a pilot experiment, we conducted individual tests in the night cages with eight individuals of group D (Table 1). The chimpanzees were visually separated from other group members to prevent social influences on their initial responses. These trials lasted 10 min, or until ten peanuts had been acquired. One observer recorded any actions directed towards the board.

Fig. 1 Food board with two stick using chimpanzees

Table 1 Order of trials

	Rattle phase			Non-rattle phase
	Individual tests	Group tests		
		1	2–7	>8[a]
Group D				
MOR	1	1	1	1
ANT	1	1	1	1
HEL	1	1	1	1
BON	1	1	1	1
SCH	1	1	1	1
SUS[b]	1	-	-	-
Alf	1	1	1	1
Dav	1	1	1	1
Xar	-	1	1	1
Group C				
CLY	-	1	1	1
GAB	-	1	1	1
PÜN	-	1	1	1
MAR	-	1	1	1
ING	-	1	1	1

Males are shown in italics, immatures (6–10 years) in small letters

1 indicates participation in the respective experiment, – that the experiment was not performed

[a] Group D was tested 7 times in the non-rattle phase, group C 3 times

[b] Female Susi was present during all experiments, but never approached the food board

Subsequent tests were conducted only in the group setting inside a group’s enclosure, with two food boards mounted at a distance of >5 m to prevent monopolisation by dominants. Both boards were baited simultaneously and then re-baited for up to 40–60 min in each test. One observer recorded behaviours at one food board, while a video camera (Sony HDR-HC1E) recorded the situation at the other. Videos were later transcribed using the program INTERACT (Mangold).

During the tests, human interference was restricted to recording behavioural data and baiting of the board without interacting with the chimpanzees. Particularly, we neither encouraged nor discouraged chimpanzees from any behaviour towards the apparatus or their group members. As chimpanzees' participation in the experiment was voluntary, the presence and behaviour of the subjects at the food boards varied within and between tests.

Group D was tested 14 times, group C 10 times (Table 1). We were forced to stop our investigations at that point, but decided to include the 'additional' four tests of group D in order to have more data on individual chimpanzees. After the seventh test we prevented rattling by fixing the food boards to the wall by a chain, so that food could be accessed only by stick use. We labelled the first seven tests 'rattle phase', and the subsequent extinction tests the 'non-rattle phase'.

Predictors

We attempted to predict innovation and the spread of techniques among group members on the basis of actual attention during the experiment. As an indicator of attention to other chimpanzees' food acquisition techniques we used 'peering', defined as looking intensely at another individual's processing behaviour (rattling or stick use) from a distance of usually an arm's reach, but never more than 2 m.

The choice between techniques might also be affected by differences in yield, dependent on features of the technique or of the individual. First, one technique may objectively be more *efficient* than another, because the average yield of individuals employing it is higher than for the other technique. Second, an individual may be more *proficient* in executing one technique than the other, e.g. as a result of familiarity and practice. The difference is especially relevant if an individual is proficient in the technique that is overall less efficient.

We called subjects who consistently used only one technique (stick or rattling) 'specialists' and those who consistently used either technique 'generalists'. We used two indicators of yield, latency to success and success rate across the first seven tests. Latency to success is the time (in seconds) that elapsed between the beginning of a processing action and the retrieval of the food item. Success rate is measured by the number of retrieved/eaten food items minus the number of food items falling off due to incompetent processing. Individual proficiency represents each individual subject's personal latency to success and success rate across the first seven tests.

Dependent variables

We distinguished two techniques, each of which included subtle variations. Stick use was coded whenever a chimpanzee pushed a stick through the mesh in order to reach food items. One 'bout' included both goal-directed moving of the stick and contacts between the stick and a food item, as well as fishing with the fingers for the food item; a bout lasted until success (i.e. food items having passed the mesh) or until the subject stopped handling the stick. We lumped various forms of stick use into this category, e.g. different ways of gripping the stick or moving it.

Rattling was coded when subjects tilted the board by sticking their fingers through the mesh, palms up, touching the bottom side of the food board and tilting it upwards by abrupt flexions of the fingers. Since even the youngest subject was able to tilt the board, effective rattling was not a matter of strength. A rattle bout included both the actual tilting of the board and fishing with fingers for the items. Rattling, too, was performed in various different ways including wrapping one finger around an obstacle and pulling the board. The bouts could consist of just one powerful rattling action or of several less powerful actions in sequence.

