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Studying Cumulative Cultural Evolution in the Laboratory

Christine A. Caldwell
Ailsa E. Millen
Department of Psychology, University of Stirling, UK

Cumulative cultural evolution is the term given to a particular kind of social learning, which allows for the accumulation of modifications over time, involving a ratchet-like effect where successful modifications are maintained until they can be improved upon. There has been great interest in the topic of cumulative cultural evolution from researchers from a wide variety of disciplines, but until recently there were no experimental studies of this phenomenon. Here we describe our motivations for developing experimental methods for studying cumulative cultural evolution, and review results we have obtained using these techniques. The results that we describe have provided insights into understanding the outcomes of cultural processes at the population level. Our experiments show that cumulative cultural evolution can result in adaptive complexity in behaviour, and also can also produce convergence in behaviour. These findings lend support to ideas that some behaviours commonly attributed to natural selection and innate tendencies could in fact be shaped by cultural processes.

1. Background

In this review, we aim to explain why there is currently a need for an experimental science of cumulative cultural evolution. We will discuss methods that we have developed which we believe can be employed in order to test experimental hypotheses about cumulative cultural evolution. We will also discuss results that we have obtained using these methods, and the implications that these findings have for our understanding of the effects of cumulative cultural evolution on human behaviour.

1.1. What is cumulative cultural evolution?

In order to explain the motivation behind our research on cumulative cultural evolution, we begin by explaining why it is an interesting behavioural phenomenon and an important topic of study. Cumulative cultural evolution is distinct from culture in the general sense in a number of ways. Whilst culture is accepted by most to refer to a socially transmitted heritage peculiar to a particular society (Boyd & Richerson 1985)[1], the definition of cumulative cultural evolution

[1] It should be noted that there are many different definitions of culture in the literature. Kroeber and Kluckhohn (1952) identified multiple different definitions from authors from a variety of disciplines. Boyd and Richerson (1985) point out that, within Kroeber and Kluckhohn's definitions, there is broad agreement on the notion of culture as socially transmitted heritage

is considerably narrower. Boyd and Richerson (1994) showed that social learning could increase the average fitness of a population if it permitted “learned improvements to accumulate from one generation to the next” (p134), essentially describing what they later termed cumulative cultural evolution (Boyd & Richerson 1996). Tomasello (1990; 1999; Tomasello et al. 1993) has coined the term “the ratchet effect” to capture a similar notion: “The process of cumulative cultural evolution requires not only creative invention but also, and just as importantly, faithful social transmission that can work as a ratchet to prevent slippage backward – so that the newly invented artifact or practice preserves its new and improved form at least somewhat faithfully until a further modification or improvement comes along.” (Tomasello, 1999, p5). Hence, cumulative cultural evolution refers to situations in which social transmission allows for successive improvements to performance over generations of learners, generated by the accumulation of modifications to the transmitted behaviours.

Cumulative cultural evolution in this sense should be distinguished from cultural evolution which does not lead to appreciable improvement in efficiency of the behaviours in question. Mesoudi et al. (2004) have argued that all of human culture constitutes an evolutionary process, since it involves variation (multiple traits that may be copied), heritability (similarity between traits as a result of copying), and competition (some traits are copied more than others), leading to the accumulation of modifications over time. However, not all such examples involve increasing efficiency or complexity. They therefore do not constitute the kind of learning that Richerson and Boyd (1994) or Tomasello (1999) were referring to, whereby each generation is provided with shortcuts to the end results of extensive trial and error learning amassed by their cultural ancestors. So, although methods developed in evolutionary biology are currently proving extremely useful in reconstructing the history of cultural products, such as textile designs (Tehrani and Collard 2002), linguistic forms (Gray and Jordan 2000), and stories (Barbrook et al. 1998), these examples do not represent the kind of process that we are referring to as cumulative cultural evolution.

