Cumulative build-up of techniques in captive orangutans is contingent on novel exigencies

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Acknowledgments

We thank Denise Nierentz and Robert Zingg at Zurich Zoo for making this study possible. The A. H. Schultz Foundation offered financial support and Beno Schoch built the foraging box. We also thank two anonymous reviewers for their constructive comments on previous drafts of this manuscript and Jo Setchell for her editorial work.

Abstract

Cumulative cultural evolution refers to cultural traditions that have cumulatively been modified over time by different individuals in the direction of greater complexity. Experimental evidence for cumulative social learning in great apes is ambiguous. We expand a previous study that showed that orangutans were able to modify a preferred technique when this became necessary, thus demonstrating high behavioral flexibility in problem solving (Lehner et al. 2011). Our main present objective was to investigate in orangutans whether ratcheting of techniques requires novel exigencies or whether they can also arise spontaneously under constant conditions; and second, if not, whether orangutans can learn ratcheted techniques through socially mediated learning if they are demonstrated to them. We presented a foraging box to nine captive Sumatran orangutans. The reward in the box could be accessed in roughly two different ways, one of which cumulatively built upon the other one and was more efficient and productive. We found that novel exigencies were indeed required for the emergence of the cumulatively built-up technique. These results show that orangutans could learn a technique by social mediation they previously failed to learn on their own.

Keywords: Cumulative build-up, cumulative culture, ratcheting, orangutan

Introduction

Striking variation in behavior in chimpanzees and orangutans at different study sites has been interpreted as evidence for culture in our closest relatives (Boesch 1996; McGrew 1992; van Schaik et al. 2003; Whiten et al. 1999). Initially, culture was considered human by definition (reviewed in McGrew 1998), whereas animals were accorded traditions; a tradition representing a behavioral practice that is shared by two or more individuals in a social unit, which persists over time and is acquired by new individuals in part through socially aided learning (Fragaszy and Perry 2003). Whiten and van Schaik (2007) defined culture as the possession of multiple traditions, spanning different domains of behavior. The number of such traditions identified in chimpanzees and orangutans (at least 39 and 24, respectively) far exceeds the cultural repertoire of other animals (van Schaik et al. 2003; van Schaik et al. 2006; Whiten et al. 1999; Whiten et al. 2001), which suggests that the basic features of culture are shared by most or all great apes (Whiten et al. 2009b). At the same time, no one doubts that human culture is characterized by many more traditions than chimpanzee and orangutan culture. However, this difference is not merely quantitative, but also qualitative, as humans use behavioral strategies and technologies that are much more complex. This vast discrepancy in cultural accomplishments between humans and great apes could be due to cumulative culture or ratcheting, i.e. the accumulation of modifications made by different individuals over time in the direction of greater complexity (Tomasello et al. 1993). By greater complexity Boesch and Tomasello (1998) meant that a wider range of functions is encompassed. More recently Dean et al. (2013) and Pradhan et al. (2012) defined behavioral complexity as the number of steps required to produce the behavior. Another way to recognize cumulative culture is by showing a low probability that naïve individuals can invent the ratcheted technique on their own (Boyd and Richerson 1996).

Arguably, cumulative culture is uniquely human (Henrich and McElreath 2003; Tomasello et al. 1993; Tomasello 1999; Tomasello 2001) and its emergence may have been facilitated by our ultrasociality (cooperative breeding and prosociality) (Burkart et al. 2009a) and our excellence, efficiency and fidelity in skill transmission (teaching, imitation) (Burkart et al. 2009a; Dean et al. 2013; Lewis & Laland 2012; Pradhan et al. 2012; Tomasello 1994). The first traceable archeological indication of cumulative build-up of technology is seen in the replacement of the Oldowan by the Acheulean stone industry (Mithen 1999). Nevertheless rudimentary forms of cumulative technology do exist in apes (as described in the following 3 paragraphs - and have also been suggested for New Caledonian crows, Hunt and Gray 2003), and the main question is to what extent great apes are spontaneously capable of such cumulative build-up, or can be coaxed into inventing or adopting ratcheted techniques. Rudimentary forms of cumulative technology have also been suggested in non-primate species: Hunt and Gray (2003) suggested that the diversification of *Pandanus* tool designs they found in New Caledonian crows are the first indication that a non-human species evolved techniques that built up on previous versions and were passed on through social learning.

Boesch (2003) and Whiten et al. (2003) suggested that some examples of chimpanzee cultures indicate that chimpanzees do have some power for cumulative build-up of techniques, at least in qualitative, modest terms. For instance, several chimpanzee populations crack nuts by hitting them directly with the hand against tree trunks or use stone hammers to break harder and smaller nuts on stone anvils, but only at Bossou (Guinea) have some individuals been observed to occasionally use an additional stone to prop up the stone anvil, thus leveling it or increasing its stability (Matsuzawa and Yamakoshi 1996; Sugiyama 1997). However, because the technique did not reach customary status, one could doubt its interpretation as cumulative culture.

Recent reports of evidence for cumulative material culture in chimpanzees are more convincing. Chimpanzees in the Congo Basin have been found to use two or more different tools in one functional sequence in termite extraction or during honey gathering. In the latter case, they use a large, club-like stick to pound open a beehive and then extract honey by dipping into the hive using a smaller stick (Sanz and Morgan 2009). While using a probe to dip into a beehive to extract honey is a widespread tactic used by chimpanzees in honey-gathering, pounding of beehives with a large club seems exclusive to populations of the Congo Basin (Sanz and Morgan 2009). The "pound-and-dip" technique includes behavioral elements of the dipping technique and probably makes additional beehives accessible that cannot be opened when only the dipping technique is available. Thus, it is reasonable to consider the "pound-and-dip" technique as cumulatively building up on the dipping technique. Nonetheless, it is remarkable (1) how rare such built-up techniques are in wild chimpanzees and (2) how limited the steps are, never building upon this two-step process by adding additional steps in all the other tool sets reported by Sanz and Morgan (2009) as well. Explaining this rarity, and this limitation to a two step-process, remain a priority if we are to explain the ape-human contrast in culture.

