Haut | ISSN: 0938 - 2216 | Vol. 23, Issue 6 | 2025

Full title: Independent Emergence of Tool-Use: Stick Pounding in Untrained Chimpanzees

Running title: Chimpanzees reinnovate tool-use behavior

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This is the peer reviewed version of the following article: Bandini, E., & Tennie, C. (2019). Individual acquisition of "stick pounding" behavior by naïve chimpanzees. American Journal of Primatology, 81(6), e22987 which has been published in final form at: https://doi.org/10.1002/ajp.22987

Abstract

Many studies investigating culture in non-human animals tend to focus on the inferred need of social learning mechanisms that transmit the form of a behavior to explain the population differences observed in wild animal behavioral repertoires. This research focus often results in studies overlooking the possibility of individuals being able to develop behavioral forms without *requiring* social learning. The disregard of individual learning abilities is most clearly observed in the non-human great ape literature, where there is a persistent claim that chimpanzee behaviors, in particular, *require* various forms of social learning mechanisms. These special social learning abilities have been argued to explain the acquisition of the relatively large behavioral repertoires observed across chimpanzee populations. However, current evidence suggests that although low-fidelity social learning plays a role in harmonizing and stabilizing the *frequency* of behaviors within chimpanzee populations, some (if not all) of the *forms* that chimpanzee behaviors take may develop independently of social learning. If so, they would be latent solutions –behavioral forms that can (re-)emerge even in the absence of observational opportunities, via individual (re)innovations. Through a combination of individual and low-fidelity social learning, the population-wide patterns of behaviors observed in great ape species are then established and maintained. This is the Zone of Latent Solutions (ZLS) hypothesis. The current study experimentally tested the ZLS hypothesis for pestle pounding, a wild chimpanzee behavior. We tested the reinnovation of this behavior in semi-wild chimpanzees at Chimfunshi Wildlife Orphanage in Zambia, Africa, (N=90, tested in four social groups). Crucially, all subjects were naïve to stick pounding before testing. Three out of the four tested groups reinnovated stick pounding – clearly demonstrating that this behavioral form does not require social learning. These findings provide support for the ZLS hypothesis alongside further evidence for the individual learning abilities of chimpanzees.

Keywords: Individual learning, social learning, chimpanzee behavior, tool-use, zone of latent solutions

Research highlights

1. *Naïve chimpanzees were provided the materials for the wild pestle pounding behavior*
2. *Chimpanzees spontaneously demonstrated the same behavioral form as wild counterparts*
3. *Individual learning, contra to previous claims, seems to be sufficient to drive this behavior in chimpanzees*

Introduction

A large body of research has focused on the tool-use repertoires of our closest living relatives, chimpanzees, as they exhibit one of the most extensive and varied tool-use repertoires in the animal kingdom (Seed & Byrne, 2010); only approximated perhaps by orang-utans (van Schaik & Pradhan, 2003), New Caledonian crows (Rutz et al., 2016) and capuchins (Mannu & Ottoni, 2009; *J. Pruetz; personal comm.*). Chimpanzees are also among the few non-human animal species that exhibit a regional variation in their tool use behaviors (Whiten, et al., 2001; Whiten et al., 1999). Despite many years of research into chimpanzee tool-use (spurred by Goodall (1986) and McGrew & Tutin's (1978) seminal reports on the behavioral repertoires of wild chimpanzees) the cognitive and cultural mechanisms behind the expression of tool-use behaviors within and across chimpanzee populations are still debated. The debate centers around two aspects of tool-use: the form and the frequency of the behavior. The form of a behavior can be defined as the action components involved in the behavior (which can be organized in both a linear and/or hierarchical relationship). The frequency of the behavior is the rate of occurrence of a behavioral form within and across populations.

Until recently, the most common explanation for the forms that chimpanzee tool-use behaviors take has been one that favors a form-copying transmission mechanism (Boesch, 1991; Boesch, 1995; Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Goodall, 1986; de Waal, 2002; Whiten et al., 2001; Whiten et al., 1999). This approach proposes that various types of social learning are *necessary* for the form of these behaviors (or, at least, some of them; Gruber, Poisot, Zuberbühler, Hoppitt, & Hobaiter, 2015; Whiten et al., 2001; Whiten et al., 1999) to spread and be maintained throughout each population. This line of thinking is best demonstrated in Whiten et al., (1999). In the original report by Whiten et al. (1999) on chimpanzee behaviors, the authors state that for some of the behaviors they identified as cultural '*it is difficult to see how such behavior patterns could be perpetuated by social learning processes simpler than imitation*' (here imitation is categorized as a high-fidelity copying social learning mechanism able to transmit the form of a behavior; Heyes, 2012; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Thus, according to what we here label the "form-copying hypothesis", when a new behavior is first shown by one individual (through innovations, see Reader & Laland, 2002), the other members of the group acquire (and *have to* acquire) the form of the behavior through social learning mechanisms that allow for the copying of behavioral forms (e.g., high-fidelity social learning). The behavioral form becomes a population-wide variant once a sufficient number of individuals have copied the innovation. The regional differences in the behavioral repertoires observed across chimpanzee populations (Whiten et al., 2001; Whiten et al., 1999) are then attributed to independent individuals in the past having innovated different behavioral forms that were then transmitted to the rest of the population via high-fidelity social learning mechanisms.

The "form-copying hypothesis" seems, at first, to fit well with data from the wild. However, it fails to explain and account for both archaeological and experimental data from wild, captive and semi-wild chimpanzees. For example, Mercader, Panger, & Boesch (2002) describe evidence from archaeological excavations of wild chimpanzee nut-cracking sites in Taï forest. The excavations at this site revealed that the general form of nut-cracking has remained constant for at least 4,000 years (and likely even longer). If this behavior were transmitted solely via social learning, then through copying error alone (which is unavoidable when copying behaviors socially; Eerkens & Lipo, 2005; Kempe, Lycett, & Mesoudi, 2012), we would expect to see changes to the form of the behavior (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Kempe, Lycett, & Mesoudi, 2012). Thus, the current archaeological evidence from chimpanzee nut-cracking sites does not seem to support the copying hypothesis.