All the same, even in these narrow terms, cumulative cultural evolution seems to pervade human society. Each generation builds on the knowledge, inventions and achievements of the previous one. Our present-day technologies exist only as a result of our ability to understand and make use of the imparted knowledge and artefacts of others. In contrast, the phenomenon of cumulative cultural evolution seems to be intriguingly rare in nonhumans. This is despite the fact that there are plenty of cases of animal culture in the more general sense. To take just one well-known example, the sweet potato washing behaviour of the Japanese macaques of Koshima (e.g. Kawai 1965; Kawamura 1959), appears to have been acquired through social learning, since the behaviour spread initially to the close associates of the first monkey to use this technique, and then on to those individuals’ associates. However, as a number of researchers have pointed out (most notably Boyd & Richerson 1996), examples of animal social learning such as this typically involve relatively simple behaviours that could also be readily

peculiar to a particular society, which is why we selected this description. Our criteria for culture in the general sense are therefore intentionally broad and inclusive.

learned through individual trial and error processes. There is little evidence of successive improvement over generations, or of the accumulation of modifications, and therefore no suggestion that the behaviours concerned could not have been invented by a single individual.

1.2. Debates in cumulative cultural evolution

A strong motivation for us in developing experimental methods for studying cumulative cultural evolution was the fact that there are a number of important unresolved issues surrounding this topic which have been the focus of much debate. The issue of whether cumulative cultural evolution is unique to humans, or merely relatively rare in nonhumans, is just one of these. In addition, there is still disagreement over the learning mechanisms upon which cumulative cultural evolution may depend, and also the extent to which it is responsible for complex adaptive human behaviours. The details of these debates are summarised below.

1.2.1. Human uniqueness. The question that has probably drawn the most attention surrounding cumulative cultural evolution is that of whether the phenomenon is unique to humans. As noted above, Boyd and Richerson (1996), amongst others, have drawn attention to the fact that although social learning is relatively common in the animal kingdom, cumulative cultural evolution appears to be extremely rare: “cumulative cultural evolution resulting in behaviors that no individual could invent on their own is limited to humans, song birds, and perhaps chimpanzees” (Boyd & Richerson 1996, p77). Likewise, Heyes (1993) has drawn a distinction between the sorts of behaviours that nonhumans appear to learn socially, in comparison with those of humans: “the human attributes that are described as ‘cultural’ in ordinary discourse, seem to be a good deal more complex than, for example, potato washing and termite-fishing…and it is plausible that their greater complexity derives from the accumulation of modifications” (Heyes 1993, p1004).

Even stronger statements have been made by others. For example, Galef (1992) has stated that “human culture accumulates over generations and can lead to invention and transmission of increasingly complex behaviours. No one has claimed that any animal learns any behaviour from conspecifics that it could not learn independently through interaction with its physical environment” (Galef 1992, p161). Along similar lines, Tomasello (1999) has asserted that “the cultural traditions and artifacts of human beings accumulate modifications over time in a way that those of other animal species do not” (Tomasello 1999, p5).

Of course, these authors are not claiming that social learning does not help animals to acquire useful behaviours. The example of the Koshima macaques illustrates how an advantageous invention can readily spread through a group. The issue is again the notion of the cultural ratchet, and of later generations exploiting the labours of previous ones in a way that allows them to make use of behaviours that they could not have learned by themselves.

All the same, some researchers have argued that there is in fact compelling evidence for cumulative cultural evolution in nonhumans. For example, Boesch (2003) cites three examples of chimpanzee behaviours which he suggests may have arisen through accumulated modifications of socially learned behaviour. One of these is nut cracking behaviour, which is observed in West African chimpanzee populations (Whiten et al. 1999). While some chimpanzees use fixed anvils, such as tree roots, others use loose stones. Furthermore, Sugiyama (1997) reported that some chimpanzees at the Bossou field site sometimes used an extra stone to stabilise the stone anvils upon which the nut is placed for cracking, perhaps indicating a refinement on the simpler technique.

