Behavioral Ecology and Sociobiology (2019) 73: 2
https://doi.org/10.1007/s00265-018-2610-7

REVIEW

Teaching and curiosity: sequential drivers of cumulative cultural evolution in the hominin lineage

Carel P. van Schaik[1] · Gauri R. Pradhan[2] · Claudio Tennie[3]

Received: 17 March 2018 / Revised: 21 August 2018 / Accepted: 12 November 2018 / Published online: 18 January 2019

Abstract

Many animals, and in particular great apes, show evidence of culture, in the sense of having multiple innovations in multiple domains whose frequencies are influenced by social learning. But only humans show strong evidence of complex, cumulative culture, which is the product of copying and the resulting effect of cumulative cultural evolution. The reasons for this increase in complexity have recently become the subject of extensive debate. Here, we examine these reasons, relying on both comparative and paleoarcheological data. The currently best-supported inference is that culture began to be truly cumulative (and so, outside the primate range) around 500,000 years ago. We suggest that the best explanation for its onset is the emergence of verbal teaching, which not only requires language and thus probably coevolved with the latter's evolution but also reflects the overall increase in proactive cooperation due to extensive allomaternal care. A subsequent steep increase in cumulative culture, roughly 75 ka, may reflect the rise of active novelty seeking (curiosity), which led to a dramatic range expansion and steep increase in the diversity and complexity of material culture. A final, and continuing, period of acceleration began with the Neolithic (agricultural) revolution.

Keywords Cumulative culture · Stone tools · Out of Africa · Imitation · Verbal instruction · Teaching

Introduction

Many animals show evidence of social learning, some show traditions, and a subset of these show multiple traditions in a range of domains, ranging from subsistence to comfort behaviors and communication, which also tend to be geographically variable (Whiten et al. 2017). Whiten and van Schaik (2007) proposed to reserve the term culture for the latter level of variation. These cultures generally consist of innovations that, once arisen, increase in frequencies via social learning until stopped by a dispersal barrier, which helps create geographic variation. However, variation may in some cases also be helped by social pressure to be similar to others (e.g., Luncz and Boesch 2014; van de Waal et al. 2017).

Despite the ubiquity of animal cultures, there is very little evidence (apart from the vocal domain, such as some bird and whale songs) for such cultures to be cumulative. A cumulative innovation is one that has a history of repeated copying plus modification of earlier forms, usually by addition (called "ratcheting" by Tomasello et al. (1993)). The paradigmatic case of a cumulative cultural effect is when an individual adds a technique used in a very different context or an entirely novel one to an existing (copied) one, and integrates the two functionally into a new technique. Cumulative culture is therefore culture that may become more complex over time as a result of the cumulation of modifications (we use this neologism to distinguish it from the more general accumulation, which refers to increased cultural diversity in the sense of multiple traits: Dean et al. 2014). Some primate technology consists of several subparts and has thus been proposed to be cumulative (e.g., Sanz and Morgan 2007). Even so, while it is

Communicated by S. Shultz

This article is a contribution to the Topical Collection Social complexity: patterns, processes, and evolution – Guest Editors: Peter Kappeler, Susanne Shultz, Tim Clutton-Brock, and Dieter Lukas

✉ Carel P. van Schaik
vschaik@aim.uzh.ch

[1] Department of Anthropology, University of Zurich, 8057 Zurich, Switzerland

[2] Department of Physics, University of South Florida, Tampa, FL 33620-7100, USA

[3] Department for Early Prehistory and Quaternary Ecology, University of Tübingen, 72070 Tübingen, Germany

cumulative in that we see compound innovations, it is as yet unclear whether it meets another frequently used definition of cumulative culture (Boyd and Richerson 1996), i.e., that a naive individual could not independently innovate the more complex variants within its lifetime. In the following, we will assume that chimpanzees, and other non-human great apes, do not have cumulative culture in this stronger sense (for a more in-depth review of the matter, see Tennie et al. (2019)).

That human culture is cumulative and thus complex for both the material and institutional components is in fact one of the key differences between human and non-human cultures. Thus, most of us use technology every day that we could not have invented from scratch and that are the incremental product of long process of cumulating modifications. While the study of cultural evolution in humans has become a thriving enterprise (Mesoudi 2016), explanations for the origin of this complexity remain elusive. The most popular idea is that cumulative culture became possible once humans evolved sophisticated imitation abilities and also special forms of teaching (Galef 1992; Tomasello 1999; Tennie et al. 2009; Lewis and Laland 2012), i.e., when they were able to pass on copies. However, when and why this happened during hominin evolution remains unresolved, despite increasing interest by behavioral biologists and psychologists (e.g., Dean et al. 2014; Kempe et al. 2014; van Schaik 2016; Laland 2017; Tennie et al. 2017).

The first hurdle is that the moment hominin technology became based on copying was not specified. By default, there is a widespread (though rarely made explicit) assumption that the smoking gun of copying can be seen in the origin of any (and thus lithic) technology in the record (Foley and Lahr 2003), although this assumption chose to treat as irrelevant obvious cases of tool use in the animal kingdom not usually seen as a product of cumulative culture (beaver dams, bird nests, etc.). And so, cumulative culture was often, and thus tellingly implicitly, assumed to have started with the onset of the Oldowan at 2.6 Ma or perhaps even with what has been called the Lomekwian at 3.3 Ma (Harmand et al. 2015). This early start has rarely been questioned, but counterarguments are on the rise. For example, Tennie et al. (2016a, b, 2017), partly drawing on great ape observations, suggested a far more recent origin of cumulative technology (at the earliest in the Acheulean, but possibly later). We will accept this assessment here, but also delineate two subsequent periods of accelerated increases in complexity and evaluate hypotheses to explain them.

At the current state of knowledge, any conclusions will have to remain tentative. Nonetheless, the value of this approach is that integrating information from living animals encourages us to consider individual, social, and demographic variables that are not always taken into account.

The origin and rise of cumulative culture

In this section, we examine the timing of the first clear signs of cumulative cultural evolution during hominin evolution (and thus of cultural complexity beyond the range of extant great apes) and of subsequent periods of apparent acceleration in the cumulation process.

Wild great apes produce innovations via others through social learning mechanisms that largely amount to socially mediated serial reinnovations (Bandini and Tennie 2017), and so innovations, even if occasionally consisting of *several* steps, nevertheless remain within the species' zone of latent solutions (Tennie et al. 2009), i.e., the set of innovations that individuals of the species can in principle independently invent during their lifetime. As a result, cultural repertoires of populations may come to differ (in the interplay between environmental and genetic differences, together with socially mediated serial reinnovations). However, while they may increase in diversity (accumulation), they tend not to increase in complexity (cumulation): there is no clear ratcheting (Tomasello 1999; Boyd and Richerson 1996).