To determine 'initial technique', we compared the results of the individual tests in group D with the first group experiment in group D. These did not differ. In group C, therefore, we assessed each subject's initial technique during the first group test. Innovation was defined as the first occurrence of rattling in the absence of prior observation of group members performing this technique.

We documented the spread of the rattling technique by recording for each subject in which test it first applied rattling and any instance of peering at another individual's performance of rattling.

The degree to which subjects employed rattling was determined by the proportion of rattle actions in the rattle, respectively the non-rattle phase (tests 8–10 for group C, respectively 8–14 for group D; however, proportions of tests 8–10 and 11–14 did not differ in the latter). The proportion of rattling was calculated in relation to total processing actions (stick and rattle) by each individual per test and per phase.

Data analysis

All statistical analyses were done with SPSS, using *t* tests, either for matched samples or independent samples, to test for differences between generalists and specialists and between techniques. For independent samples *t* tests we employed Levene's test to test for equality of variances and adjusted the degrees of freedom accordingly. The unit of analysis was the individual for whom we calculated means for the frequency, success rate and latency to success of each technique. Further, Spearman's correlations were used to assess relations between these variables. The alpha-level of significance was set at 0.05, and all tests were two-tailed.

Results

Innovation and spread

As expected on the basis of their previous exposure to stick use tasks, 10 of 13 chimpanzees immediately used sticks to access food during the first test. Five subjects (2 adult males and 3 adult females), however, spontaneously invented a novel technique, rattling (Table 2). Rattling was an innovation since it had not been seen before and no chimpanzee at *hop*E Sanctuary had ever been rewarded for performing similar actions (personal communication, keepers and investigators). Three instances of this innovation appeared during individual testing, the two others occurred nearly simultaneously and independently in the group setting on two different food boards and without previous peering by the innovators (at 4:09 min and 6:53 min in the first test). Thus, during their first exposure to the food boards, six chimpanzees spontaneously used only sticks, one employed only rattling, and four used both techniques (Table 2). The two remaining subjects did not spontaneously act on the food boards at all.

Already in the course of the first three group tests, seven more chimpanzees tried rattling in addition to the five innovators. In contrast to the innovators, these seven started rattling only after having peered at other group members while these performed rattling. Only female Bonnie peered extensively but never even tried rattling. In sum, 12 of 13 chimpanzees tested the rattling technique at least once.

After having tried either technique, however, not all chimpanzees continued to use them side by side. Three individuals gave up rattling after the first unsuccessful attempt. Another chimpanzee gave up stick use after using it inefficiently in the first (individual) test. Overall, nine individuals continued to use rattling and ten subjects continued to use sticks (Table 2). Thus, of the 13 subjects, 6 (4 adult females and the 2 juveniles) became generalists, i.e. consistently employed both techniques, whereas 4 (3 adult females, 1 subadult male) became stick specialists and all 3 adult males became rattle specialists. Remarkably, the two juveniles consistently used both techniques although each was successful in one technique only (the male in stick use, the female in rattling).

Table 2 Overview of the acquisition of the stick or the rattle technique, as generalists and specialists, and the subsequent use of technique

	Individual acquisition	Acquisition after peering	Consistent use	Successful use
MOR	r s	-	r	r
ANT	r	-	r	r
CLY	-	r	r	r
Alf	s	r	s	s
MAR	s	r	s	s
ING	s	r	s	s
BON	s	-	s	s
HEL	s	r	r s	r s
SCH	r s	-	r s	r s
GAB	r s	-	r s	r s
PÜN	r s	-	r s	r s
Xar	-	r s	r s	r
Dav	s	r	r s	s
Stick	10 (6)	1 (0)	10 (4)	10 (5)
Rattle	5 (1)	7 (6)	9 (3)	9 (4)
Generalist	4	1	6	4

Numbers in parentheses refer to the number of specialists in that category. Males are shown in italics, and immatures (6–10 years) are shown in small letters

The letters *r* and *s* indicate rattling, respectively stick use, – corresponds to none of these. *Individual acquisition* refers to the use of techniques without prior observation of others behaviours both in individual tests and in group tests, *Consistent use* stands for the subsequent performance of the techniques beyond the first acquisition, *Successful use* indicates that individuals had success in acquiring food items through the respective technique