The question of why ratcheted techniques are so rare in wild apes can be addressed experimentally with captive great apes. In a first experiment on cumulative culture in great apes, Marshall-Pescini and Whiten (2008) investigated chimpanzees' capacity for cumulative social learning by designing an apparatus whose food content could be extracted in two different ways. Both solutions were demonstrated to the subjects by a familiar human. The second technique incorporated the core actions of the first technique and was both more complex and more productive. Subjects that had previously learned the first technique did not learn the second more complex one, thus proving incapable of acquiring a cumulatively built-up technique through socially mediated learning. The authors concluded their chimpanzees had become “stuck” on a technique they had learned initially, which inhibited cumulative social learning and possibly constrains the species’ capacity for cumulative culture (Marshall-Pescini and Whiten 2008; see also Hopper et al. 2011; Hrubesch et al. 2009; Pesendorfer et al. 2009). More recently, however, positive findings regarding cumulative build-up of techniques have been reported in great apes (Lehner et al. 2011; Manrique et al. 2013). Lehner et al. (2011) found that captive orangutans in a different experiment demonstrated a high flexibility to abandon a preferred technique that had been made non-functional for solving a syrup-tube task and to switch successfully to different, functional techniques. More importantly, the study subjects invented two techniques that built up on previous ones and were thus cumulative; these were also acquired by other group members, by socially mediated learning (as suggested by the authors), indicating that modest cumulative culture is possible in captive orangutans. A critical question arising from Lehner et al.’s (2011) study is whether creating these novel exigencies by inhibiting preferred techniques was crucial for subjects to modify and improve on present solutions, and thus produce ratcheted techniques, or (whether) eventually ratcheting would also have taken place under unchanging conditions. Novel exigencies are part of Tomasello et al.’s (1993) description of cumulative culture, which suggests that without such novel exigencies there would be no cumulative build-up of techniques; however this description needs experimental validation, especially as Koops et al. (2014) reported that primate tool innovations arose from opportunity rather than necessity. Further tests of orangutans’ and great apes’ ability for cumulative build-up of techniques under *unchanging* conditions are needed to shed light on the potential for cumulative culture in these species.

The main objective of this study with captive orangutans was therefore to investigate whether novel exigencies further prove to be indispensable for cumulative build-up of techniques, or whether cumulative build-up is also possible under constant conditions. A secondary objective was to investigate whether orangutans could socially learn a technique they previously failed to invent by themselves. According to Tennie et al. (2009), chimpanzees will only socially learn what they (i.e. some individuals) could learn on their own.

We performed an experiment using an apparatus functionally similar to the one used by Marshall-Pescini and Whiten (2008), allowing us to compare results of orangutans and chimpanzees to a better extent than before. We first examined if under constant conditions subjects would spontaneously find both the simple solution first, and then also the second more complex and more productive solution that cumulatively builds up on the simple technique. Second, we investigated whether they learnt it from a familiar human demonstrator (by socially mediated learning). Third, a final phase of the experiment followed, where we created novel exigencies by making the first technique nonproductive, while demonstrations of the built-up technique were continued. Thus, we examined whether subjects that previously had not invented the cumulatively built-up technique adopted this technique demonstrated to them, if conditions of the task were changed and novel exigencies created. We used the same criteria for cumulatively built-up techniques as in a previous study (Lehner et al. 2011)

Methods

Animals and living conditions

We conducted the study on a population of Sumatran orangutans held at the Zurich Zoo (Switzerland). The study group consisted of 9 individuals: 6 females (ages: Timor 33; Selatan 26; Oceh 21; Tuah 16; Xirah 12; Cahaya 7) and 3 males (ages: Djarius 14; Dahulu 5; Hadia 1). Hadia was excluded from examination due to young age, hence sample size was N

= 8. Subjects were socially housed in one main indoor cage (480 m^3) and an outdoor cage (188 m^3). They had the possibility to retreat in boxes formerly used as sleeping boxes, out of sight of the visitors. The cages were equipped with tree trunks and ropes, which allowed the animals to show their natural locomotion, and a water source; environmental enrichment was provided almost daily. Subjects were not food or water deprived at any time. We performed all experiments in the main indoor cage with the whole group present. Their behavioral repertoire had been established previously (Lehner et. al 2010).

Apparatus

We presented subjects with a foraging box (l = 25cm, w = 15cm, h = 15cm) originally containing syrup and peanuts. A transparent window (9 x 9 cm) in the front allowed animals to look inside the wooden box. In the front of the box there was a tunnel with a recessed bolt inside that locked the lid at the top of the box. This lid had a hole (d = 1cm) that was covered by a transparent trap door; the hole led to the box's content. The size of the hole did not allow the subjects to insert a finger, as we did not want to give them the possibility to lever open the lid by any other means than inserting a stick in the hole, because this is crucial for the "Poking and Levering" technique to qualify as a ratcheted technique (see below). This is an important and intentional difference to the box used by Marshall-Pescini and Whiten (2008) where the hole happened to be wide enough for chimpanzees to insert a finger and to lever the lid open with the finger. In its home position the box's lid was locked by the recessed bolt and the trap door covered the lid's hole (Figure 1a).

We constructed the foraging task box so it could be solved in two different ways, by either "Dipping" or "Poking and Levering" (Figure 2).

(1) "Dipping" technique: Sliding open the trap door by pushing it back with a finger, thereby exposing the hole of the lid, and whilst holding on, use the other hand to dip a stick

into the revealed hole down into the syrup (Figure 1b), pull the stick out and lick the syrup from the stick. In addition to this dipping technique we distinguished two slight variations of dipping techniques where the trap door was let go before pulling the stick out or where the same stick was used to both open the trap door and dip in the revealed hole (Table 1).

(2) "Poking and Levering" technique: Using a stick to poke the recessed bolt inwards, thereby unlocking the lid at the top (Figure 1c). Slide open the trap door with a finger and use the other hand to insert a stick into the hole (as in the "Dipping" technique), let the trap door go, lever open the lid, making all the contents available (Figure 1d). Within the latter technique a variation of the first technique is contained, and while the "Dipping" technique makes only little amounts of syrup accessible (and no peanuts), the second one allows rapid access to both syrup and peanuts, making the "Poking and Levering" technique a solution cumulatively building up on the "Dipping" technique. Holding the trap door open whilst dipping a stick in and out of the hole - as in the "Dipping" technique - is in the "Poking and Levering" technique modified to letting the trap door go after having put the stick in the hole, so the stick is blocked in the hole by the trap door and the lid can be levered open with the stick. Thus, broadly summarized, the components of "Poking and Levering" are "Poking" and a modification of "Dipping" (see also Figure 2). Therefore subjects are expected to first show both "Poking" and "Dipping" before mastering "Poking and Levering".

The "Poking and Levering" technique stringently must include a variation of the "Dipping" technique, in order to qualify as a ratcheted technique. Therefore we prohibited subjects to lever the lid open in any other way than putting a stick in the lid's hole, e.g. by inserting a finger into the hole instead of a stick, or by inserting fingernails along the lid; such forms of "Poking and Levering" would not qualify as cumulatively building up on "Dipping". Table 1 gives an overview of the main behaviors that were recorded along with their descriptions.

Experimental procedure

We carried out the experiment in the group's main indoor enclosure, in a behind the scenes area of the zookeepers, nonetheless visible for zoo visitors, where subjects could put their forearms through the cage mesh. We fixed the apparatus to the outside of the enclosure, allowing subjects to watch through the box's transparent window and see the content. The content originally consisted of syrup and peanuts (or occasionally walnuts), all highly appreciated food items. We provided several sticks that were adequate to perform the two techniques.