Tennie et al. (2016a, 2017) argued that our ancestors (hominins) engaged in the same thing (socially mediated serial reinnovation) for most of their existence. The record of our early stone-tool making ancestors reveals hundreds of thousands of years of stasis (variance exists, but around a mean) in both the Oldowan and Acheulean industries, which is unlikely if they really had represented cumulative culture (i.e., the passing on of actual copies of variants which automatically would have led to variants outside the relevant species' respective zones of latent solutions - at least if there were any degrees of cultural freedom). This does not require that the ability to produce these technologies was genetically based in the sense of being developmentally strongly canalized (a view taken by Corbey et al. 2016), but that it was more likely cultural in the same sense that extant primate technology is, relying on some form of social learning/mediation and socially induced individual practice (Schuppli et al. 2016). But if the practice part receives no social inputs that provide guidance over and above what the individual will likely converge on, and if no (or not enough or too rarely) details are copied, i.e., if there is neither teaching nor imitation able to lead to *copies*, there will be a limit on the level of complexity that is achieved. Though of course, depending on factors such as a species' cognition and anatomy, concrete goals, raw material selectivity, ecological dependence on stone tools, life history (esp. maximum age), and perhaps most importantly, individual practice, the results would always show variability. But they would lack (as they do) a *fast* direction (the latter the hallmark of cumulative culture; compare Kempe et al. (2012)).

With the origin of the prepared core or mode 3 technology (grading into the Middle Stone Age), we see the emergence of even more complex tools, and with it a supposed leap in efficiency (cf. Muller and Clarkson 2016). We place this origin at ca. 500 ka because both later *Homo heidelbergensis* (a.k.a. archaic *sapiens*) and early *Homo neanderthalensis* show many similarities in technology and other aspects of culture (in the sense in which we use it here), which implies that their common ancestors around that time had similar capabilities. The technological changes included making stone points from prepared cores, and then hafting them onto wooden handles using adhesive peck (which also needs preparation) and special binding materials (Haidle et al. 2015). This complexity and interdependency at least *suggests* that new processes were at work. These tools might therefore have been outside the zone of latent solutions of the species concerned, *Homo heidelbergensis* (Mithen 1996), since it would (at least with current knowledge) seem unlikely that even a modern human could *independently* rediscover this whole interdependent sequence from scratch. Following this logic, many subsequent technologies should have been even more likely cumulative (i.e., as long as they contained even longer interdependent sequences). While this conclusion is preliminary, so far, no broadly accepted explanation has been offered for the origin of mode 3 technology, which happened when the species had reached a brain size of 1000–1200 cm^3, over twice that of the extant great apes.

Obviously, this does not mean that the cumulation process was smooth. Paleolithic archeologists have long recognized the clear uptick in complexity and diversity during the Upper Paleolithic (McBrearty and Brooks 2000; Klein 2008), which is also widely held responsible for the demographic expansion known as Out-of-Africa, which took off after ca. 75 ka and led to a massive population increase, largely through the colonization of all continents but Antarctica (Hoffecker and Hoffecker 2017), as well as increased technological complexity (Klein 2008). To Harcourt (2015), this rapid and sustained colonization of unfamiliar regions implies a sudden, dramatic leap in true *curiosity* in the form of novelty seeking and extensive exploration. Some have even claimed that this process left a genetic footprint (Matthews and Butler 2011; Gören 2016; but see Campbell and Barone 2012).

The last major increase in the rate of technological ratcheting began after the origin of sedentary life and increasingly intensive agriculture at ca. 10 ka (the Neolithic Revolution). Very soon after the Neolithic, metallurgy arose, followed by an unprecedented rise in complexity of technology and institutions. It is broadly agreed that this steep increase in the rate of cultural evolution was due to the origin of sedentism and the development of ever more efficient agricultural techniques (Scott 2017), including specialization, accompanied by a veritable population explosion and dramatic changes in social organization (Nolan and Lenski 2009; Diamond 2012). We will therefore not pursue the explanations for this last event, but focus on the first two.

Modeling cumulative culture

A variety of factors may favor cumulative cultural evolution. How are we to tie its origin and subsequent changes in its pace to the most relevant variables? Culture obviously relies on innovation and subsequent increases in the frequencies of these innovations in the form of socially mediated serial reinnovation or copying. In cumulative culture, the complexity of a particular innovation in a population is a function of the balance of cumulation through additional innovation or immigration and loss of complexity or even extinction through failure of transmission.

Theoretical attempts to understand this cumulation process follow two broad approaches. The first approach focuses on the fidelity of transmission. Lewis and Laland (2012) exemplify this approach. Pradhan et al. (2012) are similar, but explicitly derive their model from the observed natural history of great ape technology, and we will expand on it here. The model incorporates innovation rates (ε) and transmission rates, with the latter a function of the individual's ability to learn socially (α) and the number of tolerant experts and their involvement (κ). In addition, it takes into account population size (N) and life history (mortality rates and the duration of immaturity and thus learning). The goal is to think systematically about how changes in the values of the relevant variables will affect the degree of cumulation, without changes in brain size and thus intrinsic cognitive ability. In the following account, we will use previously unpublished results from this model to illustrate some conclusions (see Pradhan et al. (2012), for full details of the model).

In the Pradhan et al. (2012) model, innovation is favored by larger population sizes and exchange between populations, and by greater individual innovativeness (intelligence, curiosity). Social transmission is favored by longer contact between generations, by population size, and by social network structure (tolerance produces a greater number of role models for naïve learners). Social transmission also depends on features of the learners, especially their ability to actually pick up new innovations, i.e., by their ability to actually copy (e.g., to imitate actions and action sequences that are novel to them) and by features of the experts, in particular the degree to which they are actively aiming to pass on their skills (their levels of teaching). Finally, social transmission depends on life history, in the form of mean lifespan, and thus opportunities for social transmission of innovations (each individual is born naïve), and the duration of the immature time window of social learning.

The second approach—was introduced by Henrich (2004). The model, dubbed the treadmill model, focusses on the fate of a particular skill, which is transmitted to the next generation, whose members show a distribution of skill levels around the role model's skill level. Learners are assumed to focus on the most skilled individuals for learning, but commit errors when learning, such that the mean skill level can decrease.

