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Social organization and the evolution of cumulative technology in apes and hominins

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ABSTRACT

Culturally supported accumulation (or ratcheting) of technological complexity is widely seen as characterizing hominin technology relative to that of the extant great apes, and thus as representing a threshold in cultural evolution. To explain this divide, we modeled the process of cultural accumulation of technology, which we defined as adding new actions to existing ones to create new functional combinations, based on a model for great ape tool use. The model shows that intraspecific and interspecific variation in the presence of simple and cumulative technology among extant orangutans and chimpanzees is largely due to variation in sociability, and hence opportunities for social learning. The model also suggests that the adoption of extensive allomaternal care (cooperative breeding) in early Pleistocene *Homo*, which led to an increase in sociability and to teaching, and hence increased efficiency of social learning, was enough to facilitate technological ratcheting. Hence, socioecological changes, rather than advances in cognitive abilities, can account for the cumulative cultural changes seen until the origin of the Acheulean. The consequent increase in the reliance on technology could have served as the pacemaker for increased cognitive abilities. Our results also suggest that a more important watershed in cultural evolution was the rise of donated culture (technology or concepts), in which technology or concepts was transferred to naïve individuals, allowing them to skip many learning steps, and specialization arose, which allowed individuals to learn only a subset of the population's skills.

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Introduction

Recent studies have inferred the presence of culture, defined as multiple socially transmitted innovations, in chimpanzees and orangutans, based on geographic variation in behavior patterns or artifacts without obvious ecological or genetic correlates (Whiten et al., 1999; Boesch, 2003; van Schaik et al., 2003a; Krützen et al., 2011) and indirect indications of social learning in the field (Biro et al., 2003; Lonsdorf et al., 2004; Gruber et al., 2009; Jaeggi et al., 2010; Reader and Biro, 2010). These studies have allowed us to define more clearly what distinguishes human culture from that of the great apes, whose cultures probably closely resemble those of the last common ancestor of humans and the two chimpanzee species. Two major differences have emerged (Tomasello, 1999; van Schaik, 2004; Hill, 2009; Tennie et al., 2009): the cumulative nature of human technology, and the cumulative and normative nature of human cultural institutions. Our focus here is

to explain the origin of cumulative technology, which is widely considered to represent a watershed in cultural evolution.

The prevailing explanation is that cumulative technology is absent in great apes because they cannot imitate, and thus cannot reproduce novel actions with sufficient precision to serve as a uniform foundation for subsequent addition of accumulations. Thus, cumulative technology was thought to have arisen with Oldowan flake tools (Galef, 1992; Tomasello et al., 1993; Tomasello, 1994, 1999; Boyd and Richerson, 1996). We think this hypothesis is no longer supported, for two reasons. First, great apes in experiments can reliably transmit complex techniques, although the exact mechanisms remain debated, and second, they show some evidence of cumulative technology, if properly defined.

With respect to the imitation question, despite much recent work on nonhuman primates, no consensus on the mechanisms of observational social learning has emerged (Byrne and Tanner, 2006; Tennie et al., 2009; Whiten et al., 2009). Nonetheless, great apes have now been found to copy complex skills with sufficient reliability to maintain basic behavioral uniformity in two-target experiments in captivity despite the presence of alternative

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outcomes (reviews: Whiten et al., 2007; Whiten and Mesoudi, 2008; Dindo et al., 2011), which would suffice to maintain systematic differences in technology between nearby populations in the wild (Boesch et al., 1994; van Schaik and Knott, 2001). Although some doubt remains (Tennie et al., 2006; Claidière and Sperber, 2010), most now agree that we should look elsewhere than to mechanisms of social learning to explain the elaboration of cumulative culture in humans (Price et al., 2009; Tomasello, 2009).

To evaluate possible evidence for cumulative technology among great apes, we need a workable operational definition of cumulative technology, i.e., cumulative technological innovations that have been transmitted socially to the point of having reached high prevalence in a given population (habitual or customary status sensu Whiten et al., 1999). Cumulative innovations have been defined as those beyond what a naïve individual could invent during its lifetime (Galef, 1992; Tomasello et al., 1993; Boyd and Richerson, 1996), i.e., outside its Zone of Latent Solutions (Tennie et al., 2009). However, this definition in effect assumes that the accumulation process has already proceeded to the point that it has become impossible for naïve individuals to invent the whole series of steps. It therefore excludes the initial steps of the accumulation process, i.e., those that may still be invented by an individual, which arguably are the very steps that historically determined the difference between cumulative and non-cumulative culture.

We therefore adopted an alternative approach. The build-up “implies the existence of superordinate representations abstracted from, and maintained over, the course of multiple subordinate events” (Stout, 2011: 1051), and is therefore usually accompanied by an increase in the size of the working memory,

making the action series cognitively more challenging as it gets longer (Price et al., 2009). We accordingly defined the metric for the degree of accumulation (a.k.a. ratcheting) of a technique or learned skill as the number of distinct actions integrated as steps in a single functional sequence to reach an overall goal. One advantage of this metric is that this kind of complexity corresponds closely to that in terms of techno-units (Oswalt, 1976), which directly reflect properties of the tools themselves. It is in line with metrics developed for primate food processing (Byrne, 1995; Matsuzawa, 1996), and is also very similar to comparable metrics developed in archaeology (Haidle, 2010; Stout, 2011). However, we did not admit other criteria, such as the complexity of each individual action (which is also hard to define; Uomini, 2009) or the selectivity of the choice of raw material that is used to produce the tool. We excluded them because these aspects can be gradually improved over time through individual practice based on simple processes like associative learning, once the basic action has been put in place by ratcheting (e.g., Nonaka et al., 2010). It is important to stress that this system is preliminary and needs to be validated empirically through actual studies (for a recent attempt, see Sanz and Morgan (2010)). We will revisit this issue in the Discussion.

The paradigmatic case of ratcheting is when an individual adds an existing technique used in a different context, or an entirely novel technique, to an existing technique, and integrates them functionally. This can produce either a tool set (two or more tools used consecutively in a functionally integrated way), a composite tool (two existing tools combined directly), or a more complex tool (where subsequent actions modify an existing tool, adding functionality to it). Table 1 provides the definitions of the first

Table 1
Definitions and examples of technology levels.

| Technology level | Description | Examples sticks | Examples stones |
|------------------|--|--|---|
| TL0 | A single action (use object as tool) | Use a stick found nearby to poke into hole | Use a stone found nearby to pound nuts or bones ^a |
| TL1 | A single action, followed by other coordinated action (use object as tool on prepared substrate) | Take a stout branch found elsewhere to a suitable anvil and use as a wooden hammer | Take a stone found elsewhere to a suitable anvil, and use to pound |
| TL1 | A single action or set of closely related actions on one object, which is subsequently used as a tool (tool manufacture) | Break a twig from a branch, trim to size (and perhaps remove side-twigs, etc.), and use as tool | Hit stone on hard surface to produce flakes, through the anvil or throwing techniques ^b , and use flakes as tool |
| TL2 | Two distinct, subsequent actions on one object, which is subsequently used as tool (composite tool) | Prepare a twig to become a probe, and subsequently fray the end of the probe, thus improving its efficiency ^c | Not applicable due to body restrictions (body actions on stones are meaningless) |
| TL2 | Integrated actions on two distinct objects, which are each produced separately (tool set) | Use of a separately prepared perforating stick to create a tunnel, followed by use of separately produced probe to extract termites ^d | Not applicable due to body restrictions |
| TL2 | Co-action, two carefully integrated actions on two objects, one in each hand | Not applicable due to material restrictions (wood vs. stones) | Hitting a hand-held stone core with a stone hammer to produce an Oldowan flake (using hard-hammer percussion or bipolar technique) ^b |
| TL3 | Use a made tool to modify another tool (combining manufactured tools) | Not applicable due to material restrictions | Use an Oldowan flake, produced earlier, to sharpen a stick for more effective use ^e |
| TL3 | Use co-action (TL2) many times in a coordinated sequence | Not applicable due to material restrictions | Produce an Acheulean hand axe ^b |
| TL3 | Use two different co-actions in integrated sequence | Not applicable due to material restrictions | Use hard hammer to prepare a core, followed by soft hammer, to produce flakes off an Acheulean handaxe ^b |
| TL3 | Integrated actions on three distinct objects, which are each produced separately | Use of separately prepared pounding stick, followed by a lever tool, followed by a dip stick to obtain honey from bee nests ^d | Not applicable due to body restrictions |
| TL4 | Use two different co-actions in integrated sequence, followed by independent finishing with another tool | Not applicable due to material restrictions | As in TL3 above, followed by resharpening ^b |

As one moves down in the table, technological accumulation increases. It is assumed that each level has reached high prevalence through cultural transmission. References are given only for cases not mentioned in the description of the model.

^a As in monkeys: Ottoni and Izar, 2008; Gumert et al., 2009.