Whiten et al. (2003) have put forward similar examples of possible cumulative culture in chimpanzees, including the nut cracking behaviour just mentioned. They also suggested that the alternative tool-use techniques used to forage on ants could show evidence of ratcheting. Of the two methods used, one is more elaborate, involving bimanual coordination, and also results in a greater yield (Humle & Matsuzawa 2002) and therefore Whiten et al. (2003) suggested that this could represent an elaboration on the simpler version.

Cumulative culture has also been proposed in species other than chimpanzees. Hunt and Gray (2003) proposed that the tool manufacture skills observed in New Caledonian crows had been acquired through cumulative cultural evolution. They were able to document population specific methods of tool manufacture, which were apparently unrelated to local ecological conditions, and these different methods showed varying degrees of complexity. They therefore argued that these different techniques had been developed through cumulative cultural evolution. However, it is still unclear whether these techniques are socially learned at all, as it seems that tool manufacture abilities may be largely under genetic control in this species (Kenward et al. 2005).

There is clearly good reason to remain open-minded with regard to the question of whether cumulative cultural evolution is unique to humans. Boesch and Tomasello (1998), for example, have made the point that we have very little data on the behaviour of previous generations of chimpanzees, since long-term studies of their behaviour only began around forty years ago. This inevitably makes it difficult to judge whether their behaviour has shown any ratcheting over time.

1.2.2. The cognitive underpinnings of cumulative cultural evolution. Related to the above debate, researchers have also deliberated over the issue of the cognitive mechanisms that may or may not be necessary for cumulative culture. This is necessarily tied in with the issue of which species exhibit this phenomenon, since beliefs about which cognitive processes may be involved have typically lay behind opinions about which species possess the capacity.

For example, Boyd and Richerson (1996) have made a compelling argument that a capacity for “true imitation” is necessary for cumulative cultural evolution. By true imitation they refer to any form of learning in which individuals can learn a new behaviour by perceiving another individual’s performance of that behaviour. Boyd and Richerson (1996) also use the term “observational learning”, which may be slightly misleading in this context as visual perception is not necessarily involved, since their definition encompasses learning about vocal communication, such as the learning of grammatical rules (Richerson & Boyd 2005) and bird song learning. In any case, other types of social learning which they specify *cannot* support cumulative cultural evolution are those in which the behaviour itself is not what is learned from another individual. Similar behaviours may arise between two individuals because the actions of one individual function to draw the attention of another to a particular location (“local enhancement”) or class of objects (“stimulus enhancement”) (Whiten & Ham 1992). However, in such cases, the behaviour is learned by trial and error, and the presence of the other individual has simply made that learning more likely.

Boyd and Richerson (1996) argue that, since cumulative cultural evolution by definition must allow learners to proceed from a more advanced starting point than was possible for previous generations, true imitation is a necessary condition for its occurrence. Learning which relies upon trial and error processes will inevitably mean that each new learner has to start from scratch, thereby wiping out any useful innovations which may have been chanced upon by others.

Tomasello (e.g. Tomasello et al. 1993; Tomasello 1999) has made a similar argument, proposing that imitation and teaching, each dependent on a capacity for taking the perspective of another, are the foundations of cumulative cultural evolution. Like Boyd and Richerson, Tomasello has stressed the importance of faithful transmission (and therefore imitation) but has also emphasised the need for an understanding of the goals of other individuals. Understanding what cultural practices are *about*, such as what a tool is used for, or what a particular communicative signal means, is crucial to human cultural learning (Tomasello 1999), so he has suggested this to be another necessary feature of cumulative cultural evolution (see also Hermann et al. 2007, for a recent conceptualisation of this view).