Furthermore, the evidence for enriched captive apes: non-enculturated and non-trained (captive) chimpanzees (arguably, the only ecologically representative apes; Henrich & Tennie, 2017) possessing the assumed ability to copy behavioral forms remains highly controversial (Bandini & Tennie, 2017; Galef, 1992; Henrich & Tennie, 2017; Tennie, Call, & Tomasello, 2009; Tennie, Call, & Tomasello, 2006; Tomasello, Davis-Dasilva, Camak, & Bard, 1987). Indeed, many of the methodological approaches aiming to explicitly test for action-copying abilities in these great ape populations have failed to control for alternative non-action-copying social learning mechanisms. For example, the most commonly used method to test for action-copying in non-human animals is the "two-target" task (e.g., Custance, Whiten, Sambrook, & Galdikas, 2001; Dindo, Thierry, & Whiten, 2008; Kis, Huber, & Wilkinson, 2015; Miller, Rayburn-Reeves, & Zentall, 2009; Stoinski, Wrate, Ure, & Whiten, 2001; Whiten, 1998; Whiten, Custance, Gomez, Teixidor, & Bard, 1996; Whiten, Horner, & de Waal, 2005) in which two different *physical techniques* to access a baited apparatus are seeded into separate groups, to examine whether naïve subjects are more likely to use the demonstrated physical technique than alternative solutions. The result of these studies across an ever-growing number of species, is that many animals will preferentially adopt the seeded technique (see references above). However, besides not actually being able to identify action copying (as the tasks are grounded in differences in physical techniques; Heyes & Ray, 2000) in all cases, at least one individual in the group reinnovated the *non-seeded* technique as well (Bandini & Tennie, 2017; Tennie et al., in press), suggesting that *all* demonstrated solutions are simple enough that they can be individually learnt. Thus, these studies only test the ability for low-fidelity social learning, but not the presence of culture-dependent traits or of high-fidelity social learning (Bandini &

Tennie, 2017). Regarding the question of action copying, unconfounded tests (those that used pure actions as targets) involving unenculturated and untrained apes have, so far, failed to show evidence of action-copying abilities – at least when it comes to culture-dependent actions forms (Clay & Tennie, 2017; Claudio Tennie, Call, & Tomasello, 2012; Tomasello & Call, 1997). Additionally, recent neuroimaging work on ecologically representative non-human primates suggests that their brains are not adapted to copy action forms (Hecht et al., 2013). This evidence is further supported by a recent study that demonstrated that the necessary brain structures (e.g., changes within the fronto-parieto-temporal cortical regions of the brain) for action copying in non-human primates require ecologically invalid input (namely training by humans; Pope, Taglialatela, Skiba, & Hopkins, 2018). Therefore, wild apes, which do not receive any forms of human interaction and/or training, should not possess the necessary brain structures for action copying (according to Pope, Taglialatela, Skiba, & Hopkins, 2018).

Indeed, wild chimpanzees (and likely, due to cognitive cladistics, other great apes as well) might simply not *need* to copy the behavioral forms from their innovators in order to show the same behavior themselves. The alternative approach to the form-copying hypothesis suggests that the inferred "copying" of behaviors by chimpanzees might be an illusion.. It may be instead that the underlying mechanism that drives the acquisition of behavioral forms in chimpanzees (and other apes) is that of "socially-mediated serial reinnovations" (SMSR; Bandini & Tennie, 2017). These behavioral forms increase in frequency in populations due to low-fidelity social learning helping others reinnovate the behavior on their own. The resulting behavioral forms therefore derive individually, and do not need to be copied (this may also be the case for other primates).This approach is known as the Zone of Latent Solutions hypothesis (ZLS; Tennie et al., 2009). This may also be the case for other primates. For example, studies conducted on stone handling in wild Japanese macaques and captive rhesus macaques found that stimulus enhancement (a low-fidelity form of social learning), along with environmental and phylogenetic factors, influenced the acquisition of the behavior by infants (Huffman & Nahallage, 2007; Nahallage & Huffman, 2008).

Thus, the two possible explanations for the acquisition of behavioral patterns by wild great apes (ZLS vs. action copying) led to two lines of experimental research. The first question involves understanding and identifying whether great apes are and can ever be at least *influenced* by social learning (regardless of the specific social learning mechanism). This question has by now been unequivocally answered in the affirmative, and so it is now clear that chimpanzees, amongst many (or even most) other animal species, possess a repertoire of social learning mechanisms that they apply across various learning contexts (see review by Whiten et al., 2004) – though they seemingly lack *high-fidelity* social learning forms (see above). Thus, great apes are capable of sustaining population differences via low-fidelity social learning mechanisms, i.e. via SMSR. Indeed, several studies have now demonstrated that naïve great apes (including humans; Reindl, Beck, Apperly, & Tennie, 2016) can reinnovate wild behavioral forms in the absence of observational opportunities (Allritz, Tennie, & Call, 2013; Bandini & Tennie, 2017.; Huffman & Hirata, 2004; Huffman, Spiezio, Sgaravatti, & Leca, 2010; Menzel, Fowler, Tennie, & Call, 2013; Neadle, Allritz, & Tennie, 2017; Reindl et al., 2016; Claudio Tennie, Hedwig, Call, & Tomasello, 2008). These findings provide strong empirical support for the ZLS hypothesis, demonstrating that an individual expression approach to chimpanzee behavioral forms is justified (as surprising as it may at first seem). Thus, whilst non-copying forms of social learning facilitate the individual expression of latent solutions across individuals – and with it explains the relatively different frequencies observed – *high-fidelity* forms of social learning are not necessary for the same form of behaviors to emerge across individuals for any type of behavioral form that can be shown to arise in these kind of tests (compare Tennie et al., 2009; note that behaviours within the ZLS have a range: they can emerge almost automatically (for example, yawning, which is merely released) or they may emerge more indirectly via individual learning that is channelled in species typical ways). Therefore, instead of assuming that great apes have enhanced social leaning skills as compared to many other animals, the ZLS hypothesis implies instead that their *innovation* skills that are enhanced

Behavioral forms that emerge in the absence of social learning are classified as ‘latent solutions’ as they can be innovated as well as reinnovated (Bandini & Tennie, 2017). They lie within species’ ZLS (i.e. they represent their *potential* behavioral repertoire). Latent solutions should, technically, emerge in any typically-developed individual of such species, as long as they are in the appropriate developmental stage, are not deprived, are in the right ecology, are not negatively influenced by other pre-existing behavior patterns (e.g. functional fixedness; Hanus, Mendes, Tennie, & Call, 2011) and are motivated to show the behavior (Bandini & Tennie, 2017; Henrich & Tennie, 2017; Tennie et al., 2009; Tennie et al., 2008), amongst other potential factors (Bandini & Tennie, 2018).