^b Schick and Toth, 1993; Boysen, Personal communication.

^c Sanz et al., 2009.

^d Sanz and Morgan, 2007.

^e Dominguez-Rodrigo et al., 2001.

ratcheting steps that can be recognized using this criterion, producing increasing technology levels (TL), and provides examples for both stick and stone tools.

Although cumulative technology defined this way is absent among orangutans, various examples have recently emerged for chimpanzees (Sanz et al., 2004, 2009; Sanz and Morgan, 2007; Boesch et al., 2009). In the Goulougo Triangle, for instance, the local chimpanzees use a tool set, consisting of a stout puncturing stick and a slender probe, to exploit subterranean termite nests. It is assumed that the probing tools were already well established, since they are found in many chimpanzee populations, before the stout puncturing stick was invented. Another example from the same site is the brush-tipped termite probe, where the regular termite probe (again assumed to be the starting point, given its common presence in other populations) undergoes an additional modification in which the tip is frayed, which makes it far more effective in gathering termites (which bite into the probe, and latch on more easily if the tip is frayed). This evidence from the wild is complemented by experimental work. Recently, Lehner et al. (2011) coaxed captive orangutans into making ratcheted innovations.

By these definitions, some chimpanzee technology in nature is cumulative, although the majority is not, whereas captive orangutans can be coaxed into making it. Thus, there is some overlap with the technology of the makers of the Oldowan (Table 1). Nonetheless, whereas all orangutan and most tools in the wild are TL1 and some chimpanzee tools are TL2 and perhaps even in one case TL3, regular Oldowan tools are TL2, but Oldowan tools used to modify wooden tools are TL3. Acheulean tools, in contrast, are TL3 or higher.

Given that great apes are now known to have sufficiently accurate powers of observational learning to allow ratcheting and that they show some evidence of cumulative technology in the wild or captivity, we need a new explanation of the major difference between humans and great apes in their technology. The goal of this paper is therefore to identify the factors responsible for cumulative cultural evolution of technology.

We begin by developing a model that correctly reproduces the known great ape patterns. Modeling cumulative technology is made easier by the presence of considerable variation between orangutans and chimpanzees, the two ape species showing extensive tool use in the wild. Most orangutan populations fail to show any systematic extractive tool use, but a few do and actually do so in multiple contexts (van Schaik et al., 2003a), and even show some variation within populations, depending on exposure to suitable role models (van Schaik et al., 2003b). All chimpanzee populations, in contrast, show at least some tool use (Sanz and Morgan, 2007), and some, as noted above, show evidence of

ratcheting of technology. Having developed and tweaked the model for great apes, we then examine the hominin case by changing the model's parameter values in the direction of known or suspected changes during hominin evolution.

Methods

In this paper, we propose a novel simulation model to explain the process of accumulation of technology. It is built using the same basic framework proposed by van Schaik and Pradhan (2003) to model tool use in great apes, which replicated geographic variation in orangutan tool use, and found it to be a function of variation in opportunities for social learning (see also Enquist et al. (2010)). The current model simulates changes in a population's level of technology over time, as a result of individual opportunities for acquiring tool-use skills (either through invention or through social learning) at different levels of accumulation (TL0 through TL3). In the model, no skipping of technology levels is allowed; thus, for instance, TL2 is a prerequisite for reaching TL3, both in the innovation history and in ontogenetic acquisition. Even if this assumption does not strictly hold during ontogeny and some skipping is allowed, it remains likely that learning a skill is more difficult as TL increases.

We are interested in obtaining percentages of the total population engaged in various technology levels at every time step given suitable ecological conditions. The model's parameters are listed and defined in Table 2, as are the best estimates of these parameters for great apes (see below for justification of the actual values used). We assume that every individual of the population has an intrinsic inventive ability (ϵ). The parameter α refers to the probability that an individual learns the skill socially from any of the nearest neighbors possessing higher Tls in a given year, subject to the constraint that in a given year it can only move up one TL at best. Social learning can take place because each individual in the population can be in tolerant proximity with some close neighbors. In the model, each individual is represented as a node in a regular graph with the degree 2κ (Harary, 1969), which is the number of close neighbors for each individual. In such a social network, all of the nodes are arranged on a circle. Individuals can only learn from their nearest neighbors, i.e., the nodes to which they are directly connected. The value of κ is a function of the population's sociability, with high κ indicating high social tolerance. Note that we do not consider the effect of the number of demonstrators on skill acquisition through social learning. We chose this conservative rule because it is not known how the presence of multiple demonstrators adds up, and in the model most naïve individuals will often have only a single role model of a particular TL anyway.

Table 2
Definition of the main parameters used in the model and the best estimates of the same for great apes.

| Parameter | Description | Best estimates for great apes |
|---|--|--|
| ϵ ($0 \leq \epsilon \leq 1$) | Inventive ability: Probability of acquiring a particular skill in one time step in the absence of social influence | 0.0001 (i.e., approximately one in 500 individuals invents assuming annual mortality rate at 5%) |
| α ($0 \leq \alpha \leq 1$) | Social learning ability: Probability of learning a particular skill in one time step under social influence from any of the skilled neighbors | 0.2 (rather low value because great apes are not good copiers) |
| κ ($1 \leq 2\kappa \leq N$) | Sociability, or opportunities for social learning: Number of individuals in the social unit that are directly connected to the focal individual as possible experts from whom social learning is possible. The focal individual has 2κ nearest neighbors to learn from. The parameter κ is a constant for a given regular graph (the number of connected neighbors on one side of the individual). | 1 (i.e., association with only two individuals most of the time: mother and another associate) |
| μ | Annual mortality: proportion dying each year | 0.05 (average rate if orangutan and chimpanzee populations considered together) |
| λ | Age marking the end of active social learning | About 15 years |
| M | Maximum age reached in the wild | 50 years |
| N | Population size | About 500 |

The total number of nodes gives the size of the population (N). We could have modeled the population as a two-tiered system, with subgroups that internally show tight connections but are more loosely connected to other subgroups, but the effects would not be systematically different, except in the time it takes to reach particular TL values (see discussion).

For each combination of the parameters ε , α , and κ , we calculated the average fractions of the population that had attained the various technology levels after a suitably large number of time steps. We think of each time step as representing one year, which was also the time scale for the probabilities of innovation and acquisition through social learning. Each individual starts life at technology level 0 (TL0). It can then acquire higher technology levels through either personal innovation or social learning until it dies (implemented as reverting back to level 0). In each time step, the annual mortality rate (μ) sets the probability that the individual falls back to TL0 and age 0. Each individual has a window of active social learning (λ) that starts at birth and runs until this value is reached, representing the age at which it stops to learn socially, but after which it can still serve as role model. We also inserted a maximum age (M), although virtually no individual ever reached this. This structure produced a constant population that is roughly age-structured, but without having to introduce actual ages or other unrealistic simplifications.

As illustrated in the flow chart (Fig. 1), the simulation goes through the following steps. We generate the social graph with degree 2κ . We then initialize the model at technology level 0 (TL0) for all individuals, who are initially all at age 0. In each time step (year), we sequentially check all nodes, and for each node, we check their survival. If the node survives and is within the age range in which it is capable of social learning, we check whether the node

reaches the next TL through invention, and if not, whether it reaches the next TL through social learning. When all the nodes are traversed, we calculate the proportion of the population with TL0 through TL3 (or even higher TLs, see below). This procedure is then repeated for 10,000 steps, although equilibrium is almost always reached well before this time. To account for statistical variation in individual outcomes, the results reported in the following graphs are averages of 200 realizations of this procedure.

Parameter estimates for great apes

Because the model contains many parameters, high TL can be reached through many combinations. Thus, in order to increase the explanatory power of the simulations for hominins, we first determined the most realistic ranges for each parameter among great apes. We base these on the well-studied orangutan case of *Neesia* tool use (van Schaik and Knott, 2001; van Schaik, 2009), although we also examined the effect of each parameter over the whole range of values.