However, there is variance in the error, which is positively linked to population size, and presumably also to overall complexity (see Andersson and Read 2016). Thus, if population size is large enough, the most skilled individuals in the next generation end up being more skilled than their role models, and skill level will increase. Notice that in these models, which concentrate on the most complex skills, there is no teaching or other processes guaranteeing fidelity of transmission. However, there is a direct link between demography and skill level: that latter goes down in small populations, up in large ones. While we focus on the fidelity approach, we will bring in comparisons with the second where relevant.

Explaining the origin and elaboration of human cumulative culture

We start with the variables affecting innovation and then turn to those affecting social transmission.

Innovation: population size and social networks

Population size can affect innovation in an entirely passive way: if each individual has a particular probability of making an innovation (ε), then in a larger population (defined as a collection of individuals that are in contact), more innovations will arise per unit time ($N \times \varepsilon$). However, in a species capable of true social transmission of skill (copying) and where individuals are in contact, once innovations arise in a given population, they can then be passed on and so be retained. This leads to a higher level of cultural complexity (namely when innovations build upon earlier innovations, i.e., the ratchet effect). Figure 1 illustrates this for the model of Pradhan et al. (2012), where we imposed a maximum level of complexity of three steps of cumulation or ratcheting. Larger population size greatly speeds up the technological cumulation process, not just by favoring the emergence of new innovations but above all by improved retention. Even so, for each set of parameter values, a maximum complexity will eventually be reached, due to time constraints on learning during development. Lewis and Laland (2012) reach the same conclusion in their unbounded model, stressing that fidelity of transmission played a greater role than innovation. However, they also show that the kind of innovation with the strongest effect is trait combination, a source of innovation where two existing techniques are combined into a novel combination. Finally, as we noted above, in treadmill models (Henrich 2004; Powell et al. 2009), cumulative evolution is directly proportional to population size in both directions. Thus, larger populations should have more complex cultures, with no upper limit.

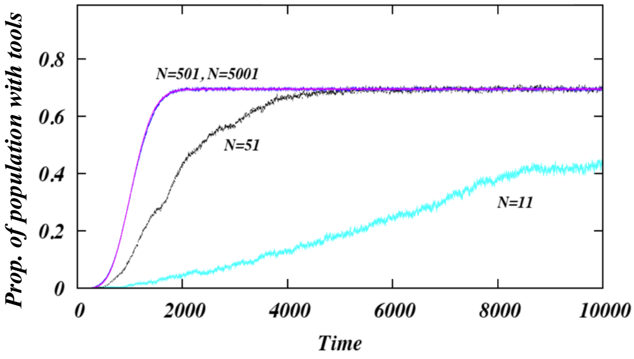

Fig. 1 Effect of population size (N) on time taken to reach complex technology (here constrained to maximum level 3) when starting from scratch. Detailed methods provided in Pradhan et al. (2012)

Perhaps surprisingly, the ethnographic evidence for a strong effect of demography is mixed (e.g., Collard et al. 2013; Andersson and Read 2016; Vaesen et al. 2016), and instead suggests that resource pressure or environmental risk may better predict innovation repertoires among foragers. One possible reason is that in a given habitat, with a particular constellation of ecological challenges, even a smaller population may eventually reach the equilibrium technology level if there is enough time and no catastrophes, especially when nomadism imposes strict limits on material culture. A recent study (Fogarty and Creanza 2017) strongly supports this interpretation, both empirically and theoretically.

This implies that demography need not have been a causal factor while all humans were still fully nomadic foragers, i.e., until well into the Upper Paleolithic. Indeed, both archeology (Klein and Steele 2013) and genetics (Li and Durbin 2011) suggest that effective population sizes were quite modest around 75 ka when humans had already developed effective new technology and began to move far out of Africa (Klein 2008). Thus, there is little empirical evidence for the proposition that population size can affect cultural evolution directly when lucky innovations start a positive feedback loop between innovation and population (cf. Laland 2017), although all approaches predict it.

A more indirect effect of demography may therefore have been more instrumental. Long-distance contact between groups can create a much larger social network and thus allow for rare innovations to spread far and wide (Henrich 2004; Powell et al. 2009). Both the number and the size of subpopulations as well as the rate of migration between them affect the cumulation process (Powell et al. 2009). We can use the Pradhan et al. (2012) model to illustrate the powerful effect of cultural diffusion. We can once a year randomly pick a single individual in a population of 500 and increase its technology level by 1. Figure 2 shows how this can massively enhance a population's technological complexity. Thus, cultural diffusion through contact can easily swamp any effects of local population size, in both directions. Such contact with other groups has been shown to be important among extant nomadic foragers, whose visits to other communities allowed them to observe hundreds of experts over a lifetime (Hill et al. 2014).

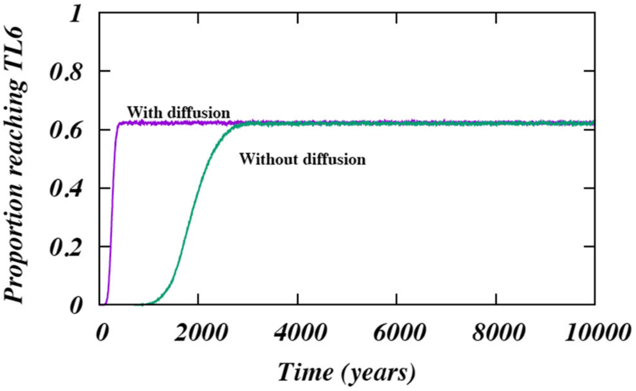

Fig. 2 Effect of diffusion on ratcheting. Diffusion was simulated by increasing a single randomly picked individual's technology level by 1 in any given year, in a population of 500 individuals, constraining the maximum technology level at 6 (where $\kappa = 2$, $\alpha = 0.4$; for details, see Pradhan et al. (2012))

But archeologically, the first unambiguous evidence of long-distance trade and thus such non-hostile contacts between societies is at 200 ka (Blegen 2017), well after the time suggested here as the appearance of the first truly cumulative technology. However, a possible origin of full-fledged language (Dediu and Levinson 2013) at around 500 ka may have facilitated non-hostile contact between neighboring communities and so facilitated cultural diffusion. Thus, indirect demographic (social network) effects may well have been stronger than actual community sizes or population densities.