To emphasize the individually derived aspect of innovations sensu Tennie et al., (2009) and in the context of the animal culture debate, we refer to latent solutions as ‘reinnovations’ (Bandini & Tennie, 2017). *Re*innovations are the behavioral forms that reappear in naïve individuals that have never observed the behavior beforehand. For example, if the same behavioral form of a wild target behavior emerges in captive, naïve individuals, i.e. those who have never seen (or been trained in) the behavior, this would count as such a ‘reinnovation’ (for examples of reinnovations see (Allritz et al., 2013; Bandini & Tennie, 2017; Menzel et al., 2013; Neadle et al., 2017; Reindl et al., 2016; Tennie et al., 2008).

Materials and Methods

Latent Solutions (LS) Testing Methodology

In order to experimentally identify the behaviors that remain within chimpanzees' ZLS, naïve, "enriched captive chimpanzees" (Henrich & Tennie, 2017) are provided with all the ecological materials of the target behavior in controlled testing conditions. These testing conditions replicate the conditions encountered by wild individuals *after* a behavior has been innovated for the first time, where the innovator leaves behind the debris of the behavior and/or attracts other subjects nearby to the necessary raw material. These conditions also mimic the stochastic nature of object location, which – by chance – are sometimes found in close proximity to their behavioral targets (thus may also recreate the situation that the first innovator might have found him/herself in by chance; e.g., see the case study described in Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, (2014), in which two new behaviors emerged after the chimpanzee population found a new waterhole that had been repeatedly flooded by a river). Therefore, LS testing conditions recreate a *possible* (albeit rare) scenario that might have been encountered by the first innovator(s) in the wild, alongside recreating the subsequent socially facilitated encounters of tool material and target once a latent solution is innovated in the population. Once the materials are introduced into the subject's enclosure, an "asocial" baseline is carried out, in which no demonstration of the behavior is provided (a classic method in ethology; e.g., Sherry & Galef, 1984). This condition allows for the behavioral form to *individually* develop without the input of any observation opportunities. If the behavioral form is reinnovated in this latent solution test, then this constitutes strong positive empirical evidence for the behavior being within the species' ZLS (because, logically, this finding demonstrates that the behavioral form does not *require* any forms of social learning to be acquired).

Target behavior: (Pestle) stick pounding

Pestle pounding is a wild behavior observed in chimpanzees in Bossou, Guinea (Yamakoshi & Sugiyama, 1995). Wild chimpanzees pull out the central shoots in the oil-palm crown of palm trees (*Elaeis guineensis)* to access the palm hearts inside. To deepen the hole and better access the palm hearts, chimpanzees use the leaf-petioles as pounding tools. The chimpanzees then extract and eat the mashed palm hearts. Pestle pounding behavior was first observed in Bossou, Guinea, in 1990, and by the time the report was published in 1995, almost half of the wild group was practicing this behavioral form (Yamakoshi & Sugiyama, 1995). As the behavior is characteristic to observe and should have been easily identified by the loud, recognizable pounding noise the chimpanzees make, the authors concluded that pestle pounding *'was* *invented recently and has since spread widely throughout the group'* (Yamakoshi & Sugiyama, 1995).

Although the same species of tree (*Elaeis guineensis*) exists across sites, pestle pounding has, so far, *only* been observed in Bossou (Whiten et al., 2001). Following the requirements laid out in Whiten et al. (1999; 2001), in which a behavior must be recorded as either '*habitual*' or '*customary*' in at least one site, and absent at but not due to ecological reasons in at least one other site, pestle-pounding has been categorized as a '*putative cultural* behavior' (ibid).

The test conditions in the current study did not include any steps *before* a tool is used for pounding. Although it would be interesting to examine the emergence of the entire pestle pounding sequence, this was not the aim of the current study. Here, we only focused on the target behavioral form itself: the use of a tool with a pounding action to mash a desirable food in a cavity, so that it can be retrieved. This is stick pounding. The behaviors surrounding the target pounding action, such as, for example, the knowledge that palm hearts are edible and can be found inside palm trees, are very likely to be driven by some forms of social learning. However, again, here we are only interested in the learning mechanisms behind *tool-use behavioral forms*, and therefore the focus of these studies must necessarily lie in the behavioral form of this tool-use itself, and not in the context of the behavior (see also Bandini & Tennie, 2017). Thus, as we focus on the crux of the tool use behavior only we refer to the target behavior as 'stick pounding' throughout this manuscript. Following the logic outlined in Tennie et al., (2009) and data from previous latent solutions tests (Allritz et al., 2013; Bandini & Tennie, 2017; Menzel et al., 2013; Neadle et al., 2017; Reindl et al., 2016; Tennie et al., 2008), we hypothesized that the target (stick pounding) behavior would be individually reinnovated by naïve individuals (therefore demonstrating this behavioral form to be a latent solution).

Subjects

The subject sample in the current study consisted of chimpanzees housed at Chimfunshi Wildlife Orphanage Trust in Zambia, Africa (henceforth: Chimfunshi; N=90: Group one: N=23: Group two: N=46; Group three: N= 10: Group four: N=11). The chimpanzees are divided into five separate groups. Four out of the five groups at Chimfunshi participated in this experiment (the last group: the so-called 'escape artists' were excluded due to their extensive contact with humans, thus potentially not making them naïve to the target behaviors. See table one in the supporting information for the demographic information of each group included in the study). Apart from groups three and four, who can occasionally see each other through a small part of the enclosures, none of the other groups can view each other.