Efficiency, proficiency, and switching between techniques

We looked at efficiency in groups of generalists and specialists separately. The success rate of rattling was much higher than that of stick use (generalists: $t = 2.866$, $P = 0.035$, $df = 5$, $n = 6$; specialists: $t = 1.445$, $P = 0.283$, $df = 2.041$, $n = 3$ rattlers + 4 stick users; Fig. 2a). The same holds true for latency to success, which was nearly three times higher for stick use, both for generalists and specialists (specialists: $t = -4.008$, $P = 0.010$, $df = 5$, $n = 3$ rattlers + 4 stick users; for generalists the sample size was too small to reveal significant results: $t = -2.735$, $P = 0.072$, $df = 3$, $n = 4$; Fig. 2b). Thus, rattling was clearly easier than stick use.

As to rattling, generalists and specialists were equally efficient, both in terms of success rate ($t = -0.130$, $P = 0.900$, $df = 7$; Fig. 2a) and latency to success ($t = -1.562$, $P = 0.169$, $df = 6$; Fig. 2b). For stick use the picture is more complex. With respect to latency to success, specialists and generalists again did not differ ($t = 0.916$, $P = 0.390$, $df = 7$; Fig. 2b). However, in terms of success

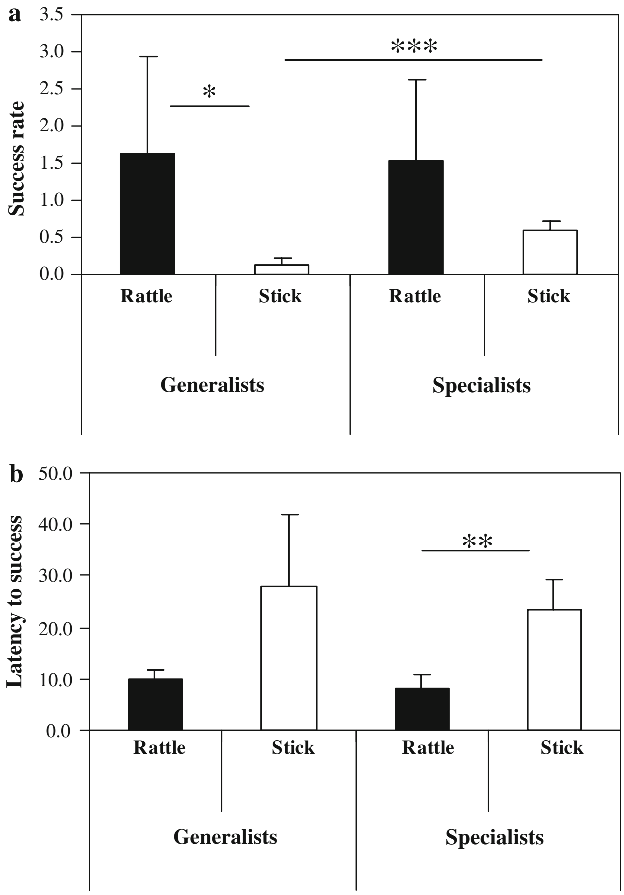

Fig. 2 Differences between generalists and specialists in the efficiency of rattling and stick use measured as mean success rate (**a**), or mean latency to success (**b**). * mark significant differences, for details see text

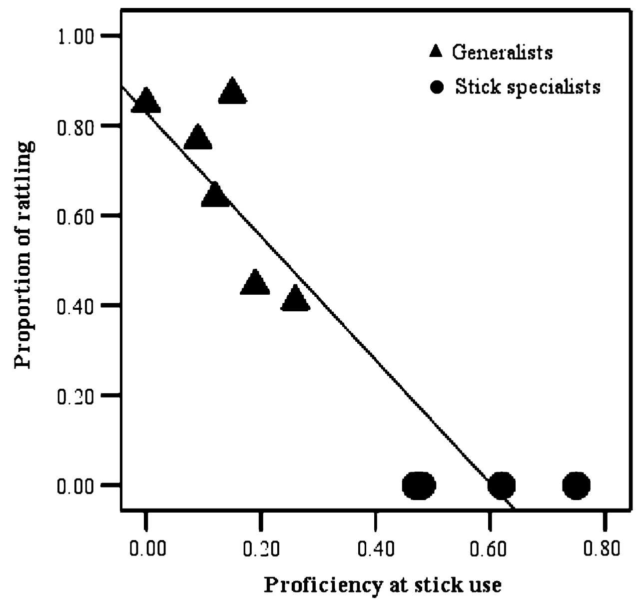

Fig. 3 Correlation of individual proficiency (mean success rate) at stick use and the inclination to adopt rattling (mean proportion of rattling) in the rattle phase. (n = 10, excluding rattle specialists)