Innovation: curiosity

In addition to external factors such as population size and contact, intrinsic factors may also affect innovation rate. Across species, various studies have found a correlation between relative brain size and the frequency of observed innovations (Reader and Laland 2002). However, this correlation need not reflect a directly causal effect of brain size on innovation tendency, because there may be a major effect of the retention of innovations helped by social learning (van Schaik et al. 2016), which is also far more likely in more encephalized species (Reader and Laland 2002). Moreover, the best evidence concerns survival upon release into novel regions, and thus need not reflect innovativeness under normal conditions (e.g., Sol et al. 2008).

We raise this more complex interpretation because wild apes show a striking lack of curiosity (novelty seeking plus extensive exploration). Thus, young orangutans are selectively curious, exploring items novel to them only after trusted older experts, initially always their mothers, have handled them (Schuppli et al. 2016). Such targeted exploration is both effective and safe. All wild orangutans strongly avoid any novel items placed in their environments (Forss et al. 2015), as do many other species (Forss et al. 2017). Gruber et al. (2009) showed experimentally that exploration of problem-solving opportunities is also minimal: adult chimpanzees in the wild do not recognize obvious alternative solutions to a problem (obtaining honey from a tree hole), even when the solution is observed and even if the solution is within reach of individuals that have not had the individual experience to develop functional fixedness (cf. Hanus et al. 2011). Overall, then, the most encephalized species in the wild stand out more by their conservatism than their innovativeness. We therefore suspect that increased brain size need not directly translate into clearly higher innovation rates in hominoids, and thus hominins.

Accordingly, despite decades of intensive field study of great apes, there is indeed remarkably little evidence for the origin of novel innovations, let alone for such that subsequently increase in frequency (e.g., Yamamoto et al. 2008). The natural examples that are well documented are minor variants on existing themes, such as moss sponging rather than the already present leaf sponging (Hobaiter et al. 2014), which may not even be cognitively distinct to the users. Stone tool use, the only known modern primate technology that left directly recognizable debris in the archeological record (plant material does not last long in these conditions), has been shown to be old. For instance, Mercader et al. (2007) showed that nut cracking by chimpanzees using stone tools is at least 4300 years old, and potentially much older, and has fundamentally remained the same since that time (Dean et al. 2014).

Wild apes thus show a remarkable conservatism and lack of curiosity (e.g., van Schaik et al. 2016). This tendency is almost certainly adaptive in that novel items are potentially dangerous and social information, when available, is therefore preferred, especially in species with a long life expectancy (Forss et al. 2017). The same conclusion might well apply to our hominin ancestors during much of human evolution. Many people may find this conclusion surprising, because when they think of apes, they have in mind *captive* apes, which are indeed rightly renowned for their innovativeness. In fact, Damerius et al. (2017a, b, see also Forss et al. 2015) showed that captive orangutans are far more curious than their wild counterparts, at least in part because captive orangutans have had extensive contact with humans from a very early age, which unleashed their curiosity. The erosion of the reluctance to explore novelty in captivity (especially when enculturated) indicates that novelty seeking is a latent ability that can be elicited by particular developmental conditions.

Because *modern* humans are often curious, the challenge is to identify when our ancestors became more like captive apes. In the wild, the dormant potential is most likely expressed under conditions of great necessity, when regular subsistence techniques have suddenly become ineffective. This would explain the increase in realized technology shown under environmental risk (Andersson and Read 2016; Fogarty and Creanza 2017), when necessity clearly acts as the mother of invention.

Social transmission: imitation

One current view holds that great apes largely lack cumulative culture because their copying abilities are not good enough: while they can individually innovate behavior (including tool making and tool use), they seem to lack the motivation and/or ability to copy the styles and forms of others' innovations (Tennie et al. 2019). It is indeed clear that a modest increase in the efficiency of social transmission due to improved social learning (or help in the form of teaching; see below) can produce a steep increase in technology level (Lewis and Laland 2012). Figure 3, based on the Pradhan et al. (2012) model, illustrates this. Indeed, given that the baseline value for wild great apes learning tool use, α, is 0.25 at best, it is clear how even a small increase in the efficiency of social transmission can provide a major boost to technological cumulation.

Indeed, it is often argued that cumulative culture requires faithful transmission so as to create a uniform platform that stays intact for long enough for subsequent modifications to happen "on top" (Tennie et al. 2009; Lewis and Laland 2012; Heyes 2018). The key improvement would involve a move away from using social learning mechanisms that are merely socially elicited individual learning (*non*-copying social learning; widespread in the animal kingdom) toward *copying* social learning (which is then able to transmit *form*, i.e., hierarchical and/or style components of demonstrations—a crucial prerequisite of the ratchet effect; Tennie et al. 2019). Once copying of actions (imitation) is in place, and especially the copying of *novel* actions (broader range), it can be applied in a broad range of conditions (e.g., communication [itself able to increase fidelity] and tool making and use), and raises transmission fidelity. And while a detailed physical understanding can theoretically allow observers to re-engineer technology (various forms of so-called emulation learning), even here action copying can be of benefit, because actions are hierarchically higher than environmental results (they *cause* these results and thus come first) and also bear an intimate correlation with their results (action A on object X may reliably produce result A), and so the simultaneous copying of both actions and results disproportionately increases fidelity (Acerbi and Tennie 2016). For these combined reasons, action copying favors cultural evolution.

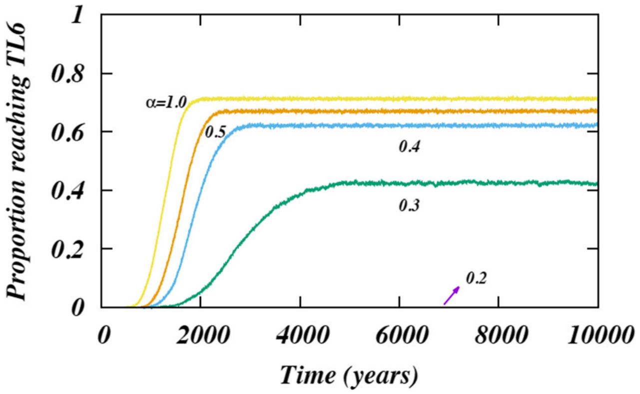

Fig. 3 The time needed to reach a complex level of cumulative technology, as a function of the efficiency of social transmission, for realistic values of great ape sociability ($\kappa = 2$) (for details, see Pradhan et al. (2012))

Do great apes copy actions in this way? Evidence for action copying in wild great apes (and, likewise, unenculturated captive apes) is debated, but weak at best (e.g, see review in Henrich and Tennie 2017), whereas *enculturated* great apes, i.e., individuals that grew up with humans and were treated much like human babies are do show evidence of action copying (Russon and Galdikas 1993; Tomasello et al. 1993; Subiaul 2016), along with the requisite *changes* in brain structure that are required and that resulted from such "training" (Bard and Hopkins 2018; Pope et al. 2018). This indicates that apes can be induced to socially construct the ability to imitate by exposure to rich inputs, perhaps especially numerous novel actions and/or long sequences of actions with unexpected outcomes. Indeed, Catmur and Heyes (2017) argue that imitation in humans is similarly constructed during development based on social inputs (i.e., is a "cognitive gadget," Heyes 2018).