Chimfunshi is located in the Copperbelt region of Northern Zambia, Africa (S12 deg 21.924 E027 deg 28.912). The chimpanzees live under semi-wild conditions in fenced enclosures ranging between 20 and 80 hectares. Individuals spend most of the day and all night outdoors, and only come indoors for their daily feeds (11.30-13.00/ 14.30-16.00). Subjects have access to water *ab libitum* and are fed a daily rich and varied diet, alongside having access to fruiting trees inside their enclosures. As interaction between keepers and visitors and the chimpanzees is kept at a minimum (to preserve a natural state of the animals), toys and/or tasks are rarely provided to the chimpanzees (thus minimizing the chance of carry-over effects in our study). However, the chimpanzees do participate in research studies such as the one presented here.

Prior to testing, the keepers at Chimfunshi and the Chimfunshi Research Advisory Board (CRAB) established that the chimpanzees did not have any previous experience with similar tasks during past experiments or enrichment exercises. Therefore, we consider the chimpanzees naïve to the pounding behavior under examination here – as is necessary for the latent solutions test. Due to the testing conditions at Chimfunshi, we were unable to use the originally described food rewards (palm hearts) to bait the apparatus. However, as mentioned previously, the aim of latent solution tests is not to examine the mechanisms behind learning which foods are edible (which may indeed be socially-mediated; e.g., Schuppli et al., 2016), instead the focus is on examining whether any social learning is necessary for the target actions (here the tool use 'pounding' action (with sticks) to mash and thus retrieve solid food). Thus, the differences in food reward type between our experimental set-up and the wild did not constitute a problem for the goal of our study (compare also Bandini & Tennie, 2017). However, we necessarily reproduced the same conceptual problem that retrieving palm hearts present. Hence, the pounding apparatus was baited with a solid, but mash-able food: for this we used boiled potatoes (to replicate the hardness, malleability and consistency of palm hearts). The chimpanzees at Chimfunshi occasionally eat potatoes, so they were familiar and motivated to retrieve the food from inside the testing apparatus.

Methods

Due to local management requirements, individuals could not be separated, so subjects were tested in their normal social groups. Thus, in order to isolate the roles of individual and social learning mechanisms, only the *first* instance of a reinnovation of the behavior is counted as data towards a ZLS-based approach. This is because, once the behavior has been reinnovated by one individual, the role of social learning in the acquisition of the behavior cannot be discounted for the rest of the group (as they might have observed the reinnovator; Bandini & Tennie, 2017).

The testing apparatus (Fig. 1) was set up near the indoor management areas when the chimpanzees were not present and out of eyesight. The testing apparatus measured 21cm x 21cm x 16cm, with the diameter of the top of the apparatus measuring approx. 1.6cm. One hard-boiled potato (boiled for approx. three minutes, all weighing between 145g to 190g) was inserted into the testing apparatus before the apparatus was attached to the mesh, and before the chimpanzees were present in the testing area. The top of the apparatus could be unscrewed to insert the bait, and then sealed again before attaching it to the mesh and starting the trial. The potato was boiled for three minutes so as to make it palatable, but was left hard enough so as to require forceful pounding with a tool to mash it into smaller pieces. The lid of the testing apparatus was sealed, apart from one small hole in the top, which was large enough to allow a tool to go through, but too small for more than one finger to be inserted into the apparatus (and in any case, the cavity was too deep for the finger to reach the potato). The testing apparatus was attached to cage mesh via a backing panel and metal wires. It was installed at a height of one meter in an area that was accessible to all the chimpanzees of the respective group. As the chimpanzees were tested in their outdoor enclosures, we did not provide any additional materials that could be used as tools. The chimpanzees had access to all the materials in their natural enclosures, including naturally occurring sticks, branches, stones, and shrubbery. Therefore, the subjects had to source their own tools from their surrounding environment without any facilitation provided by the experimental set-up.

Fig. 1

Testing was carried out over six weeks in June-August 2017 by EB. Each of the four groups was tested twice over the six weeks. Tests were carried out after the daily morning feeds (between 11.30-13.30) as the chimpanzees were most often near the indoor areas right after feeding. Behaviors were all filmed on a handheld Sony HDR-CX330E by EB. Tests started when an individual started manipulating the testing apparatus and ended after 20 minutes, unless individuals were still manipulating the apparatus, in which case testing time was extended to a maximum of 30 minutes.

Ethical statement

This study was approved by the University of Birmingham AWERB committee (reference UOB 31213) and by the host sanctuary (approved by the CRAB) following guidelines provided by the SSSMZP, EAZA, BIAZA and WAZA on animal welfare and research in zoological institutions. These studies adhered to legal requirements of the UK and Zambia, where the research was carried out, and adhered to the ASP principles for the Ethical Treatment of Primates. All the subjects in these studies voluntarily participated in the experiments, and were free to stop participating at any time. Subjects kept their regular cleaning and feeding schedules during testing and had access to water *ad libitum*. Subjects live in natural-type social groups and were fed a daily appropriate and varied diet.

Coding

All videos were first coded by EB. 20% of the videos were then second-coded by a naïve coder to assess interrater reliability. Videos for reliability coding were selected using the following procedure. During the first round of coding by EB, all the videos were assigned a sequential number (e.g., 1-*n*). After coding, the numbers were placed into a random number generator in Excel until 20% of the videos were selected for interrater reliability testing (see also Neadle et al., in prep). The second coder's observations were then compared to EB's using standard Cohen's Kappa calculation.