The experiment consisted of three phases (Table 2): (1) an innovation phase; (2) a demonstration phase; and (3) a novel-exigencies-plus-demonstration phase. Subjects were tested as a group. Experimental sessions usually lasted 90 minutes each and were performed on different days. There were a maximum of two experimental sessions per week.

(1) Experimental procedure phase 1: In the innovation phase, we ran seven experimental sessions to investigate how subjects would handle the foraging box that was attached to the outside of the enclosure.

(2) Experimental procedure phase 2: In the demonstration phase, we ran seven sessions. First we ran one session in which one box was presented in its home position as before, but a second box was also present, which was empty but had the lid opened; this was to ensure that subjects knew the lid could be opened. If subjects had learned the "Poking and Levering" technique at this stage this would have implied a form of emulation learning (i.e. learning about the environment), e.g. end-state emulation (learning about the result of the model's action and copying this product, but independently re-inventing the way to get there) or affordance learning (learning about the properties of objects) (cf. Wood 1989; Tomasello 1996; Tomasello 1998; Tennie et al., 2009; Whiten et al. 2009a). Then in the next six

sessions the complete process of the “Poking and Levering” technique was demonstrated to the subjects by a familiar human (S.L.). We carried out the demonstrations at a distance of about 1 m, in front of the whole group. For the first 20 minutes of a session, we carried out demonstrations repeatedly. After that, we put the box used by the demonstrator in its home position and fixed it to the wire mesh for subjects to interact with for the following 70-80 minutes, whilst the demonstrator used a duplicate box to demonstrate the technique “Poking and Levering” whenever a subject was watching the demonstrator or this box.

(3) Experimental procedure phase 3: In the novel-exigencies-plus-demonstration phase, we ran 10 sessions in which we paired demonstrations with changed conditions. Subjects were exposed to the foraging box, which now no longer contained syrup but only peanuts. This made the “Dipping” technique (that had so far made the syrup accessible) ineffective, leaving subjects only the “Poking and Levering” technique to access the reward. We carried out the demonstrations the same way as described for the demonstration phase. We expected that with the novel conditions subjects would be more attentive to the demonstrations of the “Poking and Levering” technique than in the demonstration phase, and that subjects would show greater effort to lever open the lid.

Data coding and analyses

We video-recorded all experiments. We undertook continuous behavior sampling (Table 1; Altmann 1974) from the video recordings. Table 1 provides descriptions of all behaviors we recorded. Amongst others we recorded for each individual the number of demonstrations of “Poke and Lever” it observed completely. More precisely, our criteria for “observing demonstration” requested that for the duration of a complete performance of the “Poke and Lever” technique a subjects eyes were directed at the human demonstrator’s (or later a successful subject’s) performance from a close distance (< 2m). The recorded data of “observing demonstrations” provides a measure for each subject’s attentiveness to the demonstrations of the “Poke and Lever” technique. The first author did all the coding of the video footage, the second author blind coded a subset, resulting in no differences. We calculated statistics in SPSS 14.0. We used Page’s L Trend Test (Page 1963) to test for successive increase in successful application of the “Dipping” technique over the seven sessions of the innovation phase.

Ethical note

All procedures of the study were performed in accordance with Swiss laws and approved by the Zurich State Veterinary Office (Nr. 2008202).

Results

In the seven sessions of the innovation phase (in total lasting 10 hours 14 minutes), seven out of eight orangutans discovered at least one of the three forms of the “Dipping” techniques that could be distinguished (complete information about latencies after which subjects successfully performed a particular behavior for the first time can be found in Appendix 1). During the course of the innovation phase subjects increasingly performed the “Dipping” techniques successfully to gain access to the syrup (Figure 3). There was a highly significant trend for subjects to gradually increase their successful use of any of the three forms of “Dipping” proportionally to their total manipulation time (Page’s L Trend Test: $L = 975.5$; $k = 7$; $N = 8$; $P < 0.01$). Two of the subjects that had used “Dipping” also discovered “Poking”, but no individual came up with the technique “Poking and Levering” in this phase.

In the demonstration phase, the technique “Poking and Levering” that cumulatively builds up on the “Dipping” techniques was still not performed by any subject. Rather, their interest in the task declined, as indicated by a lower participation with the task than in the innovation phase, measured as individuals' active manipulation with the apparatus relative to the time the apparatus was fixed to the cage in the corresponding phase (Wilcoxon signed-ranks test: Z = -1.960, N = 8, P = 0.05; Figure 4). The six individuals that had acquired "Dipping" techniques still applied them in the demonstration phase to extract some syrup from the apparatus.

In the subsequent novel-exigencies-and-demonstration phase, one subject (Selatan) eventually succeeded in performing the technique "Poking and Levering", achieving a total of six correct performances over four consecutive sessions. The first time was in the fifth session (19^{th} session overall), or after a latency of more than 27 hours. As expected, this individual had previously acquired both "Poking" and "Dipping". In the remaining sessions, no other subject acquired the "Poking and Levering" technique. Selatan did not perform the "Poking and Levering" technique during the last two sessions, despite some failed attempts.

We then investigated why most animals failed to acquire the "Poking and Levering" technique. Subjects mainly seemed to fail because they largely neglected to poke. Broadly, the components of "Poking and Levering" are "Poking" and a modification of "Dipping", thus subjects were expected to first show both "Poking" and "Dipping" before mastering "Poking and Levering". First, we therefore analyzed subjects' latencies until discovering "Poking" and "Dipping". Figure 5 shows that most subjects' latencies until the first correct performance of "Poking" were longer than for "Dipping". Five animals acquired both "Poking" and "Dipping", but of these only one succeeded to combine and modify them into the effective "Poking and Levering" technique, while four of these animals had discovered "Poking" much later than "Dipping". Two other subjects had acquired one of the "Dipping" techniques, but never acquired "Poking". Only one subject (Dahulu: male juvenile) acquired "Poking" but not "Dipping".

Second, we examined whether at some point “Poking” became common by analyzing its frequency in the three phases of the experiment. “Poking” was very rarely shown in the innovation and demonstration phases, but more often under the novel conditions of the last phase (Figure 6). We corrected the frequencies of “Poking” for the different time the apparatus was attached to the cage in the three phases (by calculating all frequencies relative to the time the foraging box was available in the demonstration phase). In the novel–exigencies-plus-demonstration phase subjects showed significantly more correct “Poking” than in both the demonstration phase (Wilcoxon signed-ranks test: Z = -2.207, N = 8, P = 0.027) and the innovation phase (Z = -2.207, N = 8, P = 0.027). Although “Poking” was most frequent in the novel-exigencies-plus-demonstration phase, its occurrence did not become common there either: except for the individual that acquired the ratcheted technique “Poking and Levering” no individual “poked” more than eight times in the 10 sessions of the novel exigencies phase (averages of correct “Poking” in phases 1-3, Selatan excluded: 0.4; 0; 2.1). Their use of social information (i.e. number of demonstrations observed) did not correlate with their frequency of successful “Poking” (Spearman’s Rho = 0.558, p = 0.151,).