Starting with N , and given that orangutan populations do not consist of loosely connected subgroups, N is realistically in the range of hundreds or more, since most natural populations are in the range of up to a few thousand (Singleton et al., 2004). We kept values of α rather low (around 0.2). Great apes may be able to copy, but they are not good copiers (see above) and many activities are not performed long enough for much observational learning to occur, explaining why some profitable innovations originate but do not seem to spread (e.g., Yamamoto et al., 2008). In addition, many aspects of the techniques cannot be seen and must be acquired by individual practice, which is bound to take time (see also Stout (2011) for humans). Finally, immatures take several years of

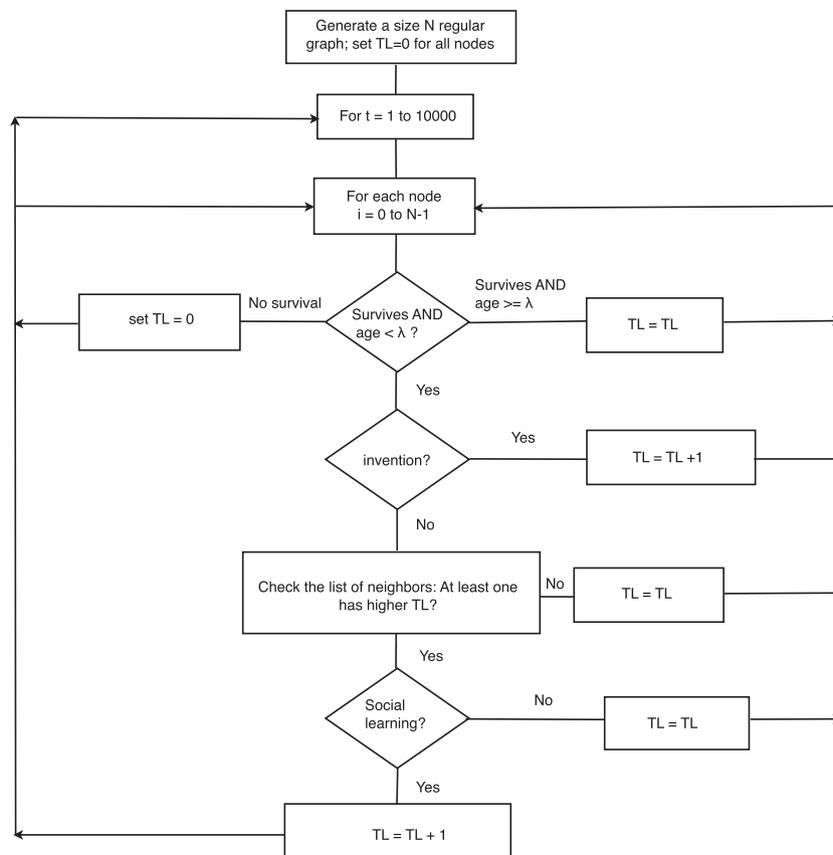


Figure 1. Flow chart showing the details of the simulation. Final results are obtained by averaging over 200 such realizations.

observation alternated with practice to acquire tool-use techniques (Matsuzawa et al., 2001; Lonsdorf et al., 2004; van Schaik, 2004; Meulman, in prep.). Therefore, it is unlikely that α is much higher than 0.2 in ape populations for the more rarely invented skills whose origin and spread is modeled here. Obviously, for simpler skills, α levels could well be far higher, but here we are modeling the most complex technology shown by these animals in the wild. In a more conservative version of the model, one could reduce α levels, as TL increases, but this would not qualitatively change the outcome of the simulations (results not presented).

We put κ at low levels, since even in the most sociable orangutan populations, which have *Neesia* tool use, immatures do not associate with others than the mother more than about 60% of time, and although only weaned individuals are counted as associates, not all of these are fully adult (van Noordwijk et al., 2009). Since many associations are with a single independent individual only, there are about two nearest neighbors on average in these populations, giving $\kappa = 1$.

Given that we tried to replicate the distribution of *Neesia* tool use first, we decided that the innovation rate, ϵ , should be low, reflecting the absence of tool use in many populations inhabiting primary forests with *Neesia* trees, where it could potentially be seen (van Schaik, 2009). Since both seed extraction and nut cracking provide more calories than any other activity in these great ape populations (van Schaik and Knott, 2001), we must assume that individuals that invented this skill would keep on using it. By putting $\epsilon = 0.0001$, we in effect assume that one in 500 individuals (given a mean annual mortality rate of 0.05, and thus an average lifespan of 20 years) will independently invent the technique, suggesting that in a large population of 500, one individual on average will come up with it. At $\epsilon = 0.001$, this probability is still one in 50, so high that tool use should be seen in most orangutan populations with *Neesia* fruits. Since it is not, ϵ should realistically be in the order of 0.0001 or less.

Sumatran orangutans can live up to at least 50 years in the wild (Wich et al., 2004), so this was the maximum age (M) in the simulation. Annual mortality rates (μ) were set at 0.05, which may be somewhat high for orangutans (Wich et al., 2004), but is certainly at the low end for chimpanzees (Hill et al., 2001).

Orangutans do not effectively use tools until weaning age (roughly seven years; van Schaik, 2004), and once adult may, like chimpanzees, gradually lose interest in learning in general, and social learning in particular (e.g., Tomasello et al., 1987; Matsuzawa et al., 2001; Hobaiter and Byrne, 2010; Tennie et al., 2010). Given that they may not be effective at learning complex techniques for the first year or two, this suggests that the social-learning window (λ) is in the order of 15 years or somewhat more. This is a rough estimate, because we do not have good estimates of how age affects social learning ability or interest.

Results

General model results

The model's output is the percentage of the population that has reached technology levels TL0, 1, 2, or 3, as a function of time (in years). In Fig. 2(a), we plot this for a hypothetical great ape population with moderate sociability ($N = 501$, $\alpha = 0.2$, $\kappa = 1$, $\epsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$). At this level of sociability, TL1 can establish itself. In Fig. 2(b), we have increased sociability to $\kappa = 2$. Now, TL1 establishes itself first, peaks, and then gives way to TL2, which in turn gives way to TL3. However, both TL1 and TL2 also stay around at low levels, reflecting the presence of individuals that have not yet reached the higher TL. This is therefore an example of a population in which ratcheted technology did evolve. We also

examine the case where sociability is moderate ($\kappa = 1$), but innovation rate is two orders of magnitude higher than what we think is the case for the normal great ape situation ($\epsilon = 0.01$). Fig. 2(c) shows that only a few members of the population reach TL3. Thus, the rate of innovation itself has far less influence on the TL reached by the average population member than the nature of the transmission conditions.

Great apes and cumulative technology

Orangutans and chimpanzees have similar cognitive abilities (Deaner et al., 2006; Herrmann et al., 2007; Tennie et al., 2010), and hence similar ϵ and α . They also have comparable life histories (Hill et al., 2001; Wich et al., 2004), and hence similar mortality rates (μ) and windows for social learning (λ), leaving only sociability (κ) and population size (N) to show enough geographic variation to affect variation in technology.

Fig. 3 shows the results when the parameters were held constant at the values selected for a great ape population (Fig. 2(a)),

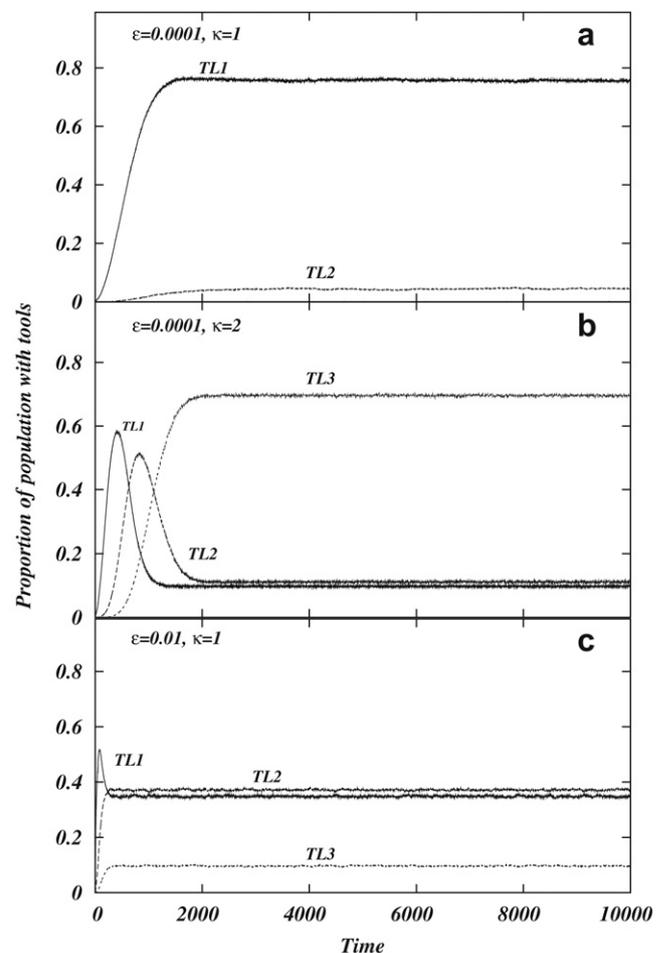


Figure 2. Examples of scenarios in which technology at various levels evolved, showing the impact of sociability in comparison with the innovative ability in hypothetical great ape populations. The plots show the equilibrium proportion of population using tools at technology levels 1 through 3 (TL1–3) as a function of time, assuming that TL3 is the highest attainable complexity of tools. (a) The parameter values representative of a hypothetical, typical great ape population ($N = 501$, $\alpha = 0.2$, $\kappa = 1$, $\epsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions). Only TL1 can establish itself. (b) If sociability is increased to $\kappa = 2$, keeping the rest of the parameters the same as in (a), the majority of the population is found to reach TL3. (c) If the sociability is still at the typical great ape level, but innovative ability ϵ is increased by two orders of magnitude ($\epsilon = 0.01$) compared with that in (a), only TL1 and TL2 are common, whereas only a small proportion reaches to TL3.

but sociability, κ , corresponding to the number of possible tolerant experts in social learning, was varied. As expected, there is a strong effect of κ . The range from 0.5 (solitary, with mother as sole companion) to 2 (on average surrounded by four knowledgeable models, one of whom is the mother) correctly reconstructs the observed patterns among great apes (van Schaik et al., 2003a). In the most solitary situation ($\kappa = 0.5$), corresponding to the orangutans in most of Borneo, we see virtually no TL1, and nothing higher, even after many years (here, 10,000). The situation with $\kappa = 1$, corresponding to the social situation in orangutans inhabiting Suaq and other swamps on Sumatra's west coast but also many chimpanzee populations, leads to customary TL1, with the odd individual reaching TL2. Once κ reaches 2, we see that TL2 or even TL3 become customary, but it is not clear whether any known chimpanzee populations reach this level of sociability.