The videos were coded for all events of interaction with the testing apparatus (see table one below for the behaviors coded and descriptions). For all tool-use bouts, the time of start of manipulation and end of manipulation were recorded, whether the tool-use bout resulted in food retrieval or not, alongside what (stick) tool was used (small or large); whether the tool was taken by another individual; and if the tool was modified in any way before or during a manipulation bout. Modification was recorded when an individual changed the state of a tool (e.g., making the tool shorter by breaking off the end, or removing any superfluous fronds or twigs from a stick). Tolerated theft of tools was coded when an individual allowed (e.g., did not resist) another one to take the tool from their hand (this does not imply active sharing or giving, but merely that the individual allowed the stick to be taken by another individual; see Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016). Furthermore, the grip of the tool (i.e., how the tool was held in the hand) was recorded (when this was clearly discernible from the video). Grip-type was coded as either: *holding the tool between the thumb and index finger* or *holding the tool in the palm, with all five fingers wrapped around the tool.* Wild chimpanzees are only described as holding the tool in both hands, but, to the best of our knowledge, no further information on grip-type of wild chimpanzees is currently available. How many times the tool was pounded was also coded (an instance of pounding started as the tool entered the apparatus and ended when it was pulled out).

Table 1: Descriptions of behaviors coded during testing

Method	Description
Interaction	Individual begins manipulating the apparatus, without a tool. This type of manipulation most often involves an individual inserting their finger into the top of the apparatus, attempting to probe inside the apparatus, or using their whole body to attempt to break or remove the apparatus from the mesh
Stick insertion	Individual holds a stick tool in hand(s), and inserts it into the apparatus. Crucially, these events are not coded as pounding, as they do not involve the forceful pounding action observed in the wild behaviors.
Pounding	Individual inserts a tool into the apparatus and performs the forceful and/or fast action of hitting it towards the bottom of the apparatus (as described by Sugiyama & Koman, 1979; Yamakoshi & Sugiyama, 1995).
Food retrieval	Some of the baited food was retrieved with the tool after being inserted in the apparatus. The food was then consumed from the tool.
Other apparatus Manipulation	Individual manipulates the apparatus in a way not described by any of the categories above (note that this manipulation never resulted in any food retrieval).
Tool modification	Tool was modified in any way (i.e., the shape was changed). For example, a stick was made shorter by biting off, or ripping off one end, or extraneous fronds or twigs were removed from the stick with hands or teeth.
Tolerated tool theft	An individual allowed (i.e., did not resist) another one to take the tool from their hand.
Grip-type	The subject either held the tool between the thumb and index finger or in the palm, with all five fingers wrapped around the tool.

ZLS Standards

In order to draw species-wide insights from population samples, the LS method applies two different standards, depending on the behavior in question (Bandini & Tennie, 2017). These two standards address the varying relative complexities of behaviors. The single-case ZLS standard is applied to relatively more complex tool-use behaviors (for example, chimpanzee nut-cracking which is a multi-step behavior organized in a clear hierarchical structure) where it is very unlikely that the behavior appears by chance. Thus, only one, spontaneous reinnovation of the behavior is required for it to be classified as a species-wide ZLS behavior. On the other hand, other chimpanzee behaviors, such as stick tool-use, are relatively simple (with some possible exceptions, such as tool-assisted hunting; Pruetz & Bertolani, 2007), and there is a slightly higher (albeit still small) possibility that they occur by chance. In these cases, the double-case standard is applied, and at least two independent reinnovations of the behavior are required for them to be considered within the species' ZLS (Bandini & Tennie, 2017). As the target behavior examined in this study is arguably relatively simple (as it only involves one tool, one fixed hole and a forceful pounding action), we applied the double-case ZLS standard, and so required at least two independent reinnovations of the behavior to classify it as a latent solution for chimpanzees.

Results

Reliability coding

20% of all the testing videos were second-coded by a naïve coder following the scheme above to assess inter-rate reliability. The reliability coder was not familiar with the methods or testing hypothesis of this study. There was very good agreement (Cohen, 1968) between coders (k=0.73) for the behaviors demonstrated, and a good agreement between coders (k=0.65) for the size of the stick-tools used and for the grip-type used by the subjects (k=0.68)

Experimental Results

In three out of four of the groups tested we identified one individual (per group) that spontaneously used tools with a pounding action with the testing apparatus. All three reinnovators (CH in Group one, MX in Group two and JK in Group four; see also supplementary information for demographic information) of the pounding behavioral form were captive born and mother-reared, ensuring that they were naïve to the behavioral form, and unenculturated (as required to draw ecologically relevant conclusions for the ZLS hypothesis; Bandini & Tennie, 2017). All of the reinnovators demonstrated the behavior within the first testing session. Thus, we identified three cases of spontaneous stick pounding behavior (see supplementary video for a clip of one individual (JK) demonstrating the pounding action). Group three was the only group that did not reinnovate the target pounding behavior. The data collected in this study fulfill the double-case ZLS standard and demonstrate that stick pounding is a behavior within chimpanzees' ZLS. As we could not control for social learning in individuals other than the first reinnovators, we only counted the first reinnovation of the behavior here. However, after the first chimpanzees acquired the behavior, other subjects in the group also interacted with the apparatus and demonstrated the target pounding action: 14% (11/79) of tested subjects showed the behavior across all three groups, which includes 14% (3/22) individuals from Group one, 11% (5/46) individuals from Group two and 27% (3/11) individuals from Group four.

Although our focus was not on the steps before the pounding action, the first step of all the chimpanzees that demonstrated the pounding action was to search for and retrieve a tool from their surroundings. The tool was then modified if necessary and inserted into the apparatus. The tool was then forcefully pounded into the apparatus one or more times. The tool was then pulled out of the apparatus and the distal end of the tool sniffed and inserted into the mouth. This process was repeated several times. The pounding action observed in this study therefore matches the descriptions of the target actions of wild pestle pounding behavior (Yamakoshi & Sugiyama, 1995) and resembles other wild tool-use behaviors, such as tool-assisted hunting (Pruetz & Bertolani, 2007).