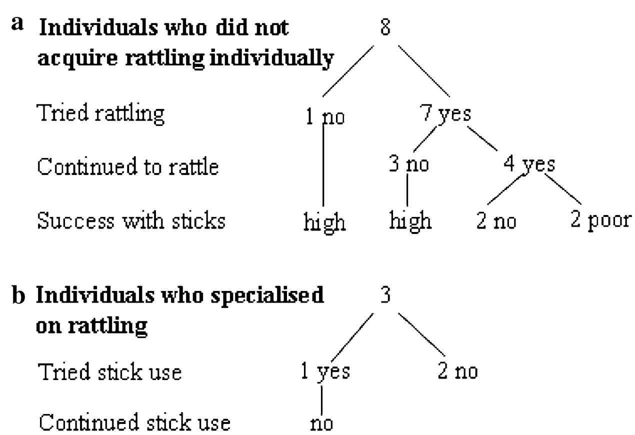

Fig. 4 Individuals abide by a technique in which they are highly proficient and refrain from adopting the alternative. *High* refers to highly successful stick users, i.e. specialists, whereas *poor* refers to poor stick users, i.e. generalists

rate, specialised stick users were over four times more successful than generalists ($t = 6.430$, $P < 0.001$, $df = 8$; Fig. 2a). These observed differences in success rates between generalists and specialists in stick use but not in rattling indicate that it was more difficult for chimpanzees to become a proficient stick user than a proficient rattler.

Although rattling was easier, as assessed by efficiency, not all individuals adopted it, and most kept using sticks as well, either as specialists or generalists. Proficiency, the individual measure of yield, however, did affect adoption decisions. The more success a chimpanzee had when using a stick, the less likely she/he was to perform rattling (Spearman's rho = − 0.894, $P < 0.001$, $n = 10$), and the most successful stick users never performed rattling at all (Fig. 3). Indeed, the tendency to abide by a technique in which one is already proficient was highly related to individual proficiency in that technique (Fig. 4). Only seven of the eight individuals who did not individually acquire rattling did acquire it after peering, whereas one female never tested the rattling technique. Of these seven subjects only four continued to use rattling, whereas three refrained from further practicing after having tried it once. All four individuals who did not perform rattling on a regular basis were successful stick users from test 1 on, whereas of the four chimpanzees who did continue to rattle two were never observed to succeed with the stick technique, the third one was the juvenile who was unsuccessful at rattling but continued to employ both techniques nonetheless, and the fourth became a generalist (Fig. 4a). The three adult males, after succeeding with rattling, never practiced stick use. Two of them did not try the stick technique even once (Fig. 4b).

The chimpanzees' responses to fixing the food board for the last 3–7 tests (non-rattle phase) support this interpretation. Individuals who had rattled much in the rattling phase,