The degree of ratcheting that can be achieved by great apes is probably limited by the 'affordance forcing' effect of the raw materials (see Table 1). This effect is expressed in the limited variability in great ape tools and the strict form–function correlation among these tools. These features reflect the biases in cognitive capacities of the species in question (the 'latent solutions'), which evolved to detect and deal with the affordances of objects in the presence of suitable problems (Tennie et al., 2009). Affordance forcing limits the amount of accumulation that can be achieved with the same raw materials, justifying stopping the simulations at a moderate level, e.g., TL3. It is also the reason why in our model we do not consider distortions in techniques, which would have arisen due to error-prone copying. However, if we allow TL to increase, at $\kappa = 2$, in equilibrium a considerable proportion of the population had reached TL4, underlining the very strong effect of sociability on ratcheting. Thus, the main finding is that increased sociability will lead to ratcheting, and thus higher TL, among great ape populations.

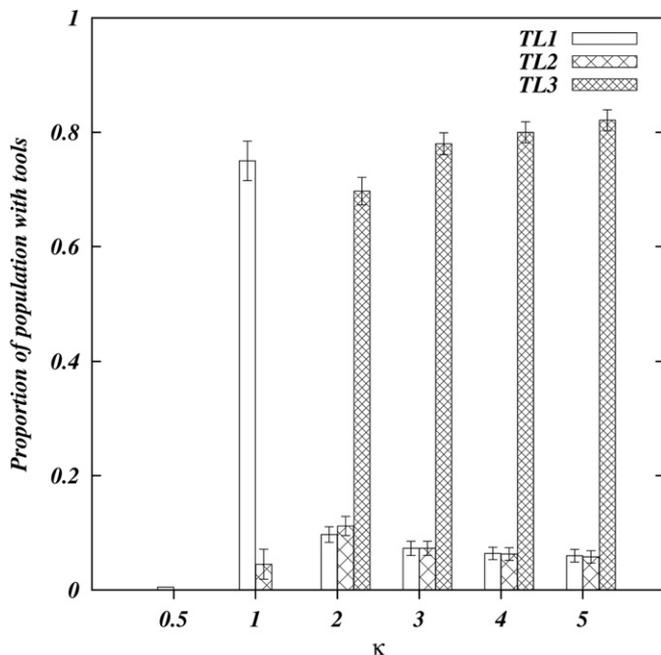


Figure 3. Variation in proportion of population using tools of varying complexity (TL1–3) as a function of sociability, κ . The error bars represent the standard deviation in the simulation outcomes. The rest of the parameter values are as in Fig. 2, viz., $N = 501$, $\alpha = 0.2$, $\epsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. For a fixed low social-learning ability, α , as κ varies from representative values for great apes to early humans, the major changes in the proportion of the population with tools at TL3 occur as κ increases from $\kappa = 1$ through $\kappa = 3$ (i.e., from 2 to 6 tolerant experts).

The effect of N , in contrast, is entirely one of timing (Fig. 4). At higher N the various TL levels are reached after a shorter number of generations, but the equilibrium levels are identical. Thus, in this model, N has no effect on the presence of the degree of accumulation of a particular technique, except in unusually small and isolated populations. This implies that a major demographic effect is expected only if populations frequently go extinct and areas are recolonized by culturally naïve individuals, initially in small populations. Both the presence for over 4000 years of nut cracking based on stone tools in chimpanzees (Mercader et al., 2002) and the unusually long temporal stability of orangutan populations in northern Sumatra (Nater et al., 2011) suggest that such demographic constraints were not ubiquitous. Moreover, known major habitat changes, such as recovery from the last glacial period, happened thousands, not hundreds, of years ago, long enough to produce equilibrium levels of cumulative technology. However, frequent local extinctions may have been an important factor in isolated populations or regions at the edge of the geographic distribution.

Hominin evolution until early Homo

Having successfully reconstructed the pattern of accumulation observed among great apes, we now examine whether the cultural

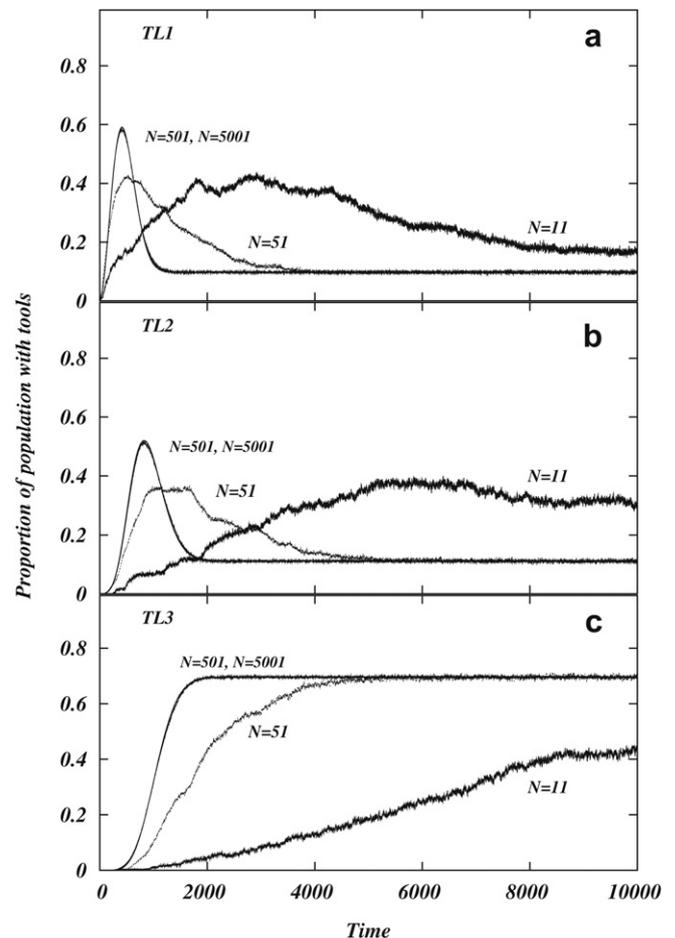


Figure 4. Proportion of the population using tools of varying complexity (TL1–3) as a function of time for varying population size. Graphs show the proportion of the population using tools of technology level TL1 (a), TL2 (b), or TL3 (c), for various values of N assuming that TL3 is the highest attainable complexity of tools. The rest of the parameters are: $\alpha = 0.2$, $\kappa = 2$, $\epsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. The total population size N affects only the time needed to reach equilibrium but not the equilibrium value.

changes in hominins with lithic technology could be a reflection of simple, immediate changes in socioecology. We do this by extending the standard great ape model as used above into parameter values known to characterize hominins. Morphological and archaeological features suggest changes in sociability, social learning through teaching, and terrestriality.

The first evidence of routine butchering of large carcasses was around by 2.5 Ma (millions of years ago) (Semaw et al., 1997; de Heinzelin et al., 1999), in a way that suggests the presence of societies with unusually high sociability, needed to either acquire the prey through hunting or defend the carcasses against large carnivores (confrontational scavenging). This suggests a clear increase in κ , which is a reliable way to get a hominin population to reach higher TL levels (Fig. 3). At $\kappa = 3$, we see that all adults reach TL3, well beyond what extant great apes can achieve. Allowing TL to move up freely yields a maximum at TL6, provided the affordances of the raw materials allow this.