These two analyses thus support the idea that most subjects failed to acquire the “Poking and Levering” technique because they largely neglected to poke. However, several other potential factors why most animals failed to acquire the “Poking and Levering” technique also had to be excluded, namely (1) subjects not paying attention to the human’s demonstration of the “Poking and Levering” technique, (2) subjects lacking motivation to lever open the lid (because they did not understand its need), and (3) limited access to the task.

First, by analyzing subjects’ attentiveness to the demonstrations of the “Poking and Levering” technique we could exclude the possibility that most subjects failed to acquire this technique because they did not watch the demonstrations. All subjects paid attention to the demonstrations of the “Poking and Levering” technique by the human demonstrator (Figure 7). A seven-year old female (Cahaya) was the most attentive individual, in total watching 92 demonstrations (thereof 2 by Selatan), followed by a 16-year old female (Tuah), who watched 39 demonstrations but both did not manage to reproduce the exact observed pattern. The individual (Selatan) that did acquire the “Poking and Levering” technique in session 19 had watched a total of 21 demonstrations before her first successful performance. Three of her correct performances of the “Poking and Levering” techniques were observed by other subjects.

Second, a simple lack of motivation (and of understanding the need to open the lid) could also be excluded as a possible explanation for most animals’ failure to show the “Poking and Levering” technique in the novel-exigencies-and-demonstration phase. Because with the novel conditions only the “Poking and Levering” technique was effective to gain a reward, we expected subjects to increase their efforts to somehow lever open the lid in the novel-exigencies-and-demonstration phase. Therefore we measured individuals’ time spent attempting to lever open the lid without succeeding (sum of Lever non-successful, Lever in vain, Lever in gaps; Table 1) and calculated its proportion of the time during which subjects could manipulate the foraging box in the corresponding phase to correct for different durations in the three phases of the experiment. Indeed, subjects’ effort to lever open the lid was greatest when the novel exigencies prevailed (Figure 8), and this effort to lever open the lid was significantly greater in the novel-exigencies-plus-demonstration phase than in the demonstration phase (Wilcoxon signed-ranks test: $Z = -2.197$, $N = 8$, $P = 0.028$). This indicates that subjects indeed recognized the need to open the lid due to the novel conditions in the novel-exigencies-and-demonstration phase and that they were motivated to do so. The conspecific demonstrator had only been observed to perform the "Poking and Levering" technique three times, indicating subjects were motivated to open the foraging box because of the environmental necessities, rather than because they had only now observed a conspecific demonstrator.

Third, limited access to the foraging box also needs to be excluded as a possible explanation for most animals' failure to show the "Poking and Levering" technique. Access to the foraging box was clearly not limited: although all subjects participated in the task in all phases of the experiment the apparatus remained unoccupied for most of the time. The only individual that acquired the "Poking and Levering" technique showed the most interaction with the task in the novel exigencies phase but by no means monopolized the apparatus (Figure 4).

Discussion

Our original aim here was to investigate whether captive orangutans (after having learned a simple technique) would under constant conditions be able to invent a more productive technique that added actions to this pre-existing technique, thus making it cumulatively built-up or ratcheted (innovation phase). We found that orangutans did not learn the cumulatively built-up technique by themselves under the constant conditions of the innovation phase. Seven subjects learned at least one of the three forms of "Dipping" techniques, and two of those also discovered "Poking“, but none combined and built up on these two techniques to invent the ratcheted technique "Poking and Levering".

We then examined whether orangutans, having previously failed to invent the built-up technique by themselves, could learn it after observing demonstrations by a human model: first still under constant conditions (demonstration phase), second under novel exigencies where the simpler technique was rendered obsolete (novel-exigencies-plus-demonstration phase). In the demonstration phase, the "Poking and Levering" technique was demonstrated to the subjects, but none acquired it. Rather, they continued using "Dipping" techniques.

Thus, orangutans did not learn the ratcheted technique “Poking and Levering” under constant conditions, neither individually in the “innovation phase“, nor socially mediated in the “demonstration phase”. Hence, under constant conditions subjects neither learned the cumulatively built-up technique by themselves, nor did they copy it from the human model.

With increased exposure to the task, and once novel exigencies were introduced, a single subject succeeded in learning the cumulatively built up technique. In the novel-exigencies-plus-demonstration phase we created novel exigencies by loading the foraging box with peanuts only rather than both syrup and peanuts, while demonstrations of the “Poking and Levering” technique were continued. By doing so, we made the “Dipping” techniques nonproductive. In order to extract any food reward from the foraging box, subjects now had to apply the “Poking and Levering” technique. Despite extensive demonstrations, all other subjects failed, although four of them had learned both one of the “Dipping” techniques and “Poking“. However, they did not combine the two components into the ratcheted technique.

These results have several implications. First and foremost, this study showed that cumulative build-up of techniques is possible in captive orangutans and not exclusive to humans, as also demonstrated by Lehner et al. (2011) and suggested by the observations on wild chimpanzees (Matsuzawa and Yamakoshi 1996; Sanz and Morgan 2009; Sugiyama 1997). Second, there was no cumulative build-up of techniques under constant conditions, i.e. when the “Dipping” techniques were still effective. This is in accordance with the experiment of Marshall-Pescini and Whiten (2008) using a similar foraging box: chimpanzees that learned the simple dipping technique did not learn the cumulatively built-up technique, although both techniques had been demonstrated to them. Third, only as novel exigencies prevailed (only) a single subject succeeded to learn the cumulatively built-up technique. This, although based on only one subject, corroborates the finding by Lehner et al. (2011), using the same subjects, that the creation of novel exigencies by inhibiting preferred techniques was likely crucial to induce subjects to modify and improve on present solutions to result in cumulative build-up of techniques. Manrique et al. (2013) have recently also shown that chimpanzees, gorillas and bonobos were able to overcome conservatism (*contra* Hrubesch et al. 2009) and abandon a previously established technique to extract food from a puzzle box when changes in the physical constraints of the task made the old technique ineffective. Interestingly, in that study orangutans were clearly outperformed by the other great ape species. Fourth, subjects still applying the unproductive “Dipping” technique in the final novel-exigencies-plus-demonstration phase obviously must have remained unsatisfied but did not copy the successful “Poking and Levering” technique, even when there was a successful conspecific model from whom the orangutans could have learned, which casts doubt on clear-cut strategies such as “copy others when unsatisfied with own currents strategy” (Laland 2004; Rendell et al. 2011; Yamamoto et al. 2013). In their review of limits to animal innovation, Brosnan & Hopper (2014) concluded that "primates will preferentially use their personal information unless there is some reason not do to so, such as when it is costly to collect or use it, or when it is unreliable or outdated" (p. 327). Perhaps social learning strategies (e.g. “copy if dissatisfied”) should be conceived as probabilistic likelihoods, just as innovations are (Lehner et al. 2010).

