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Original Article

Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture

Gillian L. Vale [a,b], Sarah J. Davis [a,b], Susan P. Lambeth [b], Steven J. Schapiro [b], Andrew Whiten [a,*]

[a] *Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology & Neuroscience, University of St Andrews, United Kingdom*

[b] *National Center for Chimpanzee Care, Michale E. Keeling Center for Comparative Medicine and Research, The University of Texas MD Anderson Cancer Center, United States*

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ABSTRACT

Cumulative culture underpins humanity's enormous success as a species. Claims that other animals are incapable of cultural ratcheting are prevalent, but are founded on just a handful of empirical studies. Whether cumulative culture is unique to humans thus remains a controversial and understudied question that has far-reaching implications for our understanding of the evolution of this phenomenon. We investigated whether one of human's two closest living primate relatives, chimpanzees, are capable of a degree of cultural ratcheting by exposing captive populations to a novel juice extraction task. We found that groups ($N = 3$) seeded with a model trained to perform a tool modification that built upon simpler, unmodified tool use developed the seeded tool method that allowed greater juice returns than achieved by groups not exposed to a trained model (non-seeded controls; $N = 3$). One non-seeded group also discovered the behavioral sequence, either by coupling asocial and social learning or by repeated invention. This behavioral sequence was found to be beyond what an additional control sample of chimpanzees ($N = 1$ group) could discover for themselves without a competent model and lacking experience with simpler, unmodified tool behaviors. Five chimpanzees tested individually with no social information, but with experience of simple unmodified tool use, invented part, but not all, of the behavioral sequence. Our findings indicate that (i) social learning facilitated the propagation of the model-demonstrated tool modification technique, (ii) experience with simple tool behaviors may facilitate individual discovery of more complex tool manipulations, and (iii) a subset of individuals were capable of learning relatively complex behaviors either by learning asocially and socially or by repeated invention over time. That chimpanzees learn increasingly complex behaviors through social and asocial learning suggests that humans' extraordinary ability to do so was built on such prior foundations.

1. Introduction

Cultural technologies have evolved across generations in human societies by the gradual buildup of modifications to, and the recombination of, existing knowledge, such that (1) artefact continuity occurs between pre-existing and 'new' artifacts, and (2) artefact complexity moves beyond what an individual can invent individually in the absence of a cultural history (Basalla, 1988; Dean, Vale, Laland, Flynn, & Kendal, 2013). This process of cumulative culture – specifically the successive addition or blending of new innovations and old, and their social spread within populations and across generations – underpins humanity's enormous success as a species and has allowed us to adapt to, inhabit, and modify (via cultural niche construction) environments we are not always biologically prepared for (Henrich, 2015; Henrich & McElreath, 2003; Odling-Smee, Laland, & Feldman, 2003; Pagel, 2012; Richerson & Boyd, 2005; Tomasello, 1999). Experimental investigations with humans have begun to shed light on how cultural change occurs over time and the factors that underpin it (e.g., Caldwell & Millen, 2010a, 2010b; Caldwell, Schillinger, Evans, & Hopper, 2012; Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Derex, Beugin, Godelle, & Raymond, 2013; Derex, Godelle, & Raymond, 2012; Zwirner & Thornton, 2015). For example, we now know that large population sizes can protect against cultural loss, enabling high levels of cultural complexity to be maintained (Derex et al., 2013), and process-copying (e.g. imitation), in many cases, can lead to superior skill acquisition than product-copying (e.g. emulation) or individual asocial learning (Derex et al., 2012; although see Caldwell & Millen, 2009; Caldwell et al., 2012). These studies have provided important insights into how human culture may have evolved and diversified by identifying particular learning mechanisms and social structures that promote the accumulation of increasingly complex cultural traits. Given the significance of cumulative culture to humanity, a major research question at an early stage of investigation is whether, and to what extent, other animals show any ratcheting in their cultural complexity.

* Corresponding author at: School of Psychology & Neuroscience, University of St Andrews, KY16 9JP, UK.
E-mail address: aw2@st-andrews.ac.uk (A. Whiten).

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The study of chimpanzees, in particular, is crucial to our understanding of the processes that have shaped hominins since the time of our last common ancestor. When it comes to the evolution of culture, numerous parallels have been drawn between chimpanzees and humans (McGrew, 1992, 2004; Boesch & Tomasello, 1998; Whiten, Hinde, Stringer, & Laland, 2011, Whiten, 2017), making them an important study species in this regard. Chimpanzees, for example, like humans, display multiple-tradition cultural repertoires that vary by geographic region (Whiten & van Schaik, 2007), and complex behaviors in the wild (e.g., complex tool sets and composite tools: Boesch, 2012; Carvalho, Biro, McGrew, & Matsuzawa, 2009; Sanz & Morgan, 2007; Sanz, Call, & Morgan, 2009; Sanz, Schoning, & Morgan, 2009) that outstrip other non-human species. Parallels have also been drawn between the social learning processes that underpin human and chimpanzee cultures. In particular, chimpanzees and humans will both engage in emulative learning, recreating cultural products from action end-products, allowing small trait modifications to occur in relatively simple tasks (Caldwell & Millen, 2009). Yet important species differences also exist, with humans often learning by imitating process or action information, a capability that appears more rarely or with less fidelity in chimpanzees (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). While research documenting chimpanzee cultures and the social learning processes that underpin them has exploded in recent years (reviewed in Whiten, 2017; Vale, Carr, Dean, & Kendal, 2017), the question of whether chimpanzee cultures become more complex is comparatively understudied.