There are many indications that extensive allomaternal care in the form of systematic food sharing or even provisioning, similar to what is seen among cooperatively breeding animals, began after the routine deployment of cooperative hunting subsequent to 2.5 Ma, and was firmly established by the appearance of *Homo erectus* around 1.7 Ma (Hrdy, 2009; van Schaik and Burkart, 2010; Isler and van Schaik, in press). Therefore, the demonstrators (already more numerous than earlier) probably also gradually began to engage in teaching, since teaching is common among cooperatively breeding animals with complex foraging techniques (Hoppitt et al., 2008; Rapaport and Brown, 2008; Burkart and van Schaik, 2010). Teaching, by definition, raises the social-learning ability, α . Fig. 5 shows the effect of raising α , at two levels of sociability, κ . An increase of α beyond the level seen in great apes (for instance as a result of opportunity teaching, largely amounting to providing opportunities for appropriate practice: Caro and Hauser, 1992) provides a strong boost to technological accumulation. At higher levels of κ , this effect reaches a ceiling, when we keep TL fixed at 3. Nonetheless, in less than 1000 years, such a population, despite having great-ape level cognitive abilities, will reach the maximum TL3 level. If we allow TL to evolve freely, a population with $\kappa = 3$ and $\alpha = 0.4$ will reach a maximum TL10, showing considerable ratcheting potential, probably well beyond what actually was possible with Oldowan techniques (see Table 1).

The processing of large animal carcasses necessarily took place on the ground. Among primates, systematic terrestriality can be shown to affect technological evolution because it leads to closer proximity (and thus higher κ) and systematic opportunities for affordance learning of the technology (and thus higher TL) (Meulman et al., 2012). By the time *H. erectus* appeared, these hominins had become systematically terrestrial (Bramble and Lieberman, 2004) and probably performed all skilled activities on the ground.

Discussion

Implications of the model

By ca 2.5 Ma, hominins already had reached lithic technology levels exceeding that of most chimpanzees (see Table 1), showing a definite advance toward cumulative technology. The simulations presented here suggest that this development in hominins was induced by changes in social organization that led to higher sociability, brought about by cooperative hunting or scavenging, followed by the adoption of full terrestriality and teaching elicited by systematic food sharing and provisioning, which further improved social transmission of skills. By the time *H. erectus* appeared, some time before 1.7 Ma, the relevant social parameters

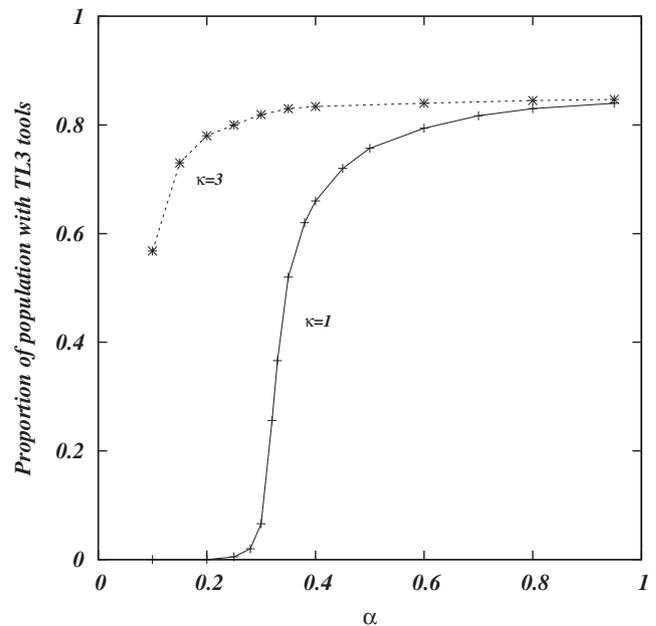


Figure 5. Proportion of the population using TL3 tools as a function of social learning ability, α . Two curves correspond to $\kappa = 1$ (solid curve; corresponds to low sociability) and $\kappa = 3$ (dotted curve; corresponds to higher sociability), respectively. The rest of the parameters are set to: $N = 501$, $\epsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. An increase of $\alpha = 0.2$ to $\alpha = 0.3$ provides a strong boost to accumulation of technology, even at low κ (solid curve). Similarly high levels could be reached at even lower α values for higher sociability (dotted curve).

(sociability κ , social learning ability α) had reached values that in the model guarantee stable cumulative technology.

The simulations imply that considerable technological accumulation can be achieved without any increase in innovation rate, population size, or development time (slower-paced life-history). The fossil and archaeological records also support this conclusion. First, the strong correlations between brain size and innovation ability in both birds and mammals (Reader and Laland, 2002; Lefebvre et al., 2004; Deaner et al., 2007) suggest that brain size can be taken as predictive of innovation level, ϵ . The Oldowan (Semaw et al., 1997) appeared well before major increases in brain size (Schoenemann, 2006). Indeed, our simulations show no effect of increased ϵ on the degree of accumulation of a particular technique (Fig. 6, in which we assume $\alpha = 0.4$ and $\kappa = 2$), except that it speeds up the time at which maximum TL is reached (similar to the effect of N). Second, these hunting or scavenging hominins occupied higher levels in the trophic pyramid, and their population sizes are therefore likely to have been smaller than those of extant great apes. However, although higher population size or connectivity would have helped, they were not required. In smaller populations the same development (ratcheting of technology) would have reached the same equilibrium level, but would merely have taken longer. The time scale of changes observed in the archaeological record indicates a very slow pace of change (Klein, 2009). Finally, the scant data on the life history of hominins predating *H. erectus*, as deduced from tooth development (Schwartz, in prep.), indicate faster development than among extant great apes, and hence higher, rather than lower, mortality.

The model therefore strongly suggests that the first stages of cumulative technology required no increases in cognitive abilities (abilities to innovate or learn socially), because populations could achieve higher ratcheting levels so long as the essential innovations arose with some non-zero probability and were passed on with some non-zero probability. Obviously, these cultural changes were

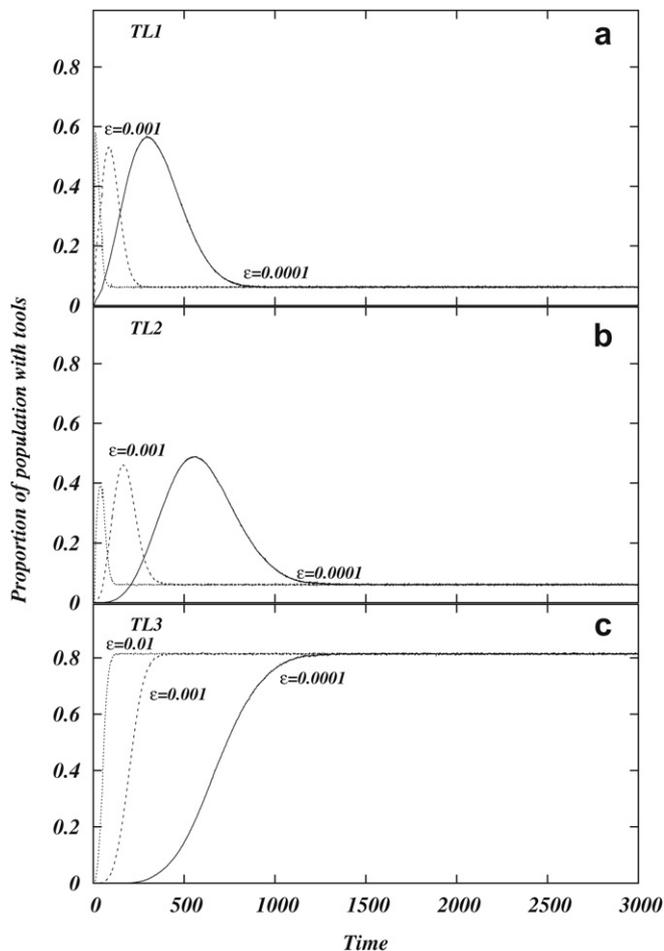


Figure 6. Proportion of the population using tools of varying complexity as a function of time for varying innovation rates: (a) TL1, (b) TL2, and (c) TL3. The inventive ability, ϵ , is varied assuming that TL3 is the highest attainable complexity of tools. The rest of the parameters are: $\alpha = 0.4$ (higher than great ape level), $\kappa = 2$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. Even orders of magnitude change in ϵ only affects the time needed to reach equilibrium but not the equilibrium value.

themselves likely to have served as the impetus for the subsequent evolution of greater cognitive abilities, especially via improved social-learning abilities, which secondarily improved innovative capacity as well (Wyles et al., 1983; van Schaik and Pradhan, 2003; Whiten and van Schaik, 2007; van Schaik and Burkart, 2011).

These results may appear to contradict the results of theoretical work on recent cultural accumulation in human evolution (Culotta, 2010), which stress the role of population expansion (Powell et al., 2009) and cognitive changes leading to increased innovation (Coolidge and Wynn, 2009). However, the pace of cultural change in (what is now visible in) the Oldowan and Acheulean was so slow that population size, which affects the time it takes for specific innovations to become established, hardly mattered. Moreover, increased innovation rate is both a direct and indirect outcome of accumulation itself. Thus, in the Middle and Upper Paleolithic, other processes may have determined cultural evolution.