The study of Marshall-Pescini and Whiten (2008) was similar to ours in design, but also differed from ours in some ways. They tested the chimpanzees individually, whereas we tested the orangutans in a group setting. They presented the task without syrup from the beginning to three naïve subjects, making only the “Poking and Levering” technique effective from the start. Two of these subjects actually discovered both the dipping technique and a poking and levering technique by themselves, leading the authors to conclude that the poking and levering technique was not too difficult for chimpanzees. However, the box used by

Marshall-Pescini and Whiten (2008) allowed chimpanzees to lever the lid open with a finger, which was not possible in our case. As a consequence, the results of the two studies are not directly comparable, because the definition for the “Poking and Levering” technique was less restrictive in their study. We would argue that such a form of poking and levering that included inserting a finger instead of a stick into the lid’s hole to lever the lid open is not really a ratcheted technique. At best it might be justifiable to suggest that such poking and levering represents a technique cumulatively building up on “dipping”, albeit only to a slight degree, if at all. In order for the “Poking and Levering” technique to qualify as cumulatively building up on the “Dipping” technique, it stringently must include a variation of the “Dipping” technique; therefore we constructed our box in a way that prohibited levering the lid open in any other way than putting a stick in the lid’s hole. Thus, our “Poking and Levering” clearly was a ratcheted technique, whereas in the study with the chimpanzees behavioral patterns whose status as “ratcheted” are questionable were also ascribed to the “Poking and Levering” technique.

Our data also suggest that captive orangutans can learn something about the foraging box or the ratcheted technique by social mediation that they previously failed to learn on their own. Innovation seemed to be the main limiting factor for cumulative build-up of techniques in this task, but social learning was also a limiting factor as the only subject that succeeded in acquiring the “Poking and Levering” technique did so after having observed quite a large number of demonstrations by the human model, 21. Individuals were given an extensive amount of time to learn the “Poking and Levering” technique by themselves (our innovation phase lasted more than ten hours), but no orangutan invented the technique, suggesting that they lacked the ability to invent it on their own. The single individual (Selatan) that acquired the technique in the novel-exigencies-and-demonstration phase had watched a total of 21 demonstrations prior to the first successful performance and seemed most focused in the two sessions right before (watching 7 demonstrations). It seems plausible that as this information was apparently gained it was then also used (in the process) to learn this technique, arguably suggesting socially mediated learning. We cannot rule out the possibility that lack of attentiveness to the demonstrations explains why the other individuals failed to learn the "Poking and Levering" technique in the novel-exigencies-and-demonstration phase; attentiveness was assessed in terms of observing demonstrations but it proved impossible to distinguish general visual orientation from more focused attention (peering).

We now turn to the question why only one of our subjects succeeded in learning the ratcheted technique. "Poking" and a modification of "Dipping" are the components of "Poking and Levering", thus subjects having mastered both these components could be expected to learn the cumulatively built-up technique. There were five animals that learned both "Poking" and "Dipping" but all but one did not succeed to build from these two the "Poking and Levering" technique. In the comparable experiment of Marshall-Pescini and Whiten (2008) chimpanzees that learned a dipping technique (which was demonstrated as first solution to them) all failed to learn the "Poking and Levering" technique (which was subsequently demonstrated to them). Thus the authors concluded that their chimpanzees had become "stuck" on a technique they had learned initially. This explanation is less likely to fit our findings, because our subjects had previously demonstrated high behavioral flexibility by showing continued interest in acquiring new solutions to a task and by switching to other techniques and relinquishing established techniques when this was advantageous (Lehner et al. 2011). Hopper et al. (2014) question a blanket classification of chimpanzees as conservative, as in their own study providing insights into chimpanzees' ability for building upon previously gained knowledge, chimpanzees demonstrated behavioral flexibility by adding steps to an already learnt sequence when "forced" into adding a step to their repertoire, and given several other recent studies where chimpanzees demonstrated behavioral flexibility (e.g. Hopper et a. 2013; Manrique et al. 2013; Yamamoto et al. 2013) However, since the only successful subject (Selatan) used the “Dipping” technique only once and also did not interact with the task at high rates prior to the final phase, Selatan possibly was less fixed on the first technique to yield a reward (i.e. “Dipping”) than other subjects (supported by observations in a previous experiment with tubes where Selatan applied the inefficient dipping technique only 7 times before changing to more efficient techniques; Lehner et al. 2011) and could possibly more easily transition to the “Poking and Levering” technique, which might explain her success, in accordance with the conclusion of Marshall-Pescini and Whiten (2008). “Poking” was crucial for the acquirement of the ratcheted technique, and subjects failed to acquire the “Poking and Levering” technique mainly because they were largely reluctant to poke; although ”Poking” was shown more frequently in the novel-exigencies-plus-demonstration phase, it never became common.

We showed that all subjects paid attention to the demonstrations of the “Poking and Levering” technique, that subjects’ effort to lever open the lid was greatest in the last phase (when the novel exigencies were in place) and that access to the foraging box was not limiting. However, even though subjects paid attention to complete demonstrations of “Poking and Levering”, they possibly focused much more on the final, levering step. This may explain why they failed to copy the complete action pattern of the ratcheted technique in the correct sequence (imitation). At the same time subjects seemed not to understand how “Poking” contributed to levering open the lid of the box, as this locking mechanism was not visible and seemed arbitrary to them, which makes the task hard (or even impossible) to be learned by product copying or affordance learning (emulation) and must therefore be learned by imitation. Chimpanzees are capable of socially learning action sequences (Bonnie et al. 2007; Whiten 1998). The fact that “Poking” alone was never rewarded is probably the most parsimonious explanation why subjects rarely "poked" and failed to learn the "Poking and Levering" technique, except for one individual.

In line with previous work (Lehner et al. 2010; Lehner et al. 2011), the present results have shown that captive orangutans are not only more innovative than their wild conspecifics, but are capable of making ratcheted innovations (i.e. innovations that are solutions cumulatively building up on previous solutions). Novel exigencies inhibiting previous solutions to the task were found to be a factor stringently required for such cumulative build-up of techniques. This suggests that the lack of cumulative culture in wild orangutans is not due to a lack of behavioral flexibility when existing solutions to tasks become impossible, or an inability to cumulatively build up on previous solutions. Rather, this critical factor of novel exigencies suddenly inhibiting previous feeding techniques is almost certainly largely missing in the wild, while at the same time other factors are in place that are impeding object manipulation and also cause the low innovation tendency in wild orangutans. The latter we suggested to be explained by the alienation from the environment experienced by zoo animals provided them with more spare time and spare energy, allowing them to play with their gratification system, as a human does (Lehner et al. 2010).