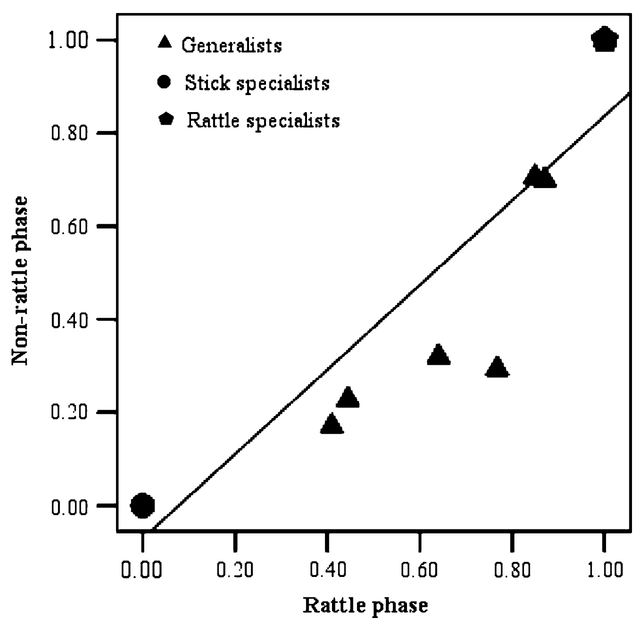

Fig. 5 Extinction resistance of rattling once rattling was made impossible (proportion of rattling in the non-rattle phase) correlated with the proportion of rattling actions when both techniques were possible (rattle phase). $n = 13$: a single point at 0 represents 4 stick specialists, the single point at 1 represents 3 rattle specialists, all other points represent one individual only

continued to rattle a lot in the non-rattle phase (Spearman's rho = 0.989, $P < 0.001$, $n = 13$; Fig. 5). However, the extent to which rattling continued after the food board was fixed was not predicted by the success at rattling itself (Spearman's rho = − 0.068, $P = 0.862$, $n = 9$), but rather by the success at stick use (Spearman's rho = − 0.919, $P < 0.001$, $n = 10$). Hence, rather than one's proficiency at the technique itself (rattling), it was being proficient in the alternative technique (stick use) that most affected the decision to give up an unsuccessful technique. In other words, the chimpanzees abided by a technique in which they had already become proficient.

Discussion

Our results demonstrate that in two groups of captive chimpanzees innovation spontaneously occurred and spread within the groups. Further, we present data that reveal the adoption rules informing chimpanzees' choices between known techniques when solving technical problems in a social setting.

Innovation and spread

Due to the small sample size, we can only provide qualitative statements on innovation and spread. First, we found that adult chimpanzees are quite capable of inventing novel solutions to problems. All our subjects were familiar with employing sticks to obtain otherwise inaccessible food. Yet, five adult chimpanzees independently invented a more efficient technique, whereas the immatures began using the novel technique only after having observed an adult performing it. These findings are consistent with Reader and Laland's review (2001), but in contrast with the common assumption of juveniles being more innovative (Gajdon and Kummer unpublished data; Kummer and Goodall 1985). Second, our data indicate that males and females were equally likely to come up with a technical innovation, in contrast to the findings of Reader and Laland (2001).

Within minutes, an innovator's performance of the novel technique was followed by peering on the part of non-innovators. In all but one case, peerers subsequently tested the technique they observed. Our third result, therefore, is that the exploration of an alternative solution was facilitated by a vivid interest in what others do.

Efficiency, proficiency, and conservatism

All individuals were familiar with using sticks before the experiment. Yet, using a stick seemed more difficult and, because rattling yielded food faster and more food overall, stick use demanded higher frustration tolerance than the new technique, rattling. Perhaps because of this, generalists using sticks were less successful than stick specialists, whereas when rattling they were just as successful as rattle specialists. The long latency to success made stick use particularly vulnerable to social influences and distractions. We regularly observed stick users being nervous about the presence of a dominant nearby or about excitement in the group and then performing poorly. This did not occur during rattling. Statistical testing of dominance effects was precluded by the absence of a clear-cut dominance hierarchy among females and small sample sizes. However, stick use specialists tended not to be high-ranking, and we almost never observed dominants displacing subordinates at the board. Nonetheless, stick users seemed sometimes to be excited and distracted by the proximity of a dominant. Thus, the higher success rate of a specialised stick user compared to a generalist was probably due to a combination of greater dexterity and patience to obtain the food. The popularity of rattling with the adult males may be linked to their lack of patience in using sticks, as well as their propensity toward brusque and energetic action. A similar sex difference among nut cracking chimpanzees at Taï, where females were found to be far more successful than males in the more demanding nut cracking techniques, was ascribed to males being more easily affected by social excitement and less concentrated and more impatient during tool use (Boesch and Boesch 1981, 1984; Boesch-Achermann and Boesch 1993). Accordingly, our females' reluctance to give up stick use may be a result of a high general motivation of chimpanzee females to use tools in foraging (see also Boesch and Boesch 1990; McGrew 1979).