The model's results also would suggest that considerable ratcheting of technology should have been possible, well beyond the Oldowan technology seen in the record for well over a million years, and should also still encompass the early Acheulean (cf. Table 1). This discrepancy may be more apparent than real because of the limitations of the archaeological record, which does not retain any use of plant-based tools, alone or in combination with stone tools. Indeed, the greatest complexity would be reached for

tool sets, functional sequences of (usually fairly simple) tools, as seen in the chimpanzees, but they likewise cannot be recognized in the archaeological record. However, if the discrepancy is real, this implies that our model cannot be applied to later stages of hominin evolution. The most likely reason for this is that neither great apes nor early hominins could reach higher TL than the moderate levels (TL3 or TL4) examined in this model, due to limits on the amount of ratcheting imposed by the nature of the raw materials in combination with the cognitive biases (see above), or the increased cognitive difficulty of producing further modifications due to constraints on working memory.

Model assumptions

The model results obviously depend on our operationalization of ratcheting. First, it assumes, with Davidson and McGrew (2005) and Wynn et al. (2011), that the cognitive challenges posed by stick tools and stone tools both depend on the technology level (TL) and thus the depth of the planning hierarchy, despite clear differences in the kinds of actions performed on sticks and stones. Thus, a clear prediction is that the same population of a given species should reach similar TL in different kinds of technology.

Table 1 might seem to indicate that this assumption is wrong, as chimpanzees, the only great ape species to use any stone tools in the wild, do not reach higher TL in such tools, in stark contrast to stick tools, which have ratcheted up to TL3 in the wild. However, the discrepancy may only be apparent. Wild chimpanzees are doubly disadvantaged when it comes to ratcheting stone tools. Chimpanzees lack the need for artificial sharp edges (their teeth are long, strong and sharp enough for the problems they face, as pointed out by Davidson and McGrew (2005) as well as Toth and Schick (2009)), and even if they would discover the need for sharp tools, their environment largely lacks the suitable stone resources that could be knapped (Carvalho et al., 2008).

It is therefore important to explore the capacity of captive apes. As it happened, besides a pioneer study on one orangutan (Wright, 1972) all work on great ape flaking has focused on bonobos, not chimpanzees. Kanzi, the main tested bonobo, developed, perfected, and later preferred, to throw the stones given to him against each other in order to produce blades. He developed this preference over the course of only 120 h of experience (Schick et al., 1999). Importantly, Kanzi invented the throwing technique without having seen it modeled (thus, this is clearly a behavior within the bonobo ZLS) – and which is a behavior that remains to be analyzed in complexity and compared to two-handed flint knapping, in the way proposed by Bril et al. (2012). Certainly, the products thus produced were not fully comparable with Oldowan artifacts. Bril et al. (2012) take this to mean that Oldowan flint knapping included some more complex behaviors than we can find in modern great apes, but did not consider the possibility that Kanzi failed in this respect perhaps because he was biomechanically restricted (Toth and Schick, 2009) in a way that chimpanzees might not be. Moreover, a female bonobo called Panbanisha was observed “making stone tools, and she appeared to calculate angles before hitting the core” (Davidson and McGrew, 2005: 799). It was also not the case that Kanzi could not flake in a hand-held, bimanual way. Kanzi may have simply realized that, for him, to flint knap in a two-handed way was less efficient than the throwing technique; perhaps not so much for cognitive, but merely for anatomical reasons.

Given the higher proficiency of tool use of chimpanzees in the wild in contrast with bonobos (e.g., Whiten et al., 1999), the best way to definitively test Bril et al. (2012) hypothesis is to test chimpanzees. At present, all we have is an unpublished study by Sarah Boysen and her team, who for the first time have provided

chimpanzees with the need (a reward box with a rope-lock) as well as the necessary raw material to flint knap (a granite hammer stone and a raw flint rock). After two short demonstrations, one of the two tested chimpanzees flint knapped with high proficiency – at a level that, at preliminary analysis, clearly outperformed previously tested bonobos (S. Boysen, personal communication). The resulting sharp edge was immediately used to cut through the rope that hindered the chimpanzee to get the reward. This to us shows the higher potential for flint knapping in chimpanzees in contrast to bonobos. Thus, the chimpanzee may not only have the cognitive capacity for Oldowan-like tools, it may also have the motor control make Oldowan-like tools (somewhat in contrast, perhaps, to the case of bonobos), consistent with the critical assumption of our modeling study (cf. Wynn et al., 2011).

A second testable prediction of this operationalization of ratcheting is that developing individuals should make simpler versions of tools before they make the more ratcheted ones. This would seem to hold true of currently living great apes and extinct hominins. Thus, we predict that immature chimpanzees should learn to make termite probes first, and then later on learn how to fray the sticks' ends to make them brushy, rather than to learn all of this at once (or if they do learn it all at once, they must learn it after longer practice, so probably at a later age than those in other populations that use simple probes). A third testable prediction is that ratcheted tools should have a more limited geographic distribution, and should often be nested inside the region of 'ancestral' simple forms from which they derive. Finally, it is to be hoped that neurobiological correlates of ratcheting can be revealed, which allow comparisons across species and tasks.

Future work should therefore test the model's assumptions. This may lead to modified conclusions. However, Sanz and Morgan (2010) recent attempt to apply different systems of accounting for complexity to tools used by Goulougo chimpanzees revealed only modest discrepancies between them. Future work should thus also show to what extent classifications of complexity must also incorporate the choice of raw materials and the complexity of actions (Haidle, 2010; Stout, 2011).

Apart from the measurement of ratcheting, the model also assumed a role for sociability, the number of available role models. As an earlier model (van Schaik and Pradhan, 2003) predicted, evidence can indeed be found for enhanced culture in groups of great apes that are more sociable (Whiten and van Schaik, 2007). However, to the best of our knowledge the parameters identified here as the major ones for the accumulation of culture have not yet been measured systematically in wild great ape populations and subsequently been correlated with the amount of ratcheting observed (let alone manipulated experimentally). This may also be due to the fact that accumulation is rare in great apes, and that thus any such correlation is hard to establish. We hope that future work in both field and captivity will test these various predictions.

Technological evolution

The results of this study suggest a new perspective on the nature and timing of the major transitions in the cultural evolution of technology in primates and humans (Fig. 7). The first phase began with the origin of simple culturally based technologies. It required the presence of extractive foraging and some cognitive abilities, enabling innovation and social learning (van Schaik et al., 1999). This level is reached by many great ape and some monkey (Otoni and Izar, 2008; Gumert et al., 2009) populations, as well several non-primate lineages of mammals and birds (Whiten and van Schaik, 2007).

The second phase began with the origin of ratcheted technology. This can be elicited in captive apes and is found among some

chimpanzee populations (and by inference early hominins), and is routinely present in late Pliocene and early Pleistocene hominins. We suggested here that this transition was made possible by increased sociability and terrestriality, and subsequently teaching (see also Tomasello (2009)). However, this process probably also reaches some ceiling, set by material, cognitive (especially size of working memory), demographic and life-history limitations, reached by early *Homo*. The complexity of each particular technique may also reach a ceiling because an individual may have to learn various different techniques simultaneously, and thus cannot fully concentrate on any single technique. It may be difficult to break through this ceiling because each individual must learn to produce all the technology used in its society and is therefore constrained by learning time (although this gets longer as life-history pace slows down, and especially as the learning window expands). It is still possible, of course, that adaptations could have enabled hominins to move beyond this ceiling. For instance, lengthening the duration of the learning period (λ) will help. Nonetheless, some limitation should emerge, and our model strongly suggests that the prime mover was not cumulative culture per se.

Because of the constraints on learning time, we propose a third transition in cultural evolution to explain levels of accumulation beyond the ones we have modeled here. Moving beyond the results of our models, we speculate that it was caused by the appearance of donated technology, which relied on two major components: technology transfer and specialization (Fig. 7). In technology transfer, naïve individuals would receive implements or concepts that they did not invent and could not design and produce themselves, allowing them to skip many steps in the ratcheting process and use these technologies to invent further ratcheted technologies. Thus, here we can begin to encounter cumulative culture in the sense of the appearance and subsequent routine use of innovations well beyond the innovative reach of individuals (cf. Galef, 1992; Tomasello et al., 1993; Boyd and Richerson, 1996). Specialization, or advanced division of labor, means that individuals no longer need to learn all of the technology used in a particular society, but can instead focus on acquiring a particular subset of skills. This almost inevitably produces higher technology levels in the population as well. Specialization can be recognized ethnographically by examining the TL level at which requests for help with the repair of tools and implements are made. One can also recognize it in the archaeological record with the onset of long-distance trade (which presupposes specialization, unless the traded items were naturally occurring resources that were traded prior to processing them).