Our study investigated whether groups of captive chimpanzees adopt a tool modification behavior that is built upon simpler tool behavioral foundations. Documentation of the use of tool sets and composite tools in wild chimpanzees (Boesch, 2012; Sanz & Morgan, 2007; Sanz, Call et al., 2009; Sanz, Schoning et al., 2009) is suggestive of some degree of cultural modification. Brush-tipped probes, used for termite fishing, provide one interesting case. Here, chimpanzees of the Goualougo Triangle deliberately modify herb stem probes by chewing one end to create a new tool surface that increases the tool efficiency in gathering termites, relative to unmodified tools (Sanz, Call et al., 2009). Thus, we see a modification, in terms of complexity and efficiency, of an existing cultural behavior. However, investigation with captive chimpanzees concluded that cumulative learning of increasingly complex skills may be absent in chimpanzees (Dean et al., 2012; Marshall-Pescini & Whiten, 2008) or limited to small modifications in behavioral efficiency that may easily be invented by a few adept individuals (Yamamoto, Humle, & Tanaka, 2013). In Dean et al. (2012) groups of capuchins, chimpanzees, and nursery school children were presented with a puzzle box containing three, increasingly difficult, task solutions. The first solution simply required participants to push open a door to reveal a low-value reward; the second solution required the depression of a button before pushing the door even further revealing a medium-value reward; and lastly, the most complex action was completed by turning a dial and pushing the door even further to reveal a high-value food reward (but note that these solutions had to occur in this sequence). Social demonstrations of the complex behavior did not greatly enhance the chimpanzees or capuchins' performances, whereas children progressed through the complex task solution. The authors concluded that the nonhuman primates of this study lacked cumulative learning, contrasting with the children who learned increasingly more complex solutions (albeit, note that this study lacked an asocial control condition and thus it is unknown whether children could have progressed through the three solutions independently). Given that the variability in the complexity of wild chimpanzee tool use and manufacture hints at a possibility of some cumulative learning, it is possible that the absence of evidence in controlled settings may be an artefact of failure to provide the right task conditions for its expression. In the wild, chimpanzees manufacture tools by detaching sticks and leaves to create tools of different lengths and diameter for specific task uses (Boesch & Boesch, 1990). Accordingly, and in contrast to previous culture studies that have required the manipulation of multiple defenses to access increasingly desirable rewards (e.g. opening doors and depressing buttons: Dean et al., 2012; Marshall-Pescini & Whiten, 2008), here we presented chimpanzees with a tool modification task that required the detachment of tool material. Specifically, we examined whether social learning from a trained model on a tool detachment behavior promotes the acquisition of this behavior relative to (1) groups of chimpanzees not seeded with such a model and (2) chimpanzees, tested individually, that received no social information at all (asocial controls); as well as (3) whether complex behaviors build on simpler foundations.

Previous investigation has shown that chimpanzees, provisioned with straws and a container of juice, may switch from a relatively inefficient "dip" technique to a more efficient, but readily invented, "suck" technique, either through social learning or independently through trial and error (Yamamoto et al., 2013; see also Manrique & Call, 2011 and Manrique, Gross, & Call, 2010 for similar cases of apes switching from dipping behaviors to suck techniques). Building on this, we presented six groups of chimpanzees with a large juice container and multiple tools affording dipping and/or suck behaviors, with the addition that a modification of removing a stop valve attached to one end of a tube meant that it could then be used as a 'straw' – i.e. a tube for sucking juice. Removal of the stop valve required chimpanzees to turn ('unscrew') the valve. Modification and use of this tool allowed efficient juice gain relative to tools that did not require modification. As our chimpanzee population shows great difficulty in socially learning turn behaviors (Dean et al., 2012), the behavioral steps of valve removal and subsequent use of the modified straw tool were considered a relatively complex behavior for our sample. Chimpanzees could alternatively use comparatively simple behaviors such as 'dipping' their hands into the juice, or using unmodified tools on the task. There were three study phases: (1) 10 h of open diffusion during which three groups were exposed to a model trained to perform this tool modification before using the tool as a straw (hereafter referred to as a behavioral sequence of 'unscrew and suck'), and three groups were not (remaining non-seeded and all group members were task naive); (2) groups subsequently received a further 10 h of task exposure but this time the three seeded groups were exposed to 10 h of video demonstrations of the unscrew and suck behavioral sequence prior to, and during, open diffusion, while the three non-seeded groups received no such video exposure of the tool modification; (3) groups subsequently received an additional 10 h of exposure to a modified version of the task that minimized the use of simpler tool behaviors. Phase 3 allowed an assessment of whether chimpanzees would be motivated to learn the unscrew and suck behaviors when other task solutions were unavailable to them. This is of interest given that one driver of behavioral modification is environmental fluctuation or risk, which may encourage behavioral change when past behaviors become inefficient or redundant (Buchanan, O'Brien, & Collard, 2015; Collard, Buchanan, & O'Brien, 2013; Collard, Kemery, & Banks, 2005; Smaldino & Richerson, 2013). Behavioral change in nonhuman primates who otherwise show conservative behavior (Marshall-Pescini & Whiten, 2008) has been found to be facilitated as past behaviors become obsolete (Lehner et al., 2011; Manrique, Volter, & Call, 2013) or difficult to perform (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016). Again, during this phase, the three seeded groups had access to a trained model and the non-seeded groups did not. Importantly, we compared group performances to those of asocial controls that had no access to social information. This allowed testing of whether the unscrew and suck behavior could be independently learned by invention alone. This is crucial to the study of cumulative culture in which behavioral complexity must supersede what individual innovative abilities can achieve.

2. Method

2.1. Participants

Out of the fifty-six chimpanzees (M age = 32.04, 36 female) who participated in this investigation, 21 chimpanzees were in the seeded