Pounding tools

The stick tools used by the chimpanzees could not always be retrieved by the experimenter after the study as the chimpanzees often carried them away into the forested area (which cannot be accessed due to health and safety regulations). However, a small sample of tools used by different individuals was retrieved from Group four (n=4; 28% of the overall number of tools used during testing). The tools measured between 60-90cm long (M=76.9; SD=9.37) and .5-1.5cm wide (M= 1.02; SD=0.499). Although it was not possible to record the exact dimensions of the tools from video, sticks on video could be classified as either ‘small’ or ‘large’. Small sticks measured approx. between 60-75cm long and .5-.7cm wide. Large sticks measured approx. between 75-90cm long and .7-1.5cm wide (see supplementary video for a clip of two individuals using a large and small tool). 55% (11/21) of pounding events were carried out with a ‘large’ tool, which may have made the forceful action potentially more efficient, due to the larger diameter of the stick tools. We only recorded instances of subjects changing from a small tool to a large one during testing. Once the subject found a larger tool than the first one, they did not change the tool again (even if other tool types were available). The difference between time spent pounding with a large and a small tool was not statistically significant (Wilcoxin signed rank test; Z= -1.362, p=0.173). Mean number of times the tool was pounded was recorded for each pounding bout. Across all groups, individuals pounded on average 4.0 times (SD=1.3) per tool-use bout.

Interaction with the testing apparatus

The accumulated interaction time with the apparatus (including both manipulation with and without tools) was measured per each group. Subjects in Group one spent 14:19 minutes interacting with the testing apparatus; Group two: 17:13 minutes; Group three: 18:03minutes; Group four: 27:34minutes. In total, all four groups spent 1:17:27 manipulating the testing apparatus. A Kruskal-Wallis H test demonstrated no significant difference between the total interaction time of each group, $\chi^2(2)=2.424$, $p=0.524$, with a mean rank score of 37.21 for Group one, 33.75 for Group two, 29.44 for Group three and 40.32 for Group four.

Out of all interactions with the testing apparatus, 26% (19/74) of manipulations were pounding bouts. Individually, pounding made up 33% (5/15) of Group one's interactions, 27% (6/22) of Group two's and 28% (8/28) of Group four's interactions (no pounding behavior was recorded for Group 3). No observations of tool insertion (defined as the insertion of tool into the apparatus without demonstrating the target pounding action) were recorded in these groups. The time spent pounding was recorded for the three reinnovators. In Group one, CH spent 1:29 minutes pounding, in Group two MX spent 1:10 minutes pounding and in Group four JK spent 2:10 minutes pounding. Including other individuals in the group, time spent pounding was 4:06 minutes for Group 1, 4:12 minutes for Group 2 and 8:41 minutes for Group 4 (totaling 16.59minutes for all three groups). Collective average time spent pounding was 1:05 minutes (SD= 0.34).

Grip type

Grip type was recorded every time an individual used a tool. However, not all videos allowed for a clear enough view to determine the grip-type of each individual, so only clear videos were coded (14% (3/21) of cases were excluded due to the view of the grip being blocked). Across all groups, two different grips were recorded: *holding the tool between the thumb and index* and *holding the tool in the palm, with all five fingers wrapped around the tool*. Of these two grip-types, palm grip was recorded in 67% (14/21) of cases, whilst holding the tool between the index and thumb was recorded in 19% (3/21) of cases. Subjects always held the tool in one hand, contrary to the wild, where chimpanzees have occasionally been observed holding the tools with two hands (Yamakoshi & Sugiyama, 1995). However, it may have been difficult for the subjects to hold the tool with both hands due to the experimental set-up (as they also had to hold on to the mesh or the apparatus to maintain balance whilst pounding).

Tolerated theft of tools

Bouts of tolerated theft of tools were also recorded across all four groups (see also Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016 for a description of tool transfers or tolerated thefts of tools in the wild). Tolerated theft was only observed in Groups one and four. In Group one, tolerated theft events occurred in 41% (8/19) of pounding bouts, and in Group four, tolerated theft of tools occurred in 36% (7/19) of bouts. Tolerated theft of tools was never recorded in Group two, and no active food-sharing bouts in any group were observed during testing. There was no discernable pattern between individuals who allowed their tools to be taken. However, all individuals who took a tool then always went on to use the same tool to interact with the testing apparatus (c.f. Hopper, Kurtycz, Ross, & Bonnie, 2015).

Tool modification

Any instances of tool modification were also recorded. Modifications of the tools were rare, and only ever observed in Group 4. In only 15.8% (3/19) of pounding bouts in Group 4 was a modification of the tool recorded. Modification occurred, for example, when a chimpanzee (JK) brought the first tool to the apparatus, which was a frond made of several smaller tools. JK then proceeded to remove the other fronds with his teeth, and used the middle (and largest) one to insert into the apparatus.

Food retrieval

Additionally, the weight of the potato before and after testing was recorded after all remnants of the potato were retrieved from the testing apparatus. The potatoes weighed between on average 171g (SD= 17.26) before testing, and 144g (SD=9.45) after testing.

Discussion

At least three individual naïve chimpanzees spontaneously reinnovated the stick pounding behavioral form in this study (one individual each in Groups one, two and four). In all three groups, the naïve chimpanzees used tools and the target pounding action to retrieve part of the bait at the bottom of our testing apparatus. All the chimpanzees that first reinnovated the behavior were captive-born and mother-reared, thus further ensuring that they were naïve to the target stick pounding behavioral form. These findings surpass the double-case ZLS standard (Bandini & Tennie, 2017, and see methods above) and demonstrate that stick pounding is a behavioral form that can be reinnovated by naive chimpanzees. Thus, this study adds to the growing body of evidence for the view that many chimpanzee tool-use behavioral forms are most likely reinnovated by naïve individuals, in which the frequency of reinnovation is mediated by low-fidelity forms of social learning (SMSR; Bandini & Tennie, 2017). Although three individuals reinnovated the behavior, and despite no significant difference in mere interaction time with the apparatus across groups, no individuals in Group three reinnovated the target stick pounding behavior.