Both of these novel features imply larger societies with a high level of cooperation and enough of a food surplus to support specialists that are not full-time food producers. Moreover, the high

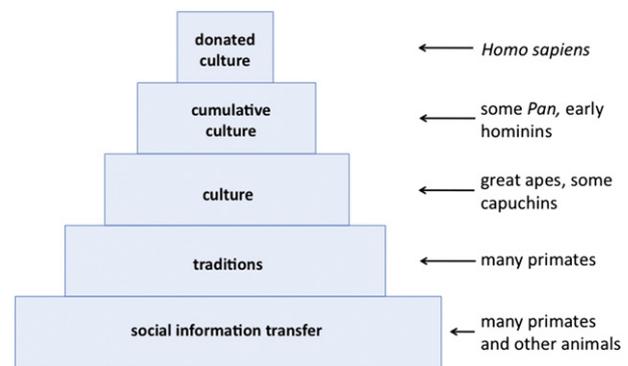


Figure 7. The culture pyramid (modified after Whiten and van Schaik (2007)), showing the hierarchical or nested-subset nature of various manifestations of culture.

technology implies at least part-time sedentism and presumably trading of specialist products.

Because individuals can skip technology levels by using implements produced by other experts, and because different specialists acquire different skills, this third phase has a far greater potential to produce run-away cumulative technology. Hence, it is in this phase that demographic limitations (and therefore also time) become important, as stressed by recent archeological models that focus on relatively recent changes in the technology of *Homo sapiens* (Shennan, 2001; Henrich, 2004; Powell et al., 2009).

Conclusions

This modeling study showed that we could explain variation among orangutans and chimpanzees in the presence and degree of accumulation of their (mainly wood-based) technology with reference to varying sociability, which affects the opportunities for social learning. The degree of accumulation of technology well into levels shown by the most complex Oldowan tools can plausibly be attributed to further increases in sociability, and the introduction of teaching, which increases the probability of acquiring a skill through social learning. Thus, according to the model, no major cognitive changes, relative to extant great apes, were needed to explain the origin and initial elaboration of lithic technology in the hominin lineage, consistent with the observation that the two taxa had similar brain sizes. Our model also indicates that population (network) size is less important than previously thought – though it can be still important in timing, especially with regard to the rate of environmental change (d'Errico and Stringer, 2011). However, once populations consistently began to have highly ratcheted technology, selection may have begun to favor enhanced cognitive abilities, allowing faster developmental acquisition and (as a byproduct) the innovation of more complex techniques. Indeed, by the time the Acheulean appeared, hominin brain sizes exceeded those of extant great apes. This argument suggests that the seemingly autocatalytic increase in brain size during the early evolution of *Homo* was driven by technological evolution rather than by other factors such as social complexity per se.

Because considerable cumulative cultural evolution is possible with great ape sized brains, as implied by results from the wild and experiments in captivity, the ratcheted technology of hominins should no longer be considered qualitatively unique, although they subsequently pushed it to much higher levels than the extant great apes. We speculate that a truly qualitative change in technological evolution came much later, in the form of donated technology, when individuals could use the products of others' efforts as their starting point, allowing them to skip many steps in the learning process, and individuals could also specialize in acquiring particular subsets of the skills present in the population as a whole.

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References

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., Matsuzawa, T., 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* 6, 213–223.

Boesch, C., 2003. Is culture a golden barrier between humans and chimpanzee? *Evol. Anthropol.* 12, 82–91.

Boesch, C., Head, J., Robbins, M.M., 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *J. Hum. Evol.* 56, 560–568.

Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., Joulain, F., 1994. Is nut cracking in wild chimpanzees a cultural-behavior? *J. Hum. Evol.* 26, 325–338.

Boyd, R., Richerson, P.J., 1996. Why culture is common, but cultural evolution is rare. *Proc. Brit. Acad.* 88, 77–93.

Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432, 345–352.

Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata, S., Roux, V., 2012. Functional mastery of percussive technology in nut-cracking and stone-flaking actions: experimental comparison and implications for the evolution of the human brain. *Phil. Trans. R. Soc. B* 367, 59–74.

Burkart, J.M., van Schaik, C.P., 2010. Cognitive consequences of cooperative breeding in primates. *Anim. Cogn.* 13, 1–19.

Byrne, R.W., 1995. *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford University Press, Oxford.

Byrne, R.W., Tanner, J.E., 2006. Gestural imitation by a gorilla: evidence and nature of the capacity. *Int. J. Psych. Psychol. Ther.* 6, 215–231.

Caro, T.M., Hauser, M.D., 1992. Is there teaching in nonhuman animals? *Q. Rev. Biol.* 67, 151–174.

Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaines operatoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J. Hum. Evol.* 55, 148–163.

Claidière, N., Sperber, D., 2010. Imitation explains the propagation, not the stability of animal culture. *Proc. Roy. Soc. B* 277, 651–659.

Coolidge, F.L., Wynn, T., 2009. *The Rise of Homo sapiens: The Evolution of Modern Thinking*. Wiley-Blackwell, Oxford.

Culotta, E., 2010. Did modern humans get smart or just get together? *Science* 328, 164.

d'Errico, F., Stringer, C.B., 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures? *Phil. Trans. R. Soc. B* 366, 1060–1069.

Davidson, I., McGrew, W.C., 2005. Stone tools and the uniqueness of human culture. *J. Roy. Anthropol. Inst.* 11, 793–817.

Deaner, R.O., Isler, K., Burkart, J.M., van Schaik, C.P., 2007. Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behav. Evol.* 70, 115–124.

Deaner, R.O., van Schaik, C.P., Johnson, V., 2006. Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evol. Psychol.* 4, 149–196.

de Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-Million-year-old Bouri hominids. *Science* 284, 625–629.

Dindo, M., Stoinski, T., Whiten, A., 2011. Observational learning in orangutan cultural transmission chains. *Biol. Lett.* 7, 181–183.

Dominguez-Rodrigo, M., Serrallonga, J., Juan, J., Alcalá, L., Luque, L., 2001. Wood-working activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *J. Hum. Evol.* 40, 289–299.

Enquist, M., Strimling, P., Eriksson, K., Laland, K.N., Sjostrand, J., 2010. One cultural parent makes no culture. *Anim. Behav.* 79, 1353–1362.

Galef Jr., B.G., 1992. The question of animal culture. *Hum. Nat.* 3, 157–178.

Gruber, T., Muller, M.N., Strimling, P., Wrangham, R., Zuberbuhler, K., 2009. Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Curr. Biol.* 19, 1806–1810.

Gumert, M.D., Kluck, M., Malaivijitnond, S., 2009. The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. *Am. J. Primatol.* 71, 594–608.

Haidle, M.N., 2010. Working-memory capacity and the evolution of modern cognitive potential: implications from animal and early human tool use. *Curr. Anthropol.* 51, S149–S166.

Harary, F., 1969. *Graph Theory*. Addison-Wesley Publishing Company, Reading.

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

Herrmann, E., Call, J., Hernandez-Lloreda, M.V., Hare, B., Tomasello, M., 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317, 1360–1366.

Hill, K., 2009. Animal 'culture'. In: Laland, K.N., Galef, B.G. (Eds.), *The Question of Animal Culture*. Harvard University Press, Cambridge, pp. 269–287.

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., Wrangham, R., 2001. Mortality rates among wild chimpanzees. *J. Hum. Evol.* 40, 437–450.

Hobaiter, C., Byrne, R.W., 2010. Able-bodied wild chimpanzees imitate a motor procedure used by a disabled individual to overcome handicap. *PLoS ONE* 5, e11959.

Hoppitt, W.J.E., Brown, G.R., Kendal, R., Rendell, L., Thornton, A., Webster, M.M., Laland, K.N., 2008. Lessons from animal teaching. *Trends Ecol. Evol.* 23, 486–493.

Hrdy, S., 2009. *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Harvard University Press, Cambridge.

Isler, K., van Schaik, C.P. How our ancestors broke through the gray ceiling: comparative evidence for cooperative breeding in early *Homo*, *Current Anthropology*, in press.

Jaeggi, A., Dunkel, L., van Noordwijk, M.A., Wich, S.A., Sura, A.A.L., van Schaik, C.P., 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am. J. Primatol.* 72, 62–71.

Klein, R., 2009. *The Human Career: Human, Biological and Cultural Origins*, third ed. Chicago University Press, Chicago.

Krützen, M., Willems, E.P., van Schaik, C.P., 2011. Culture and geographic variation in orangutan behavior. *Curr. Biol.* 21, 1808–1812.