In sum, this study supports earlier results (Lehner et al. 2011) showing that cumulative build-up of techniques is possible in captive orangutans and not limited to humans, at least if they have to deal with novel conditions. Second, under constant conditions subjects failed to acquire the ratcheted technique, which corroborates the suggestion that cumulative build-up of techniques requires novel exigencies, so that previous solutions to the task are inhibited. Third, our results indicate captive orangutans can learn (or at least learn much faster) by social mediation something they previously failed to learn on their own.

References

Altmann, J. (1974). Observational study of behaviour: sampling methods. Behaviour, 49**,** 227-267.

Boesch, C. (1996). The emergence of cultures among wild chimpanzees. In: W. G. Runciman, J. Maynard-Smith, & R. I. M. Dunbar (Eds.), Evolution of Social Behaviour Patterns in Monkeys and Man (pp. 251-268). London: British Academy.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? Evolutionary Anthropology, 12, 82-91

Boesch, C., & Tomasello, M. (1998). Chimpanzee and human cultures. Current Anthropology, 39, 591-614

Bonnie, K. E., Horner, V., Whiten, A, & de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. Proceedings of the Royal Society B, 274, 367-372

Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. In: W. G. Runciman, J. Maynard-Smith, R. I. M. Dunbar (Eds.), Evolution of Social Behaviour Patterns in Monkeys and Man (pp. 77-93). Oxford: Oxford University Press.

Brosnan, S. F., & Hopper, L. M. (2014). Psychological limits on animal innovation. Animal Behaviour, 92, 325-332

Burkart, J. M., Hrdy, S. B., & van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. Evolutionary Anthropology 18, 175-186

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2013). Human cumulative culture: a comparative perspective. Biological Reviews, 89, 284-301

Fragaszy, D. M. & Perry, S. 2003. The Biology of Traditions: Models and Evidence. Cambridge, UK: Cambridge University Press.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. Evolutionary Anthropology, 12, 123-135

Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. Animal Behaviour, 81, 1195–1202

Hopper LM, Lambeth SP, Schapiro SJ, Brosnan SF (2013) When given the opportunity, chimpanzees maximize personal gain rather than ''level the playing field''. PeerJ 1:e165

Hrubesch, C., Preuschoft, S., & van Schaik, C. P. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). Animal Cognition, 12, 209-216

Hunt, G. R. & Gray, R. D. 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. Proceedings of the Royal Society B, 270**,** 867-874

Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). The ecology of primate material culture. Biology Letters, 10, 20140508

Laland, K. N. (2004). Social learning strategies. Learning and Behavior, 32, 4-14

Lehner, S. R., Burkart, J. M., & van Schaik, C. P. (2010). An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans. Primates, 51,101-118

Lehner, S. R., Burkart, J. M., & van Schaik, C. P. (2011). Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques? Journal of Comparative Psychology, 125, 446-455

Lewis, H. M., & Laland, K. N. (2012). Transmission fidelity is the key to the build-up of cumulative culture. Philosophical Transactions of the Royal Society B, 367, 2171-2180

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. Animal Behaviour, 85, 195-202

Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. Animal Cognition, 11, 449-456

Matsuzawa, T., & Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: A. E. Russon, K. A. Bard, S. T. Parker (Eds.), Reaching Into Thought (pp. 211-232). Cambridge: Cambridge University Press.

McGrew, W. C. (1992). Chimpanzee Material Culture: Implications for Human Evolution. Cambridge: Cambridge University Press.

McGrew, W. C. 1998. Culture in nonhuman primates? Annual Review of Anthropology, 27**,** 301-328.

Mithen, S. (1999). Imitation and cultural change: a view from the Stone Age, with specific reference to the manufacture of handaxes. In: H. O. Box, & K. R. Gibson (Eds.), Mammalian Social Learning: Comparative and Ecological Perspectives (pp. 389-399). Cambridge: Cambridge University Press.

Page, E. B. (1963). Ordered hypotheses for multiple treatments - a significance test for linear ranks. Journal of the American Statistical Association, 58, 216-230

Pesendorfer, M. B., Gunhold, T., Schiel, N., Souto, A., Huber, L., & Range, F. (2009). The maintenance of traditions in marmosets: individual habit, not social conformity? A field experiment. PLoS One, 4, e4472

Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. Journal of Human Evolution, 63, 180–190

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. Trends in Cognitive Sciences, 15, 68-76

Sanz, C. M., & Morgan, D. B. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. International Journal of Primatology, 30, 411-427

Sugiyama, Y. (1997). Social tradition and the use of tool-composites by wild chimpanzees. Evolutionary Anthropology, 6, 23-27

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. Philosophical Transactions of the Royal Society B, 364, 2405-2415

Tomasello, M. (1996). Do apes ape? In: C. M. Heyes, & B. G. Galef (Eds.), Social Learning in Animals: The Roots of Culture (pp. 319-346). London: Academic Press.

Tomasello, M. (1998). Emulation learning and cultural learning. Behavioral and Brain Sciences, 21, 703-704

Tomasello, M. (1999). The human adaptation for culture. Annual Review of Anthropology, 28, 509-529

Tomasello, M. (2001). Cultural transmission – A view from chimpanzees and human infants. Journal of Cross-Cultural Psychology, 32, 135-146

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. Behavioral and Brain Sciences, 16, 495-511

Tomasello, M. (1994). The question of chimpanzee culture. In: R. Wrangham, W. McGrew, F. de Waal, & P. Heltne (Eds.), Chimpanzee Cultures (pp. 301-317). Cambridge MA: Harvard University Press.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. Science, 299, 102-105

van Schaik, C. P., van Noordwijk, M. A., & Wich, S. A. (2006). Innovation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). Behaviour, 143, 839-876

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology, 112, 270-281

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. 1999. Cultures in chimpanzees. Nature, 399, 682-685

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (2001). Charting cultural variation in chimpanzees. Behaviour, 138, 1481-1516

Whiten, A., Horner, V., & Marshall-Pescini, S. (2003). Cultural panthropology. Evolutionary Anthropology, 12, 92-105

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009a). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. Philosophical Transactions of the Royal Society B, 364, 2417-2428

Whiten, A., Schick, K., & Toth, N. (2009b). The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. Journal of Human Evolution, 57, 420-435

Whiten, A. & van Schaik, C. P. 2007. The evolution of animal 'cultures' and social intelligence. Philosophical Transactions of the Royal Society B, 362**,** 603-620.

Wood, D. (1989). Social interaction as tutoring. In: M. H. Bornstein, J. S. Bruner (Eds.), Interaction in Human Development (pp. 59-80). Hillsdale, NJ: Lawrence Erlbaum Associates.

Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. PLOS ONE, 8, e55768

Figure 1: Foraging box and its techniques. a) Overview of box in its home position. b) “Dipping” technique. c) “Poke and Lever” technique: Poke. d) “Poke and Lever” technique: Lever.

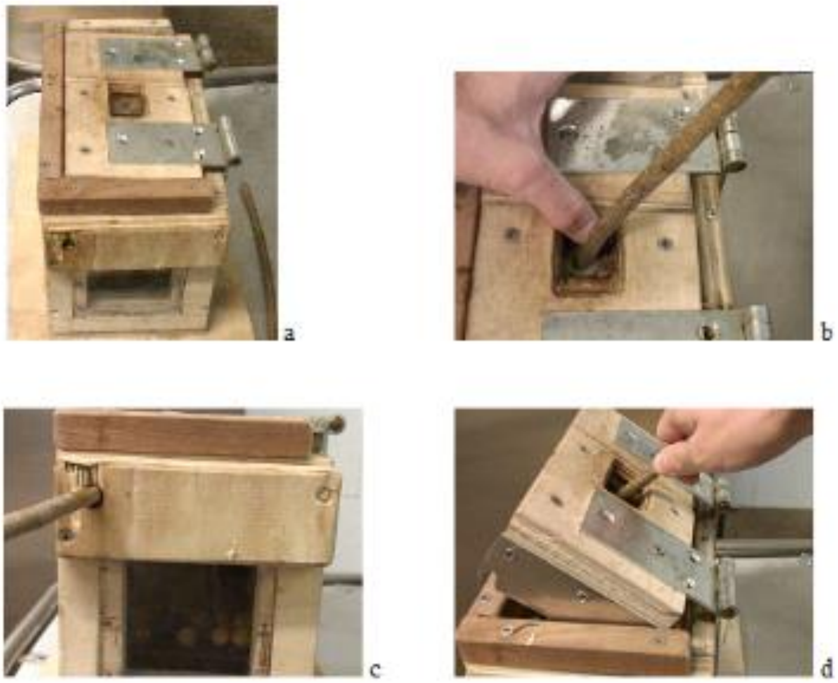


Figure 2: The task could be solved by two techniques: 1) Dipping, 2) Poke and Lever. For a detailed description see Table 1.

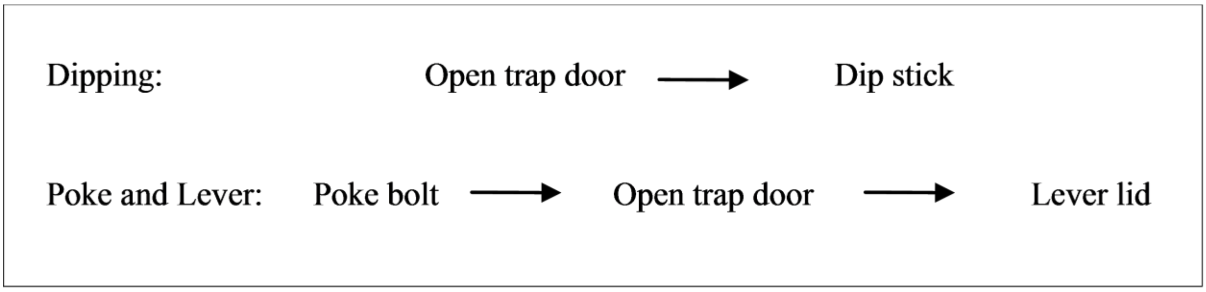


Figure 3: Successful performance of the “Dipping” techniques as proportion of subjects’ (N = 8) total manipulation durations in the seven sessions of the innovation phase. Medians and quartiles are shown.

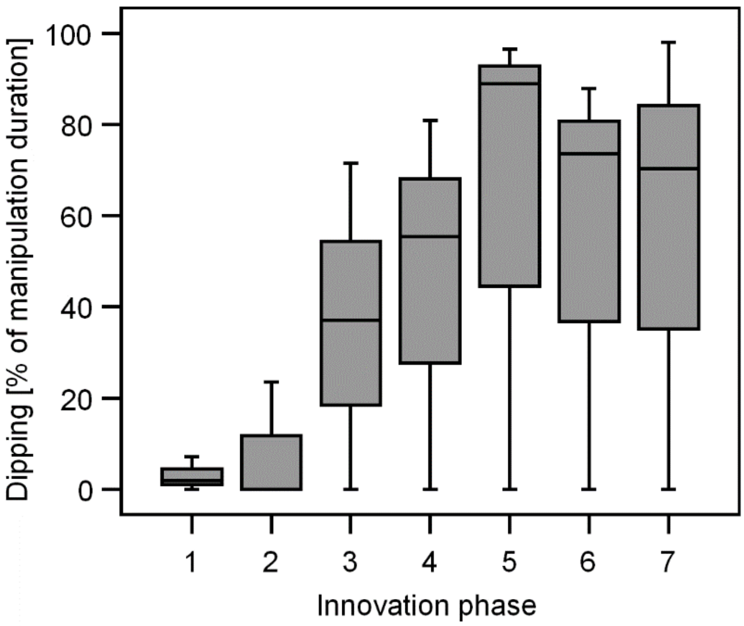


Figure 4: Individuals’ participation in the three phases of the experiment, the innovation phase, the demonstration phase, and the novel-exigencies-plus-demonstration phase, presented as duration of active manipulation with the apparatus proportionate to the time the apparatus was fixed to the cage in the corresponding phase (32h 12min).