Social tolerance

One possible explanation for the lack of reinnovation in Group three is that this group has been found to be less socially tolerant than the other three groups at Chimfunshi. Social tolerance has been suggested to foster tool-use behaviors in both human and non-human animals (Cultural Intelligence hypothesis; (Ashton, Ridley, Edwards, & Thornton, 2018; Forss, Willems, Call, & van Schaik, 2016; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; van Schaik & Burkart, 2011; Whiten & van Schaik, 2007). Models have demonstrated that 'high intelligence' (often equated with innovation) may be linked to social tolerance, with the most innovative groups also having the highest levels of social tolerance (van Schaik & Pradhan, 2003). This may be due to the fact that more highly tolerant groups allow for more individual exploration without interruptions, in turn fostering individual innovations and reinnovations (van Schaik & Pradhan, 2003). Cronin, Van Leeuwen, Vreeman, & Haun (2014) measured the levels of social tolerance in Groups one to four at Chimfunshi by examining both the naturally occurring social dynamics and experimentally testing their resource-sharing strategies. Whilst Groups one, two and four had similar levels of social tolerance, Group three demonstrated the least socially cohesive structure and a general tendency to be less tolerant and more avoidant of the other group members (Cronin, Van Leeuwen, Vreeman, & Haun; 2014). Therefore, it is possible that the individuals in Group three did not reinnovate stick pounding due to their relatively low levels of social tolerance. This interpretation fits with previous studies on the role of social tolerance in performance in novel behavior acquisition tasks (Ashton et al., 2018; Damerius et al., 2017; Forss et al., 2016; Lonsdorf, Ross, Linick, Milstein, & Melber, 2009; van Schaik, Deaner, & Merrill, 1999). However, experimental applications of the cultural intelligence hypothesis are still relatively rare and controversial, so whilst providing a potential explanation for Group three's behavior, other interpretations should also be explored. It should also be noted that cultural intelligence might be a misnomer if it turns out that tolerance merely increases individual exploration rate, and in turn unleashes innovative skills through individual means.

Additional influences

Whilst the ZLS approach predicts that all individuals are technically *capable* of reinnovating behaviors that are *within* their ZLS, this does not suggest that all individuals must always reinnovate the behavior, even when they are in the appropriate ecological circumstances. Other factors, such as genetics, developmental stage, levels of motivation, pre-existing techniques and even personality may play a role in whether some behaviors are reinnovated or not (e.g., see also Bandini & Tennie, 2018). Indeed, these external factors may hinder the emergence of behaviors even when opportunities for social learning are provided. For example, several studies on the reinnovation of behaviors in both captive and wild populations across species have reported that even after extensive exposure to knowledgeable demonstrators, the rest of the group does not always reliably acquire the target behavior (e.g. see: (Anderson, 1985; Antinucci & Visalberghi, 1986; Bandini & Tennie, 2018; Beck, n.d.; Biro, Haslam, & Rutz, 2013; Geissmann, 2009; Hayashi, Mizuno, & Matsuzawa, 2005; Hirata, Morimura, & Houki, 2009; Marshall-Pescini & Whiten, 2008; E. W. Menzel, Davenport, & Rogers, 1970; Nakamichi, 1999; Overington, Cauchard, Côté, & Lefebvre, 2011; Smith, Appleby, & Litchfield, 2012; Sumita, Kitahara-Frisch, & Norikoshi, 1985; Taylor, Hunt, Holzhaider, & Gray, 2007; Tebbich, Taborsky, Fessl, & Blomqvist, 2001; Tokida, Tanaka, Takefushi, & Hagiwara, 1994; Visalberghi, 1987; Visalberghi & Trinca, 1989; Yamamoto, Yamakoshi, Humle, & Matsuzawa, 2008; Zuberbühler, Gygax, Harley, & Kummer, 1996). Thus, the lack of reinnovation of stick pounding observed in some of the subjects tested in this study does not necessarily suggest that these individuals are incapable of expressing the behavior, but simply that they may have been limited in their reinnovation by some of the factors mentioned above.

Crucially, however, three individuals did reinnovate the target behavioral form without prior experience of the actions required for stick pounding. Thus, it is likely that this behavioral form is within chimpanzees' ZLS. The pounding behavioral form observed in this study is also similar to other wild chimpanzee behaviors, such as hive pounding (Sanz & Morgan, 2009) and tool-assisted hunting (Pruetz & Bertolani, 2007). Chimpanzees in Goualougo Triangle (Republic of Congo) adopt several different strategies to retrieve honey from hives, one of which is a pounding action, generally used to open the hive (Sanz & Morgan, 2009). The chimpanzees then use other stick tools to perform the other actions of the behavior (e.g., they will use a smaller stick to dip for the honey once they have pounded open the entrance; Sanz & Morgan, 2009), however the pounding action with a large stick to open the hive is similar to the behavioral form observed in this study. Similarly, the chimpanzee community of Fongoli, in Southeastern Senegal, hunt *Galago* using a large stick which they pound into tree cavities where the *Galago* are found (Pruetz et al., 2015). This pounding action is again similar to the behavior reinnovated in the current study. As the pounding action observed in this study is so similar to other wild behaviors, it is also possible that these other pounding behaviors can also be reinnovated, and do not strictly require high-fidelity social learning to emerge, as has been demonstrated for stick pounding here (however this remains to be tested for each of the behaviors). This does not, however, suggest that social learning (of a low-fidelity type) does not play a role in facilitating the individual expression of this behavior after the first innovation. As emphasized by Bandini & Tennie (2017), although social learning is not strictly required for a latent solution to be reinnovated (as demonstrated by the findings of this study, and several previous work into the ZLS of different species: Allritz et al., 2013; Bandini & Tennie, 2017; Menzel et al., 2013; Neadle et al., 2017; Reindl et al., 2016; Tennie et al., 2008), opportunities for social learning greatly facilitate the release/expression of the behavior in naïve individuals.

Indeed it seems likely that individual and social learning are based on the same associated mechanisms (Heyes, 2012; Reader, Hager, & Laland, 2011). Great ape cultures may be catalyzed and sustained by an interplay of individual learning and non-copying forms of social learning – they are minimal, or soft, cultures (Neadle et al., 2017).

Acknowledgments

The authors, EB & CT, are very grateful to Chimfunshi Wildlife Orphanage Trust and the members of the CRAB research board for approving the study, and for helpful suggestions on the methodology. The authors also thank Innocent Mulenga and Thalita Calvi for facilitating the research, and Goodson Muletele, Felix Chinyama, Patrick Mwika, Mumba Kawele and Joseph Kasongo for all their help during testing. EB is also very grateful to Linda Oña, Ruth

Sonnwebber, Catherine Crockford and Katja Liebal for their invaluable advice and support during testing. EB is also grateful to Eva Reindl and Damien Neadle for their support and to Margherita Bandini for reliability coding.