There is no doubt that our subjects could assess the difference in yield of the two techniques as various field and laboratory studies have confirmed the chimpanzees' capacity for numerical assessment (e.g. Beran 2001; Boysen and Berntson 1995; Boysen et al. 1996; Tomonaga 2008; Wilson et al. 2002). Thus, if adoption decisions were based on overall efficiency levels of a technique, we should have found that over time all chimpanzees converged on rattling. However, this was not the case: in group D there were four generalists, two stick specialists and two rattle specialists, and in group C one rattle specialist, two stick specialists and two generalists. Instead, the chimpanzees' choice of technique was predicted by their individual proficiency. The more proficient a subject was at stick use, the less likely she/he was to adopt rattling. Subjects who were successful at a technique remained faithful to it, whereas only those who had not mastered it were willing to switch. One stick user did not try rattling even once, although she extensively peered. Of the 12 individuals who did experiment with rattling, 3 ceased using it without further practice and continued instead to use the stick technique at which they were already proficient. The six individuals who learnt to successfully use either technique kept using both, without switching to the one with the higher and quicker yields. Most strikingly, the three rattle specialists, i.e. the adult males, never even attempted to use sticks to obtain the food after rattling had been made ineffective, but simply continued to try rattling the food board. Likewise, generalists, who were less proficient at stick use, tried to rattle in the extinction phase more often than did the highly proficient stick users.

The chimpanzees participating in our study comprise only one population, and may not be representative of chimpanzees in general. Although they do not differ in their behaviour from many other captive chimpanzees (K. Pieta and C. Hrubesch, unpublished data), it is possible that chimpanzees who were mother-reared, normally socialised and free respond differently and are less stuck to known tool use techniques. Nonetheless, some findings of field studies might be outcomes of individual conservatism among great apes. Free chimpanzees (Kummer and Goodall 1985) and orangutans (Jaeggi et al., submitted) are reluctant to explore unknown potential foods. Furthermore, adult female chimpanzees at Bossou seem to exhibit conservatism in their harvesting for driver ants with tools. It might be that they are more proficient in one technique and therefore reluctant to adopt the alternative (Humle et al., submitted).

Moreover, Marshall-Pescini and Whiten (2008) studied the propensity of immature peer-reared chimpanzee orphans to adopt an alternative higher-yielding technique, which was an extension of the first technique. Their subjects turned out to be reluctant to use this technique, even though additional experiments showed it was within their capacity. The authors discussed the possibility that young chimpanzees would only show a willingness to adopt alternatives when they are dissatisfied by their initial technique (copy-if-dissatisfied: cf. Galef et al. 2008; Laland 2004). This is in line with our results that highly successful stick users did not adopt the higher-yielding rattling technique, whereas unsuccessful or less successful individuals did adopt it. However, because rattlers did not switch to the alternative technique even when rattling had been made impossible, a simple 'copy-if-dissatisfied'-strategy does not sufficiently explain the chimpanzees' conservatism in the recent investigation.

Conservatism may also explain individual specialisation. A recent field study of tool use in New Caledonian Crows (Hunt and Gray 2007) produced evidence for within-population individual specialisation in tool use in nonhuman animals. In fact, 8 of 12 crows were specialists in 1 of 2 alternative techniques. This pattern may be based on the same process: an individual specialises on the technique in which it fortuitously reaches proficiency first, with a minority reaching proficiency in multiple techniques, probably based on the success of initial attempts. The present study shows that also in great apes several tool use alternatives can coexist in one population.

Conservatism or conformity?

Cultural uniformity and stability may have at least two causes: the conservatism described here, and conformity imposed by society. Whiten and colleagues interpreted within-group uniformity despite the availability of an alternative technique as evidence of conformity (Bonnie et al. 2007; Horner et al. 2006; Whiten et al. 2005; 2007). However, their findings could also indicate a reluctance to explore alternatives after having successfully mastered the first technique (i.e. conservatism), as implied by this study. Moreover, in all four studies exceptions from the group norm exist that can be explained by individual conservatism. Thus, we need experiments specifically designed to differentiate between conformity and conservatism.

The same two processes are also found in humans. As Boyd and Richerson (1985) have shown, conformist transmission can maintain similarities within and differences between cultural groups. However, humans also have an inherent resistance to changing their opinion (Ehrlich and Levin 2005). Indeed, a model by Ghirlanda et al. (2006) suggests that when adoption rules are evolvable, populations become conservative, as individuals become reluctant to copy others but promote being copied by others. It will therefore be interesting in future work to disentangle the effects of conservatism and conformity on spatial and temporal variation in cultural systems.