However, not all theorists see things in this way. Heyes (1993), for example, has stated that there is no reason why imitation should be particularly crucial to the generation of cumulative behavioural change. Heyes (1993) proposed that the particular learning mechanism involved is in fact irrelevant to the issue of faithful transmission, and that what really matters is whether or not a behaviour will extinguish once learned. Heyes (1993) cited Galef et al.’s (1986) data from a two-action study on budgerigars: subjects that observed conspecifics accessing hidden food using either their beak or their foot tended to match the demonstrated technique for only the first two trials post-demonstration. In later trials, the difference between the groups disappeared. Therefore she has argued that behaviours learned via imitation, like any other, will be subject to modification from trial and error learning. Heyes (1993) proposed that in fact cumulative culture would be more likely to be supported by a separate insulating mechanism which protects socially learned information against the influence of trial and error learning.

Laland and Hoppitt (2003), similarly, have argued that there is currently no reason to believe that either imitation or teaching are particularly significant to cumulative cultural evolution. Laland (2004) has instead suggested that an ability to evaluate the relative effectiveness of behavioural alternatives would be a more plausible cognitive precursor to cumulative culture. Along similar lines, Enquist and Ghirlanda (2007) have argued for the importance of an “adaptive filtering” mechanism. Modelling populations of social learners, Enquist and Ghirlanda (2007) concluded that, without such a filter, cumulative culture would result in the acquisition of many maladaptive traits and therefore could not evolve. However, a capacity to filter out maladaptive traits causes adaptive traits to accumulate preferentially, generating the ratchet effect which is characteristic of human culture.

In conclusion therefore, there are a range of different views regarding the cognitive abilities upon which cumulative cultural evolution may depend. However, experimental work on this topic could contribute greatly to addressing this question, as we hope to elucidate later, and such work will also have implications for questions about human uniqueness.

1.2.3. The origins of complex human behaviour

Just as there is disagreement over the precursors to cumulative cultural evolution, as detailed above, there are also conflicting views on the outcomes of this process, which we will outline here. There is broad agreement that cumulative cultural evolution is responsible for a number of particularly interesting human traits. Indeed, this goes some way to explaining why so many researchers have been fascinated by this phenomenon. Tomasello (e.g. 1999) has argued that, given that our species shared a common ancestor with chimpanzees a mere six million years ago, the cognitive achievements of modern humans (such as written language, mathematics, and complex technologies) have developed implausibly rapidly to be attributed to natural selection on behaviour. Instead he has proposed that cumulative cultural evolution may have played a significant role, and that this would have allowed for much more rapid behavioural change than would genetic evolution. Boyd and Richerson (1996) have emphasised the influence of cumulative cultural evolution in terms of the success of humans as a species. Our ability to exploit a range of habitats has allowed us to become the most widespread animal on the planet.

However, recently arguments have been put forward which propose a role for cumulative cultural evolution in the origins of behaviours which have been popularly believed to be largely dependent on naturally selected innate tendencies. For example, the structural properties shared by many different languages (usually referred to as linguistic universals) have been often been argued to be good evidence of innate language-specific capabilities, common to all humans (e.g. Pinker & Bloom 1990). However, this view has recently been challenged by Christiansen and Chater (in press) and Kirby et al. (2007), amongst others (see also Smith and Kirby this issue).

Kirby et al. (2007) have argued that even extremely weak biases in learning (such as an expectation of regularity) can, over generations of learners, result in languages which are strongly adapted to those biases. The result of this is that no language-specific capacity is necessary in order to explain the existence of linguistic universals, as universals could arise from slight biases in general purpose learning mechanisms. Within this view, languages are therefore seen as shaped by the brain (Christiansen & Chater in press) through the repeated cycle of learning and use over many generations, rather than the brain being adapted to language.

The crucial question here really is whether cumulative cultural evolution, driven by general learning mechanisms, can account for cross-cultural universals in behaviour. Universality in complex adaptive human behaviour is often taken as a hallmark of highly specialised innate predispositions (e.g. Buss 1991; Pinker & Bloom 1990). However, since cumulative cultural evolution can similarly result in complex adaptive behaviour, the issue is really whether it also results in convergence in behaviour, such that separate populations independently invent and retain similar behaviours. Whilst culture is generally viewed as a source of behavioural variation between cultures, under certain circumstances it may result in cross-cultural convergence. We explain in section 5 how our experimental work has so far contributed to this question.