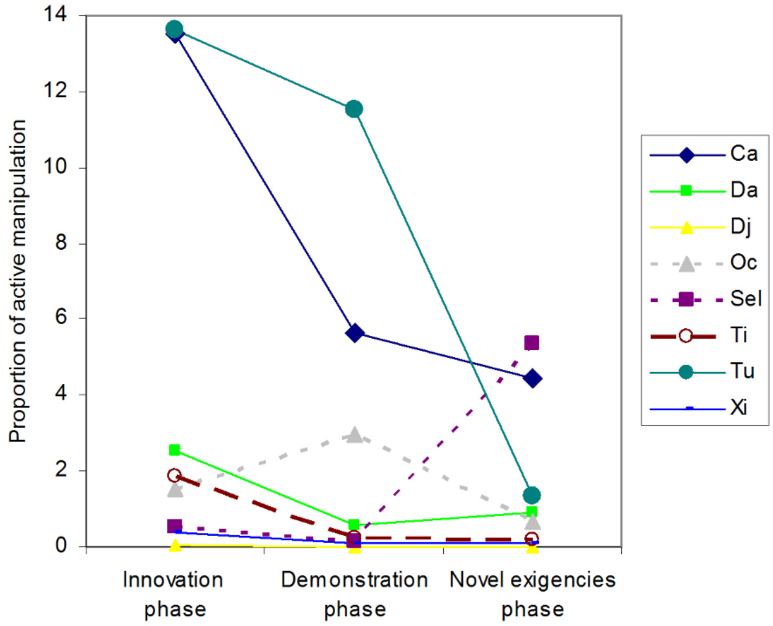
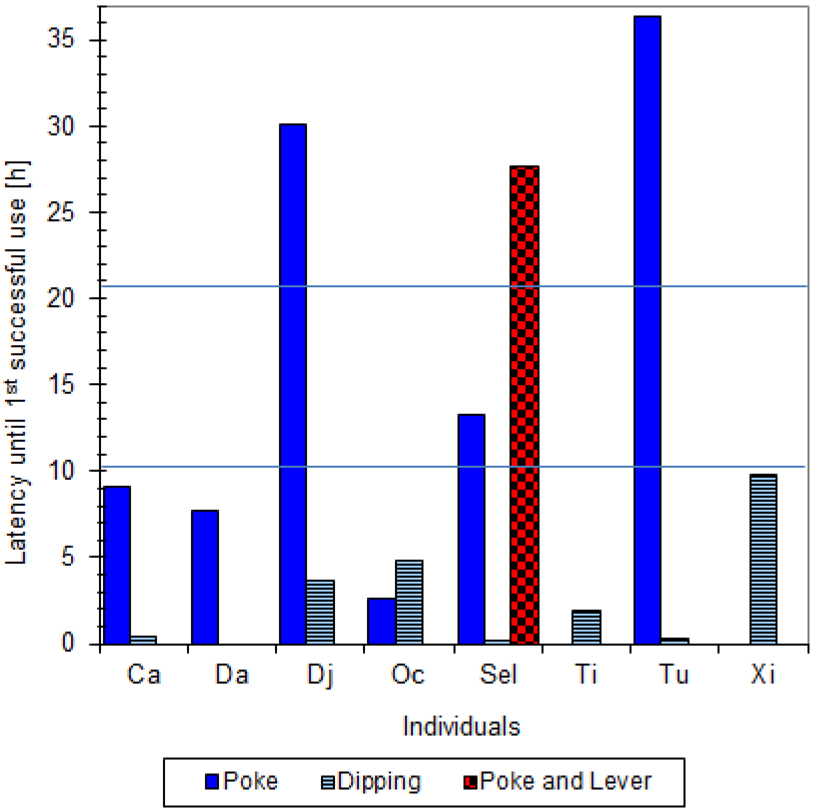


Figure 5: Latencies (h) until individuals' (N = 8) first successful performance of a "Dipping" technique, the first successful "Poke", and the first correct cumulative build-up on these two resulting in the ratcheted technique "Poke and Lever". Horizontal lines indicate the beginning of phases 2 and 3.


Latency until 1st successful use [h]
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Individuals
Poke
Dipping
Poke and Lever

Figure 6: Subjects' (N = 8) successful performance of "Poke" in the innovation phase, the demonstration phase, and the novel-exigencies-plus-demonstration phase. Frequency corrected for different durations of the three phases. The positive outliers represent the performance of the only individual (Sel) that mastered the "Poke and Lever" technique. Medians and quartiles are shown.

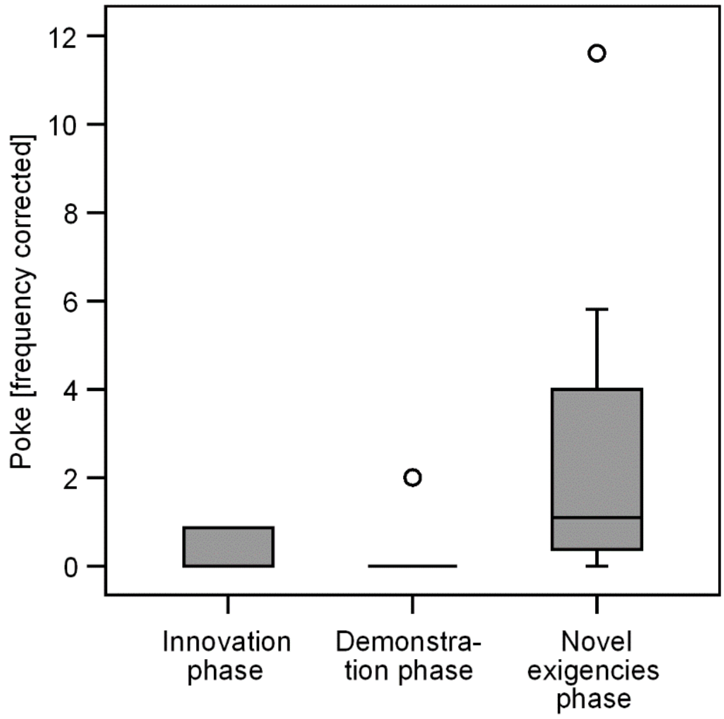

Figure 7: Frequency of "Poke and Lever" demonstrations watched by individuals (N = 8) per sessions in the demonstration phase and the novel-exigencies-plus-demonstration phase. The "Poke and Lever" technique was demonstrated by the human model. Means and SD are shown.

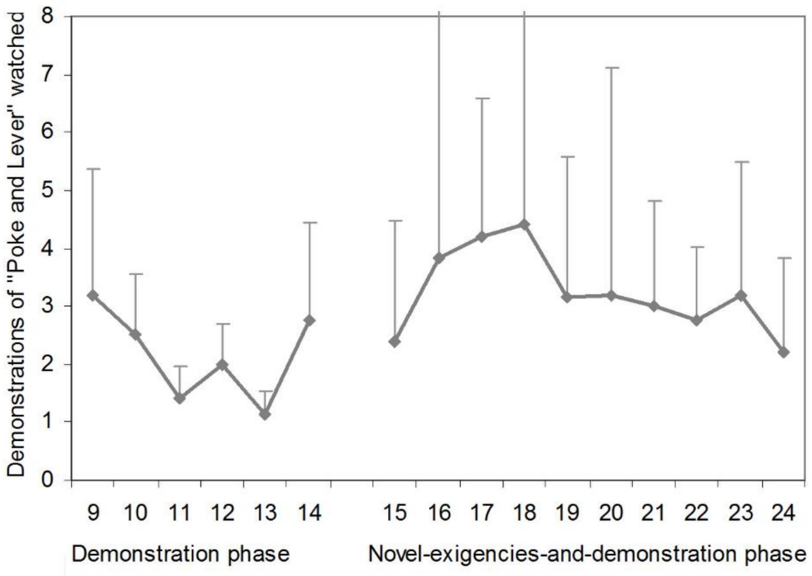

Figure 8: Effort to lever open the lid without succeeding as proportion of the time during which subjects (N = 8) could interact with the apparatus for the innovation phase, the demonstration phase, and the novel-exigencies-plus-demonstration phase. Medians and quartiles are shown.