- Lefebvre, L., Reader, S.M., Sol, D., 2004. Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* 63, 233–246.
- Lehner, S.R., Burkart, J.M., van Schaik, C.P., 2011. Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques? *J. Comp. Psychol.* 125, 446–455.
- Lonsdorf, E.V., Eberly, L.E., Pusey, A.E., 2004. Sex differences in learning in chimpanzees. *Nature* 428, 715–716.
- Matsuzawa, T., 1996. Chimpanzee intelligence in nature and in captivity: isomorphism of symbol use and tool use. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, New York, pp. 196–209.
- Matsuzawa, S., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., 2001. Emergence of culture in wild chimpanzees: education by master apprenticeship. In: Matsuzawa, S. (Ed.), *Primate Origins of Human Cognition and Behavior*. Springer, Tokyo, pp. 557–574.
- Meulman, E.J.M., Sanz, C.M., Visalberghi, E., van Schaik, C.P., 2012. The role of terrestriality in promoting primate technology. *Evol. Anthropol.* 21, 58–68.
- Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296, 1452–1455.
- Nater, A., Nietlisbach, P., Arora, N., van Schaik, C.P., van Noordwijk, M.A., Willems, E.P., Singleton, I., Wich, S.A., Goossens, B., Warren, K.S., Verschoor, E.J., Perwitasari-Farajallah, D., Pamungkas, J., Krutzen, M., 2011. Sex biased dispersal and volcanic activities shaped phylogeographic patterns of extant orangutans (genus: *Pongo*). *Mol. Biol. Evol.* 28, 2275–2288.
- Nonaka, T., Bril, B., Rein, R., 2010. How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. *J. Hum. Evol.* 59, 155–167.
- Oswalt, W.H., 1976. *An Anthropological Analysis of Food-Getting Technology*. John Wiley, New York.
- Ottoni, E., Izar, P., 2008. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Evol. Anthropol.* 17, 171–178.
- Powell, A., Shennan, S., Thomas, M.G., 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science* 324, 1298–1301.
- Price, E.E., Lambeth, S.P., Schapiro, S.J., Whiten, A., 2009. A potent effect of observational learning on chimpanzee tool construction. *Proc. Roy. Soc. B* 276, 3377–3383.
- Rapaport, L.G., Brown, R.B., 2008. Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evol. Anthropol.* 17, 189–201.
- Reader, S.M., Biro, D., 2010. Experimental identification of social learning in wild animals. *Learn. Behav.* 38, 265–283.
- Reader, S.M., Laland, K.N., 2002. Social intelligence, innovation and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U S A* 99, 4436–4441.
- Sanz, C.M., Morgan, D.B., 2007. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *J. Hum. Evol.* 52, 420–433.
- Sanz, C., Morgan, D., 2010. The complexity of chimpanzee tool using behaviors. In: Lonsdorf, E.V., Ross, S.R., Matsuzawa, T. (Eds.), *The Mind of the Chimpanzee*. University of Chicago Press, Chicago, pp. 127–140.
- Sanz, C., Morgan, D., Gulick, S., 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *Am. Nat.* 164, 567–581.
- Sanz, C.M., Schöning, C., Morgan, D.B., 2009. Chimpanzees prey on army ants with specialized tool set. *Am. J. Primatol.* 71, 1–8.
- Schick, K.D., Toth, N., 1993. *Making Silent Stones Speak: Human Evolution and the Dawn of Technology*. Simon and Schuster, New York.
- Schick, K.D., Toth, N., Garufi, G., Savage-Rumbaugh, S., Rumbaugh, D., Sevcik, R., 1999. Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *J. Archaeol. Sci.* 26, 821–832.
- Schoenemann, P.T., 2006. Evolution of the size and functional areas of the human brain. *Annu. Rev. Anthropol.* 35, 379–406.
- Semaw, S., Renne, P., Harris, J.W.K., Feibel, C.S., Bernor, R.L., Fesseha, N., Mowbray, K., 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385, 333–336.
- Shennan, S., 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Camb. Archaeol. J.* 11, 5–16.
- Singleton, I., Wich, S.A., Husson, S., Stephens, S., Utami-Atmoko, S.A., Leighton, M., Rosen, N., Traylor-Holzer, K., Lacy, R., Byers, O., 2004. Orangutan Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialists Group, Apple Valley.
- Stout, D., 2011. Stone toolmaking and the evolution of human culture and cognition. *Phil. Trans. R. Soc. B* 366, 1050–1059.
- Tennie, C., Call, J., Tomasello, M., 2006. Push or pull: imitation vs. emulation in great apes and human children. *Ethology* 112, 1159–1169.
- Tennie, C., Call, J., Tomasello, M., 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* 364, 2405–2415.
- Tennie, C., Call, J., Tomasello, M., 2010. Evidence for emulation in chimpanzees in social settings using the floating peanut task. *Plos One* 5, e10544.
- Tomasello, M., 1994. The question of chimpanzee culture. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G., Marquardt, L.A. (Eds.), *Chimpanzee Cultures*. Harvard University Press, Cambridge, pp. 301–318.
- 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, K.N., Galef Jr., B.G. (Eds.), *The Question of Animal Culture*. Harvard University Press, Cambridge, pp. 198–221.
- Tomasello, M., Davis-Dasilva, M., Camak, L., Bard, K.A., 1987. Observational learning of tool-use by young chimpanzees. *Hum. Evol.* 2, 175–183.
- Tomasello, M., Kruger, A.C., Ratner, H.H., 1993. Cultural learning. *Behav. Brain Sci.* 16, 495–552.
- Toth, N., Schick, K., 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *Annu. Rev. Anthropol.* 38, 289–305.
- Uomini, N.T., 2009. The prehistory of handedness: archaeological data and comparative ethology. *J. Hum. Evol.* 57, 411–419.
- van Noordwijk, M.A., Sauren, S.E.B., Nuzuar Abulami, A., Morrogh-Bernard, H., Utami Atmoko, S.S., van Schaik, C.P., 2009. Development of independence. In: Wich, S.A., Mitra Setia, T., Utami Atmoko, S.A., van Schaik, C.P. (Eds.), *Orangutans Compared: Geographic Variation in Behavioral Ecology and Conservation*. Oxford University Press, Oxford, pp. 189–203.
- van Schaik, C.P., 2004. Among Orangutans: Red Apes and the Rise of Human Culture. Harvard University Press, Cambridge.
- van Schaik, C.P., 2009. Geographic variation in the behavior of wild great apes: is it really cultural? In: Laland, K.N., Galef Jr., B.G. (Eds.), *The Question of Animal Culture*. Harvard University Press, Cambridge, pp. 70–98.
- van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami-Atmoko, S.S., Merrill, M.Y., 2003a. Orangutan cultures and the evolution of material culture. *Science* 299, 102–105.
- van Schaik, C.P., Burkart, J.M., 2010. Mind the gap: cooperative breeding and the evolution of our unique features. In: Kappeler, P.M., Silk, J. (Eds.), *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Berlin, pp. 477–496.
- van Schaik, C.P., Burkart, J.M., 2011. Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B* 366, 1008–1016.
- van Schaik, C.P., Deaner, R.O., Merrill, M.Y., 1999. The conditions for tool use in primates: implications for the evolution of material culture. *J. Hum. Evol.* 36, 719–741.
- van Schaik, C.P., Fox, E.A., Fechtman, L.T., 2003b. Individual variation in the rate of use of tree-hole tools among wild orang-utans: implications for hominin evolution. *J. Hum. Evol.* 44, 11–23.
- van Schaik, C.P., Knott, C., 2001. Geographic variation in tool use on *Neesia* fruits in orangutans. *Am. J. Phys. Anthropol.* 114, 331–342.
- van Schaik, C.P., Pradhan, G.R., 2003. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *J. Hum. Evol.* 44, 645–664.
- Wich, S.A., Utami-Atmoko, S.S., Mitra Setia, T., Rijksen, H.D., Schurmann, C., van Hooff, J.A.R.A.M., van Schaik, C.P., 2004. Life history of wild Sumatran orangutans (*Pongo abelii*). *J. Hum. Evol.* 47, 385–398.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. *Nature* 399, 682–685.
- Whiten, A., McGuigan, N., Marshall-Pescini, S., Hopper, L., 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* 364, 2417–2428.
- Whiten, A., Mesoudi, A., 2008. Establishing an experimental science of culture: animal social diffusion experiments. *Phil. Trans. R. Soc. B* 363, 3477–3488.
- Whiten, A., Spiteri, A., Horner, V., Bonnie, K.E., Schapiro, S.J., de Waal, F.B.M., 2007. Transmission of multiple traditions within and between chimpanzee groups. *Curr. Biol.* 17, 1–6.
- Whiten, A., van Schaik, C.P., 2007. The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* 362, 603–620.
- Wright, R.V.S., 1972. Imitative learning of a flaked tool technology: the case of an orangutan. *Mankind* 8, 296–306.
- Wyles, J.S., Kunkel, J.G., Wilson, A.C., 1983. Birds, behavior, and anatomical evolution. *Proc. Natl. Acad. Sci. U S A* 80, 4394–4397.
- Wynn, T., Hernandez-Aguilar, R.A., Marchant, L.F., McGrew, W.C., 2011. "An ape's view of the Oldowan" revisited. *Evol. Anthropol.* 20, 181–197.
- 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 virus*) at Bossou, Guinea. *Am. J. Primatol.* 70, 699–702.