Clearly therefore, there are currently some extremely interesting intellectual disputes within the field of cumulative cultural evolution, each of which could benefit from empirical studies of this phenomenon. In the next section we will examine existing approaches to studying cumulative cultural evolution, and what these studies have so far been able to contribute.

2. Approaches to studying cumulative cultural evolution

2.1. Studying cumulative cultural evolution in the field

In order to study the phenomenon of cumulative cultural evolution in natural populations, it is necessary to have access to fairly accurate information about the past forms of behaviours. This can be difficult as many behaviours leave no discernable trace. However, it is possible to study cumulative cultural evolution from cultural artefacts, including archaeological finds. For example, we can infer from the archaeological record (or rather, the lack of it) that any tools used by hominids up until about two million years ago, were probably comparable to those used by other great apes, such as chimpanzees (Ambrose 2001). We also know that, around a quarter of a million years ago, tools manufactured by humans began to show rapid change and development. Around this time, a wide variety of different stone tools were being used by humans, each tailored to a specific function.

Some authors have documented progress in science and technology in explicitly evolutionary terms (e.g. Basalla’s 1988 *The Evolution of Technology*, and Wilder’s 1968 *Evolution of Mathematical Concepts*). In other texts the notion of accumulation is more implicit. Inventions and discoveries are dated, and advancement is assumed (e.g. Bunch & Hellemans 2004). However, irrespective of the source consulted, evidence can readily be found for ratcheting, with new developments building on previous ones. Loss of information or skills from a population is very much the exception, rather than the rule (although it is worth noting that such loss certainly has been documented; the decline in complexity of the Tasmanian toolkit is probably the best known example, e.g. Henrich 2004).

Consider two examples, the wheel and mathematical notation. The invention of the wheel as an aid to transportation is generally dated between five and six thousand years ago, with early wheels constituting simple wooden disks with a hole for the axle. The spoked wheel was only invented more recently (around four thousand years ago). The invention of the wheel then gave rise to a number of other technological innovations including cogs and pulleys (Basalla 1988; Bunch & Hellemans 2004). Mathematical systems of notation have also developed considerably over time, with simple tally systems recorded from around thirty thousand years ago. However, more abstract symbolic representations are much more recent. Place value notation was being used by the Mesopotamians by around four thousands years ago, but also seems to have been independently invented by the Indians within the last two thousand years, leading to our current “Arabic” notation. The invention of a symbol to represent zero (which made the place notation system considerably more informative) was more recent still, in both cultures (Wilder 1968; Bunch & Hellemans 2004).

Clearly, valuable information can be gleaned from studying cumulative cultural evolution in natural populations. Important insights can be gained into the kinds of behaviours which show cumulative cultural evolution over time, and the nature of the changes that occur. These can, up to a point, address certain issues raised in the previous section. For example, adequate information on the past forms of behaviour in populations which have had little contact with one another could enhance our understanding of convergence in cumulative cultural evolution, and therefore extent to which it may explain cross-cultural universals. However, there are limitations to the kinds of questions one can ask when using these kinds of data. Mesoudi (Mesoudi 2007; Mesoudi & O’Brien 2008) has argued that historical methods have several drawbacks when it comes to studying cultural variation, and the same apply for investigations of cumulative cultural evolution. The main weakness of this approach, certainly from the perspective of addressing some of the debates listed above, is that it does not allow for manipulation of variables of interest. We can ask questions about how cumulative cultural evolution *has* occurred, but we cannot ask what *might* have happened, had circumstances been slightly different. In contrast, using an experimental approach, we can explicitly manipulate factors believed to be crucial in generating cumulative cultural evolution, to test hypotheses about necessary precursors. Likewise we can set out to study the outcomes of cumulative cultural evolution in multiple replicated populations under controlled conditions.