We conclude that our results point to conservatism as an important adoption criterion in chimpanzees: a reluctance to give up a well-grasped technique, even if a more efficient one is available and the individual knows it is available, and even after the mastered technique is made ineffective. It appears that previous mastery of one technique inhibits the willingness to explore and thus adopt another technique. This mechanism may even account for cases of apparent conformity.

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References

Beran MJ (2001) Summation and numerousness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). J Comp Psychol 115:181–191

Boesch C, Boesch H (1981) Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. J Hum Evol 10:585–593

Boesch C, Boesch H (1984) Possible causes of sex-differences in the use of natural hammers by wild chimpanzees. J Hum Evol 13:415–440

Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. Folia Primatol (Basel) 54:86–99

Boesch-Achermann H, Boesch C (1993) Tool use in wild chimpanzees: new light from dark forests. Curr Dir Psychol Sci 2(1):18–21

Bonnie KE, Horner V, Whiten A, de Waal FBM (2007) Spread of arbitrary conventions among chimpanzees: a controlled experiment. Proc R Soc B 274:367–372. doi:10.1098/rspb.2006.3733

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. University of Chicago Press, Chicago

Boysen ST, Berntson GG (1995) Responses to quantity—perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). J Exp Psychol Anim Behav Process 21:82–86

Boysen ST, Bernston GG, Hannan MB, Cacioppo JT (1996) Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). J Exp Psychol Anim Behav Process 22:76–86

Byrne RW (2002) Imitation of novel complex action: what does the evidence from animals mean? Adv Study Behav 31:77–105

Ehrlich PR, Levin SA (2005) The evolution of norms. PLoS Biol 3: e194 DOI 10.1371/journal.pbio.0030194

Galef BG Jr, Kristina ED, Whiskin EE (2008) Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. Anim Behav 75:631–637

Ghirlanda S, Enquist M, Nakamaru M (2006) Cultural evolution develops its own rules—the rise of conservatism and persuasion. Curr Anthropol 47:1027–1034

Horner V, Whiten A, Flynn E, de Waal FBM (2006) Faithful copying of foraging techniques along cultural transmission chains by chimpanzees and children. Proc Natl Acad Sci USA 103:13878–13883. doi:10.1073/pnas.0606015103

Hunt GR, Gray RD (2007) Parallel tool industries in New Caledonian crows. Biol Lett 3(2):173–175. doi:10.1098/rsbl.2006.0603

Kummer H, Goodall J (1985) Conditions of innovative behaviour in primates. Phil Trans R Soc Lond B 308:203–214

Laland KN (2004) Social learning strategies. Learn Behav 32(1):4–14

Marshall-Pescini S, Whiten A (2008) Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. Anim Cogn 11:449–456. doi:10.1007/s10071-007-0135-y

McGrew WC (1979) Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg DA, McCown ER (eds) Perspectives on human evolution, vol. 5: the great apes. Benjamin/Cummings Publishing Co, Menlo Park, pp 441–463

Reader SM, Laland KN (2001) Primate innovation: sex, age and social rank differences. Intern J Primatol 22:787–805. doi:10.1023/A:1012069500899

Tomonaga M (2008) Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): evidence for approximate numerical representations. Anim Cogn 11:443–457. doi:10.1007/s10071-007-0089-0

van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M (2003) Orangutan cultures and the evolution of material culture. Science 299:102–105. doi:10.1126/science.1078004

Whiten A (1998) Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). J Comp Psychol 112:270–281

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. Nature 399:682–685. doi:10.1038/21415

Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in chimpanzees. Nature 437:737–740. doi:10.1038/nature04047

Whiten A, Horner V, Litchfield CA, Marshall-Pescini S (2004) How do apes ape? Learn Behav 32:36–52

Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FBM (2007) Transmission of multiple traditions within and between chimpanzee groups. Curr Biol 17(2):1038–1043. doi:10.1016/j.cub.2007.05.031

Wilson ML, Britton NF, Franks NR (2002) Chimpanzees and the mathematics of battle. Proc Biol Sci 269:1107–1112