The upshot of this recent increase in our understanding of ape imitation is that imitation is possibly no longer the (or the only) magic bullet for the evolution of cumulative culture. The ability to engage in imitation, including perhaps production imitation (sensu Byrne 2002), lies—as a potential—dormant in every great ape, and can be constructed when the social inputs are right - or perhaps even if they require it (we postpone asking about the origin of these complex inputs to the discussion).

Social transmission: teaching

In species capable of social learning of copying type(s), teaching—social learning with an actively involved demonstrator—provides a major boost in transmission efficiency (Fogarty et al. 2011; Dean et al. 2014; Morgan et al. 2015) and perhaps also in the possible complexity of innovations that can be copied. Teaching in this way is seen in large-scale human societies (Csibra and Gergely 2011) and, albeit less pervasively, also in hunter-gatherers (Kline 2015; Hewlett and Roulette 2016), whereas despite all efforts to detect it, the evidence for great apes is extremely thin (Hoppitt and Laland 2013; Moore and Tennie 2015). However, (non-intentional) teaching is common among primates that are cooperative breeders (Humle and Snowdon 2008; Rapaport 2011). Because teaching can provide a boost to transmission fidelity, and can initially do so without requiring the evolution of complex cognitive machinery, it is among the most important drivers of cultural complexity (Tomasello 2009; Pradhan et al. 2012; Dean et al. 2014). Thus, the timing of the origin of teaching may hint at the origin of cumulative technology (Fogarty et al. 2011; Laland 2017). Note however that teaching should always be split up by the underlying social learning mechanisms (Hoppitt et al. 2008). Here, we are interested in teaching forms that use social learning mechanisms involving copying (which is why we do not elaborate on the occurrences of other, non-copying forms of teaching in the animal kingdom; see, e.g., Hoppitt et al. 2008).

Discussion

When trying to identify the variables leading to cumulative technology, it is generally most profitable to look for changes in the external variables, either the habitat (as driven by the rate and amplitude of climate change: Richerson and Boyd 2000) or other, habitat-driven aspects of the social system, such as the rearing system (van Schaik and Burkart 2010) and environmental risk (Andersson and Read 2016). Above, we suggested that the archeological record does not support increased population size or a positive feedback loop between population size and innovation as the sole cause for the onset of cumulative technology. Of course, it remains possible that a relatively short period of favorable climate pushed up (some) hominin populations, and so gave rise to innovations that raised carrying capacity enough to unleash a positive feedback loop between population size and innovation repertoires. However, the lack of clear evidence for a sustained increase in population size during the Middle Pleistocene does not support this possibility. Instead, we identified the onset of language-buttressed teaching involving copying of novel actions and, later, curiosity as key variables for the onset of cumulative culture and its acceleration before Out-of-Africa, respectively (Table 1).

The dawn of cumulative cultural evolution

Roughly following Tennie et al. (2016a), we tentatively pinpointed the period after around 500 ka (as the earliest) to mark the onset of the first cumulative technology. This suggests that *Homo heidelbergensis* evolved a new lifestyle. Indeed, around this time or somewhat later (the latter perhaps due to the incomplete record in most of Africa), the first solid evidence is found for systematic controlled use of fire (Roebroeks and Villa 2011), and especially for new technology, including composite tools (Wilkins et al. 2012), the use of throwing spears (Thieme 1997), and the inferred use of full-fledged language (Dediu and Levinson 2013). This latter factor may hold the key.

The classic candidate processes to explain the origin of cumulative culture are high-fidelity copying (especially imitation) and teaching (Tennie et al. 2009; Laland 2017). We tentatively discount imitation as the sole limiting factor since great apes can be led to developmentally construct the ability (as a "cognitive gadget" sensu Heyes 2018) in socially structured conditions where more complex actions or action sequences must be learned. This further highlights a role for teaching (cf. Tomasello 2009; Fogarty et al. 2011). Because teaching improves transmission and so retention of innovations, it favors increased innovation capacity whenever innovations enhance fitness. Modern humans, in addition to silently providing examples and physically shaping others' behavior (an understudied form of true social transmission, leading to copies), often rely on language in instruction. Indeed, experiments have shown that learning to make stone tools becomes far more efficient when verbal instruction is added to the mix (Morgan et al. 2015; cf. Zwirner and Thornton 2015). This suggests that effective teaching, especially of functionally opaque actions that are part of a longer chain and which require copying for their acquisition, could only become prominent after language had evolved to a sufficient level of complexity to make this possible. Once it was in place, correlated evolution between teaching, imitation, and cumulative culture could ensue (Laland 2017).

Language did not evolve overnight, and precursors must have existed (Tomasello et al. 2012). Teaching is more common among cooperative breeders (Rapaport 2011), and hominins may have become cooperative breeders and thus more cooperative than extant great apes (Tennie et al. 2016b) well before they invented the prepared core technique (Hrdy 2009; Isler and van Schaik 2012). The fundamentally prosocial attitudes toward fellow group members that characterize cooperative breeding (Burkart et al. 2014) will have favored the evolution of both teaching and language (Burkart et al. 2018), as teaching is, in essence, prosocial (Tennie et al. 2009; van Schaik and Burkart 2010). Thus, the combination of teaching and language produced cumulative

Table 1 The major leaps in the pace of cultural evolution during human evolution

Major transition	When?	Major driver
Homo heidelbergensis	After 500 ka	*Intensive cooperation*: involving potential use of language and teaching of young, both driven by extensive allomaternal care and systematic food sharing
Out-of-Africa	ca. 75 ka	*Curiosity unleashed*: sudden failure of regular foraging, leading to need to invent new resource exploitation methods, leading to novel niche dimensions
Neolithic	ca. 10 ka	*Incentives for specialization*: after development of sedentism and then agriculture, producing increased incentives to innovate, due to private benefits from specialization and trade, and need for effective wars

culture. The plausibility of this model is enhanced by the fact that the external factor producing the onset of cumulative culture was not a cognitive one but rather a change in the rearing and social system (van Schaik and Burkart 2010; Laland 2017). Assuming an externally caused increase in cognition merely moves the question to the source of this increase. However, cooperative breeding (and, with it, teaching) may plausibly have been elicited by increasing climate fluctuations (cf. Richerson and Boyd 2000), because it is known to be favored when productivity declines (Griesser et al. 2017) and, among mammals, is overrepresented in the most inhospitable climates (Lukas and Clutton-Brock 2017).