2.2. Theoretical studies of cumulative cultural evolution

In contrast, theoretical studies of cumulative cultural evolution permit researchers to manipulate as many variables as they desire, and controlling extraneous factors is of course not an issue. There are many theoretical models involving social learning, but only a few have tested hypotheses relevant to the debates detailed above. For instance, Boyd and Richerson’s (1996) paper included a theoretical analysis of why cumulative cultural evolution seems to be a rare phenomenon within the animal kingdom. Their models showed that an ability to copy the behaviour of others only becomes more useful than a capacity for individual learning when other members of the population are themselves engaging in behaviours with higher payoffs than would be achieved with individual learning alone. Hence there is a significant obstacle to the evolution of such capabilities since they are only valuable once they are widespread in the population. Enquist and Ghirlanda (2007) have addressed the issue of the cognitive abilities necessary for cumulative cultural evolution. As mentioned above, their models indicate that a mechanism which can selectively filter out maladaptive behaviours would be crucial for cumulative cultural evolution to evolve. Work by Kirby and colleagues (e.g. Kirby et al. 2007; Kirby & Christiansen 2003; Smith et al. 2003; Smith and Kirby this issue) has investigated the question of whether complex innate competencies are a necessary feature for the evolution of structured language. Modelling iterated learning of communication systems, they have shown that structural features, such as compositionality, can arise through cultural transmission over multiple generations.

However, the great strength of theoretical models, in terms of the flexibility afforded, is also to an extent their weakness. The constraints imposed on the models are those selected by their creator, and the conclusions drawn necessarily depend on the underlying assumptions, which may or may not be accurate. In contrast, in experimental studies with human subjects, one can gain important insights into the likely results of real learning processes repeated over multiple generations. In the following sections we detail experimental approaches which can be used to study culture in the laboratory (Section 3), and explain how we have applied these methods to test hypotheses about cumulative cultural evolution (Section 4).

3. Studying culture in the laboratory

There are a variety of methods which have been used for studying culture under laboratory conditions (for reviews see: Mesoudi 2007; Mesoudi & Whiten this issue; Whiten & Mesoudi this issue). The aim of such approaches is essentially to simulate cultural phenomena on a small scale, allowing researchers to study how behaviours change over time as a result of repeated learning and transmission between individuals. Whilst experimental approaches inevitably have imperfections of their own, we consider that the power to manipulate variables, and collect precisely the data that is required, constrained and informed by the behaviour of real participants, strikes a very constructive balance.

The utility of such methods is best illustrated with an example of this kind of study. Jacobs and Campbell (1961) used laboratory “microcultures” (Gerard, Kluckhohn & Rapoport 1956) aiming to “demonstrate a perpetuation of ‘cultural’ characteristics that transcends the replacement of individual persons” (p649). Their study therefore involved simulating generational succession through the repeated removal and replacement of participants within small groups. Jacobs and Campbell (1961) wanted to determine whether participants’ tendencies to conform to majority opinion could result in long-lasting traditions of counterintuitive beliefs. Groups were founded by experimental confederates, instructed to respond with a significant overestimation of their true perception of the strength of a visual movement illusion, but these were gradually replaced by naïve participants. In an example of one of Jacobs and Campbell's (1961) conditions, there were three individuals present in the test group at any one time, and at the start of the experiment two of these individuals were confederates and one was a naïve participant. Each individual from the group was asked to estimate the degree of the illusory movement perceived, starting with the confederates, and their responses were recorded. This was repeated thirty times, after which one of the confederates was removed and replaced by another naïve participant. Thirty more trials were then carried out with this new group, and the remaining confederate was then removed and replaced with a further naïve participant. This procedure continued for a total of ten "generations". Jacobs and Campbell (1961) also ran further conditions, manipulating the size of the test group (varying between one individual and four), and the number of confederates in the first generation (varying between zero and three). Each experimental condition was replicated three times each. Jacobs and Campbell (1961) found that the overestimation bias induced by the confederates persisted for several generations after the final confederate had been removed.