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Supporting information

Table S1: Demographic information on the subjects included in this study (Courtesy of *T.Calvi*)

Group	**Name**	**Sex**	**Approx.DoB**	**Origin**	**Rearing**
1	BJ	Female	07/02/2007	Captive	Mother
1	Bob	Male	04/18/2001	Captive	Mother
1	Booboo	Male	01/01/1982	Wild	Hand
1	Brenda	Female	08/12/1995	Captive	Mother
1	Chrissy	Female	12/14/2006	Captive	Mother
1	Genny	Female	02/19/1997	Captive	Mother
1	Gerald	Male	04/14/2002	Captive	Mother
1	Girly	Female	01/01/1982	Wild	Hand
1	Gonzaga	Male	04/05/2008	Captive	Mother
1	Ilse	Female	05/07/2002	Captive	Mother
1	Ian	Male	01/25/2015	Captive	Mother
1	Ingrid	Female	01/10/1991	Captive	Mother
1	Innocentia	Female	01/10/2007	Captive	Mother
1	Ireen	Female	11/02/2011	Captive	Mother
1	Josephine	Female	01/01/1983	Wild	Hand
1	Pal	Male	01/01/1981	Wild	Hand
1	Rachel	Female	06/28/2012	Captive	Mother
1	Regina	Female	12/21/2006	Captive	Mother
1	Renata	Female	01/10/1997	Captive	Mother
1	Rita	Female	01/01/1983	Wild	Hand
1	Rusty	Male	10/14/2006	Captive	Mother
1	Tara	Male	01/01/1983	Wild	Hand
1	Tobar	Male	01/01/1982	Wild	Hand
2	Carol	Female	12/06/1996	Captive	Mother
2	Charity	Female	08/13/2007	Captive	Mother
2	Chitalu	Female	01/01/2014	Captive	Mother

2	Claire	Female	05/15/2002	Captive	Mother
2	Coco	Female	01/01/1985	Wild	Hand
2	Daisy	Female	10/17/2004	Captive	Mother
2	Danny	Male	04/23/2012	Captive	Mother
2	Darwin	Male	03/27/2007	Captive	Mother
2	David	Male	09/12/2001	Captive	Mother
2	Debbie	Female	12/11/2015	Captive	Mother
2	Diana	Female	01/01/1991	Wild	Hand
2	Diz	Female	10/12/2007	Captive	Mother
2	Dolly	Female	10/28/1996	Captive	Mother
2	Donna	Female	01/01/1984	Wild	Hand
2	Dora	Female	01/01/1989	Wild	Hand
2	Doug	Male	01/19/2003	Captive	Mother
2	Little Jack	Male	03/22/2012	Captive	Mother
2	Little Jane	Female	01/01/1985	Wild	Mother
2	Little Jenkins	Male	02/19/2007	Captive	Mother
2	Little Jones	Male	09/16/2010	Captive	Mother
2	Little Judy	Female	05/16/1995	Captive	Mother
2	Long John	Male	11/07/2006	Captive	Mother
2	Maggie	Female	01/01/1986	Wild	Mother
2	Martin	Male	04/14/2012	Captive	Mother
2	Mary	Female	09/04/2005	Captive	Mother
2	Mavis	Female	01/10/2013	Captive	Mother
2	Max	Male	08/29/2006	Captive	Mother
2	Maxine	Female	05/19/2001	Captive	Mother
2	May	Female	12/20/2012	Captive	Mother
2	Masya	Female	01/01/1991	Wild	Hand
2	Mikey	Male	01/01/1988	Wild	Hand
2	Misha	Female	01/01/1988	Wild	Hand
2	Moyo	Male	08/15/2007	Captive	Mother
2	Nikkie	Female	11/12/1997	Captive	Mother

2	Nina	Female	03/21/2003	Captive	Mother
2	Noel	Female	01/01/1977	Wild	Hand
2	Pan	Male	01/01/1989	Wild	Hand
2	Pippa	Female	01/01/1989	Wild	Hand
2	Taylor	Female	09/16/2004	Captive	Mother
2	Tess	Female	08/26/1998	Captive	Mother
2	Tina	Female	05/10/2015	Captive	Mother
2	Tilly	Female	01/24/2001	Captive	Mother
2	Tom	Male	02/25/2015	Captive	Mother
2	Toni	Female	01/23/2003	Captive	Mother
2	Trixie	Female	01/01/1990	Wild-born	Hand-raised
2	Violet	Female	01/01/1991	Wild	Hand
2	Vis	Male	04/05/2004	Captive	Mother
2	Zsabu	Male	01/01/1990	Wild	Hand
3	Barbie	Female	01/01/1995	Wild	Hand
3	Brent	Female	01/03/2014	Captive	Mother
3	Brian	Male	01/01/1994	Wild	Hand
3	Bruce	Male	12/21/2009	Captive	Mother
3	Buffy	Female	01/01/1985	Wild	Hand
3	Bussy	Male	06/23/2004	Captive	Mother
3	Clement	Male	01/01/1993	Wild	Hand
3	E.T	Female	01/01/1995	Wild	Hand
3	Lods	Female	06/01/2010	Captive	Mother
3	Roxy	Female	01/01/1995	Wild	Hand
4	Bobby	Male	01/01/1993	Wild	Hand
4	Commander	Male	01/01/2001	Wild	Mother
4	Jack	Male	04/16/2008	Captive	Mother
4	Jewel	Male	05/19/2013	Captive	Hand

4	Kambo	Female	01/01/1996	Wild	Hand
4	Kathy	Female	01/01/1999	Wild	Mother
4	Kenny	Male	05/25/2011	Captive	Mother
4	Kit	Male	01/12/2005	Captive	Mother
4	Miracle	Female	07/13/2000	Captive	Hand
4	Nicky	Male	01/01/1991	Wild	Mother
4	Sinkie	Male	01/01/1994	Wild	Hand