This leaves the question how the adoption of language-buttressed teaching may have led to greater innovativeness in our ancestors. Once effective teaching exists, selection will favor individuals who acquire the local population's set of innovations as fully and rapidly as possible. However, this selection also automatically improves individual or asocial learning skills (van Schaik and Burkart 2011; Heyes 2012), leading to better and faster innovation, which in turn may have favoured the developmental construction of imitation (see above). These mutual positive influences create a positive feedback loop, leading to coevolving innovation and imitation abilities. This loop also includes changes in life history (e.g., by slowing down development and expanding the learning period to beyond sexual maturity) and brain size. This process may bring about a quantum leap in the complexity of technology because teaching (due to its potential for highly increased fidelity) allows naïve individuals to bypass the historical sequence of innovation steps that led to the current, complex technique and simply skip to the current technique. Such shortcutting also increases the likelihood that young individuals make additional innovations (often by mistake; cf. Henrich 2004; Eerkens and Lipo 2005) that improve upon the existing technique.

Overall, then, the process that produced both effective language and teaching in a coevolutionary process is the most plausible candidate for the origin of complex and truly cumulative material culture in hominin evolution.

The origin of curiosity

The idea that a gradual increase in cumulative culture in Africa was the root cause of the rich and complex material culture of the humans that appeared in Europe at ca. 42 ka (McBrearty and Brooks 2000) suggests no stepwise change in the cumulation process. Nonetheless, many suggest that some major new factor underlies by the rapid, sustained Out-of-Africa dispersal that began around 75 ka, and by the continuing rapid increase in complexity since then. As discussed above, a sudden increase in novelty seeking or curiosity was recently suggested as the key underlying change.

We noted that in great apes, curiosity can be elicited (in captivity) even when it normally lies dormant. This idea lends greater plausibility to the novelty-seeking hypothesis, because the existence of a phenotypic switch to turn on curiosity enables rapid responses during a brief period in which regular techniques have become ineffective. If the onset of curiosity had required genetic responses, local populations would probably have gone extinct well before they could respond adaptively. It is also possible, as suggested by the geographic gradient in variants of the dopamine receptor gene (Matthews and Butler 2011; Gören 2016), that selection on the suppression of previously maladaptive curiosity was relaxed, allowing the variant alleles of the dopamine receptor gene to spread during to the dramatic range expansion.

Obviously, future work is needed to evaluate this radical idea, in particular with respect to the event that elicited this shift in some local population(s). For example, the Toba eruption may not have led to a population collapse in Africa and adjacent regions, as previously claimed (Ambrose 2003), but it may have produced a brief ecological crisis, serious enough to lead some individuals to lose their neophobia and try out unusual resources or habitats.

The Neolithic revolution

The origin of agriculture was preceded by a period in which foragers in some regions became more sedentary. Sedentary foragers have more, and more complex, technology than nomadic ones (Torrence 2001). Agriculture added another major impetus to expand technology, partly made possible by specialization, but also led to a strong increase in population size and contact between societies through trade or conquest (Scott 2017). Large populations produce more innovations passively (by greater numbers or greater diffusion), by allowing specialization or by producing wars and ecological crises that necessitated innovations (Fogarty and Creanza 2017). In this phase, clearly the feedback loop between population size, social exchange, and the accompanying cultural diffusion had become major engines of cumulative culture, with seemingly open-ended outcome (Laland 2017).

Acknowledgments We thank Peter Kappeler for the invitation and Kevin Laland and an anonymous reviewer for valuable comments.

Funding information This work has received funding from the Swiss National Science Foundation (grant 310030B_160363/1) and European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no. 714658; STONECULT project)

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Acerbi A, Tennie C (2016) The role of redundant information in cultural transmission and cultural stabilization. J Comp Psychol 130:62–70

Ambrose SH (2003) Did the super-eruption of Toba cause a human population bottleneck? Reply to Gathorne-Hardy and Harcourt-Smith. J Hum Evol 45:231–237

Andersson C, Read D (2016) The evolution of cultural complexity: not by the treadmill alone. Curr Anthropol 57:261–286

Bandini E, Tennie C (2017) Spontaneous reoccurrence of "scooping", a wild tool-use behaviour, in naïve chimpanzees. PeerJ 5:e3814

Bard KA, Hopkins WD (2018) Early socioemotional intervention mediates long-term effects of atypical rearing on structural covariation in gray matter in adult chimpanzees. Psychol Sci 29:594–603

Blegen N (2017) The earliest long-distance obsidian transport: evidence from the ≈ 200 ka Middle Stone Age Sibilo School Road Site, Baringo, Kenya. J Hum Evol 103:1–19

Boyd R, Richerson PJ (1996) Why culture is common, but cultural evolution is rare. Proc Brit Acad 88:77–93

Burkart JM, Allon O, Amici F et al (2014) The evolutionary origin of human hyper-cooperation. Nat Commun 5:4747

Burkart JM, Martins EG, Miss F, Zürcher Y (2018) From sharing food to sharing information: cooperative breeding and language evolution. Interact Stud 19:135–150

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

Campbell BC, Barone LM (2012) Evolutionary basis of human migration. In: Crawford MH, Campbell BC (eds) Causes and Consequences of Human Migration. Cambridge University Press, New York, pp 45–64

Catmur C, Heyes C (2017) Mirroring "meaningful" actions: sensorimotor learning modulates imitation of goal-directed actions. Q J Exp Psychol 19:1–13

Collard M, Buchanan B, O'Brien MJ, Scholnick J (2013) Risk, mobility or population size? Drivers of technological richness among contact-period western North American hunter-gatherers. Philos Trans R Soc B 368:20120412

Corbey R, Jagich A, Vaesen K, Collard M (2016) The Acheulean handaxe: more like a bird's song than a Beatles' tune? Evol Anthropol 25:6–19

Csibra G, Gergely G (2011) Natural pedagogy as evolutionary adaptation. Philos Trans R Soc B 366:1149–1157

Damerius LA, Forss SIF, Kosonen ZK et al (2017a) Orientation towards humans predicts cognitive performance in orang-utans. Sci Rep 7: 40052

Damerius L, Graber SM, Willems EP, van Schaik CP (2017b) Curiosity boosts orang-utan problem-solving ability. Anim Behav 134:57–70

Dean LG, Vale GL, Laland KN, Flynn E, Kendal RL (2014) Human cumulative culture: a comparative perspective. Biol Rev 89:284–301

Dediu D, Levinson SC (2013) On the antiquity of language: the reinterpretation of Neandertal linguistic capacities and its consequences. Front Psychol 4:397

Diamond J (2012) The world until yesterday: what we can learn from traditional societies. Viking, New York

Eerkens JW, Lipo CP (2005) Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. J Anthropol Archaeol 24:316–334

Fogarty L, Creanza N (2017) The niche construction of cultural complexity: interactions between innovations, population size and the environment. Phil Trans R Soc B 372:20160428

Fogarty L, Strimling P, Laland KN (2011) The evolution of teaching. Evolution 65:2760–2770

Foley R, Lahr MM (2003) On stony ground: lithic technology, human evolution, and the emergence of culture. Evol Anthropol 12:109–122

Forss SIF, Schuppli C, Haiden D, Zweifel N, van Schaik CP (2015) Contrasting responses to novelty by wild and captive orangutans. Am J Primatol 77:1109–1121

Forss SIF, Koski SE, van Schaik CP (2017) Explaining the paradox of neophobic explorers: the social information hypothesis. Int J Primatol 38:799–822

Galef BG Jr (1992) The question of animal culture. Hum Nat 3:157–178

Gören E (2016) The biogeographic origins of novelty-seeking traits. Evol Hum Behav 37:456–469

Griesser M, Drobniak SM, Nakagawa S, Botero CA (2017) Family living sets the stage for cooperative breeding and ecological resilience in birds. PLoS Biol 15:e2000483

Gruber T, Muller MN, Strimling P, Wrangham RW, Zuberbühler K (2009) Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. Curr Biol 19:1806–1810

Haidle MN, Bolus M, Collard M et al (2015) The nature of culture: an eight-grade model for the evolution and expansion of cultural capacities in hominins and other animals. J Anthropol Sci 93:43–70

Hanus D, Mendes N, Tennie C, Call J (2011) Comparing the performances of apes (*Gorilla gorilla, Pan troglodytes, Pongo pygmaeus*) and human children (*Homo sapiens*) in the floating peanut task. PLoS One 6:e19555

Harcourt A (2015) Humankind: how biology and geography shape human diversity. Pegasus Books, New York

Harmand S, Lewis JE, Feibel CS et al (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521:310–315

Henrich J (2004) Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case. Am Antiq 69:197–214

Henrich J, Tennie C (2017) Cultural evolution in chimpanzees and humans. In: Muller M, Wrangham R, Pilbeam D (eds) Chimpanzees and Human Evolution. Harvard University Press, Cambridge

Hewlett BS, Roulette CS (2016) Teaching in hunter-gatherer infancy. R Soc Open Sci 3:150403

Heyes C (2012) What's social about social learning? J Comp Psychol 126:193–202

Heyes C (2018) Cognitive gadgets: the cultural evolution of thinking. Harvard University Press, Cambridge

Hill KR, Wood BM, Baggio J, Hurtado AM, Boyd RT (2014) Hunter-gatherer inter-band interaction rates: implications for cumulative culture. PLoS One 9:e102806

Hobaiter C, Poisot T, Zuberbühler K, Hoppitt W, Gruber T (2014) Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. PLoS Biol 12:e1001960

Hoffecker JF, Hoffecker IT (2017) Technological complexity and the global dispersal of modern humans. Evol Anthropol 26:285–299

Hoppitt WJE, Laland KN (2013) Social learning: an introduction to mechanisms, methods, and models. Princeton University Press, Princeton

Hoppitt WJ, Brown GR, Kendal R, Rendell L, Thornton A, Webster MM, Laland KN (2008) Lessons from animal teaching. Trends Ecol Evol 23:486–493

Hrdy SB (2009) Mothers and others: the evolutionary origins of mutual understanding. Harvard University Press, Cambridge

Humle T, Snowdon CT (2008) Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. Anim Behav 75:267–277

Isler K, van Schaik CP (2012) How our ancestors broke through the gray ceiling: comparative evidence for cooperative breeding in early *Homo*. Curr Anthropol 53:S453–S465

Kempe M, Lycett S, Mesoudi A (2012) An experimental test of the accumulated copying error model of cultural mutation for Acheulean handaxe size. PLoS One 7:e48333

Kempe M, Lycett SJ, Mesoudi A (2014) From cultural traditions to cumulative culture: parameterizing the differences between human and nonhuman culture. J Theor Biol 359:29–36

Klein RG (2008) Out of Africa and the revolution of human behavior. Evol Anthropol 17:267–281

Klein RG, Steele TE (2013) Archaeological shellfish size and later human evolution in Africa. Proc Natl Acad Sci U S A 110:10910–10915

Kline MA (2015) How to learn about teaching: an evolutionary framework for the study of teaching behavior in humans and other animals. Behav Brain Sci 38:e31

Laland KN (2017) Darwin's unfinished symphony: how culture made the human mind. Princeton University Press, Princeton

Lewis HM, Laland KN (2012) Transmission fidelity is the key to the build-up of cumulative culture. Philos Trans R Soc B 367:2171–2180

Li H, Durbin R (2011) Inference of human population history from individual whole-genome sequences. Nature 475:493–496

Lukas D, Clutton-Brock TH (2017) Climate and the distribution of cooperative breeding in mammals. R Soc Open Sci 4:160897

Luncz LV, Boesch C (2014) Tradition over trend: neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. Am J Primatol 76:649–657

Matthews LJ, Butler PM (2011) Novelty-seeking DRD4 polymorphisms are associated with human migration distance Out-of-Africa after controlling for neutral population gene structure. Am J Phys Anthropol 145:382–389

McBrearty S, Brooks AS (2000) The revolution that wasn't: a new interpretation of the origin of modern human behavior. J Hum Evol 39: 453–563

Mercader J, Barton H, Gillespie J, Harris J, Kuhn S, Tyler R, Boesch C (2007) 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proc Natl Acad Sci U S A 104:3043–3048

Mesoudi A (2016) Cultural evolution: a review of theory, findings and controversies. Evol Theor 43:481–497

Mithen S (1996) The prehistory of the mind: the cognitive origins of art, religion and science. Thames and Hudson, London

Moore R, Tennie C (2015) Cognitive mechanisms matter - but they do not explain the absence of teaching in chimpanzees. Behav Br Sci 38: 32–33

Morgan TJH, Uomini NT, Rendell LE et al (2015) Experimental evidence for the co-evolution of hominin tool-making teaching and language. Nat Commun 6:6029

Muller A, Clarkson C (2016) Identifying major transitions in the evolution of lithic cutting edge production rates. PLoS One 11:e0167244

Nolan P, Lenski G (2009) Human societies: an introduction to macrosociology, 11th edn. Paradigm Publishers, Boulder

Pope SM, Taglialatela JP, Skiba SA, Hopkins WD (2018) Changes in frontoparietotemporal connectivity following do-as-I-do imitation training in chimpanzees (*Pan troglodytes*). J Cogn Neurosci 30: 421–431

Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. Science 324:1298–1301

Pradhan GR, Tennie C, van Schaik CP (2012) Social organization and the evolution of cumulative technology in apes and hominins. J Hum Evol 63:180–190

Rapaport LG (2011) Progressive parenting behavior in wild golden lion tamarins. Behav Ecol 22:745–754

Reader SM, Laland KN (2002) Social intelligence, innovation and enhanced brain size in primates. Proc Natl Acad Sci U S A 99:4436–4441

Richerson PJ, Boyd RT (2000) Climate, culture, and the evolution of cognition. In: Heyes C, Huber L (eds) Evolution of Cognition. MIT Press, Cambridge, pp 329–346

Roebroeks W, Villa P (2011) On the earliest evidence for habitual use of fire in Europe. Proc Natl Acad Sci U S A 108:5209–5214

Russon A, Galdikas B (1993) Imitation in ex-captive orangutans. J Comp Psychol 107:147–161

Sanz CM, Morgan DB (2007) Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. J Hum Evol 52:420–433

van Schaik CP, Burkart JM (2010) Mind the gap: cooperative breeding and the evolution of our unique features. In: Kappeler PM, Silk J (eds) Mind the Gap: Tracing the origins of Human Universals. Springer, Berlin, pp 477–496

Schuppli C, Meulman EJM, Forss SIF, Aprilinayati F, van Noordwijk MA, van Schaik CP (2016) Observational social learning and socially induced practice of routine skills in immature wild orangutans. Anim Behav 119:87–98

Scott JP (2017) Against the grain: a deep history of the earliest states. Yale University Press, New Haven

Sol D, Bacher S, Reader SM, Lefebvre L (2008) Brain size predicts the success of mammal species introduced into novel environments. Am Nat 172:S63–S71

Subiaul F (2016) What is special about human imitation? A comparison with enculturated apes. Behav Sci 6:13

Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Philos Trans R Soc B 364:2405–2415

Tennie C, Braun DR, Premo LS, McPherron SP (2016a) The island test for cumulative culture in the Paleolithic. In: Haidle MN, Conard NJ, Bolus M (eds) The Nature of Culture: Based on an Interdisciplinary Symposium ‘The Nature of Culture’, Tübingen. Germany. Springer Science+Business Media, Dordrecht, pp 121–133

Tennie C, Jensen K, Call J (2016b) The nature of prosociality in chimpanzees. Nat Commun 7:13915

Tennie C, Premo LS, Braun DR, McPherron SP (2017) Early stone tools and cultural transmission: Resetting the null hypothesis. Curr Anthropol 58:652–672

Tennie C, Hopper L, van Schaik CP (2019) On the origin of cumulative culture: consideration of the role of copying in culture-dependent traits and a reappraisal of the zone of latent solutions hypothesis. In: Ross S, Hopper L (eds) Chimpanzees in context: a comparative perspective on chimpanzee behavior, cognition, conservation, and welfare. Chicago University Press, Chicago

Thieme H (1997) Lower Palaeolithic hunting spears from Germany. Nature 385:807–810

Tomasello M (1999) The cultural origins of human cognition. Harvard University Press, Cambridge

Tomasello M (2009) The question of chimpanzee culture, plus postscript (chimpanzee culture 2009). In: Laland KN, Galef BG (eds) The Question of Animal Culture. Harvard University Press, Cambridge, pp 198–221

Tomasello M, Kruger A, Ratner H (1993) Cultural learning. Behav Brain Sci 16:495–511

Tomasello M, Melis AP, Tennie C, Wyman E, Herrmann E (2012) Two key steps in the evolution of human cooperation: the interdependence hypothesis. Curr Anthropol 53:673–692. https://doi.org/10.1086/668207

Torrence R (2001) Hunter-gatherer technology: macro- and microscale approaches. In: Panter-Brick C, Layton RH, Rowley-Conwy P (eds) Hunter-Gatherers: An Interdisciplinary Perspective. Cambridge University Press, Cambridge, pp 73–98

Vaesen K, Collard M, Cosgrove R, Roebroeks W (2016) Population size does not explain past changes in cultural complexity. Proc Natl Acad Sci U S A 113:E2241–E2247 van de Waal E, van Schaik CP, Whiten A (2017) Resilience of experimentally seeded dietary traditions in wild vervets: evidence from group fissions. Am J Primatol 79:e22687

van Schaik CP (2016) The primate origins of human nature. John Wiley & Sons, Hoboken

van Schaik CP, Burkart JM (2011) Social learning and evolution: the cultural intelligence hypothesis. Philos Trans R Soc B 366:1008–1016

van Schaik CP, Burkart JM, Damerius L, Forss SIF, Koops K, van Noordwijk MA, Schuppli C (2016) The reluctant innovator: orangutans and the phylogeny of creativity. Philos Trans R Soc B 371: 20150183

Whiten A, van Schaik CP (2007) The evolution of animal 'cultures' and social intelligence. Philos Trans R Soc B 362:603–620

Whiten A, Ayala FJ, Feldman MW, Laland KN (2017) The extension of biology through culture. Proc Natl Acad Sci U S A 114:7775–7781

Wilkins J, Schoville BJ, Brown KS, Chazan M (2012) Evidence for early hafted hunting technology. Science 338:942–946

Yamamoto S, Yamakoshi G, Humle T, Matsuzawa T (2008) Invention and modification of a new tool use behavior: ant-fishing in trees by a wild chimpanzee (*Pan troglodytes verus*) at Bossou, Guinea. Am J Primatol 70:699–702

Zwirner E, Thornton A (2015) Cognitive requirements of cumulative culture: teaching is useful but not essential. Sci Rep 5:16781