Similar methods, involving the removal and replacement of participants within groups, have since been adopted by Insko and colleagues (Insko et al. 1980; 1983) and also more recently by Baum et al. (2004). The benefit of this method lies not only in the power to manipulate certain key variables (e.g. size of group and number of confederates for Jacobs and Campbell 1961), but also in the timescale required for the study. Whilst cultural evolution is generally assumed to occur on a timescale of multiple human lifespans, these experiments seek to study cultural phenomena over learner generations, rather than reproductive generations. For this reason such methods have also been applied within the literature on animal social learning (e.g. Galef & Allen 1995; Laland & Williams 1997; 1998).

As well as methods involving removal and replacement of participants in groups, there are also other methods which can be used to study culture under experimental conditions (for a comprehensive reviews see Mesoudi 2007; Mesoudi & Whiten this issue; Whiten & Mesoudi this issue), but these are less relevant in terms of finding an experimental model for studying cumulative cultural evolution. For example Bartlett (1932) made use of the "method of serial reproduction" in his studies of human memory, a method which has been recently revived by Mesoudi and colleagues (Mesoudi & Whiten 2004; Mesoudi et al. 2006). Although chains of multiple generations are involved, with new participants learning from previous learners, it is quite different from the method detailed above in a number of important respects. In this type of research, participants are explicitly instructed to copy, in that their aim is to reproduce information as accurately as they possibly can. The focus is therefore on the degradation of the information originally provided to the first participant. Whilst this is an excellent method for revealing people's unconscious cognitive biases (as it allows researchers to investigate what sort of information is omitted, or introduced, when participants are actively trying to reproduce material as accurately as possible), it is clearly considerably less appropriate for studying cumulative cultural evolution. Any laboratory model of cumulative cultural evolution must involve behaviours which can show measurable improvement over generations, and it is also important that participants understand that the choice of whether or not to copy is their own.

Until recently, even the experimental work which has been carried out using the replacement method has fallen short of providing an adequate model of cumulative cultural evolution. As noted above, the behaviours to be transmitted must be capable of showing measurable improvement over generations, as a consequence of accumulated modifications. The perceptual judgement task used by Jacobs and Campbell (1961) is therefore far too simple a behaviour. Work carried out by Baum et al. (2004) (as well as other work from the same group, e.g. McElreath et al., 2005; Efferson et al., 2007; Efferson et al., 2008; McElreath et al. this volume) does show increasingly adaptive choices made by participants over generations, but these experiments involve participants choosing between two options each of which has an unpredictable payoff. This method has been used to elucidate participants' strategies in gauging their use of socially- and individually-acquired information in order to make best guess choices. In terms of studying cumulative cultural evolution however, the method is less appropriate. Whilst the average payoffs seem to increase over time, as a result of participants gravitating towards the choice which is the best on average, the behaviours themselves (of one choice over another) are not ideal candidates in terms of demonstrating the accumulation of modifications.

Interestingly, in Insko's studies (Insko et al. 1980; 1983), which involved between-group trading of paper origami products manufactured by group members, groups made increasingly greater profits over generations, suggesting more efficient methods of production were being passed on. However, it is unclear what the nature of the improved efficiency was, and whether this was definitely attributable to transmission between generations. In the following section we detail the method that we have developed for studying cumulative cultural evolution experimentally. Within this issue, studies reported by Fay et al. and Flynn show similar effects to ours which may also provide promising approaches for studying cumulative cultural evolution.

4. A method for studying cumulative cultural evolution in the laboratory

4.1. The tasks

As explained above, the task presented to participants must be chosen very carefully in order to create an effective laboratory model of cumulative cultural evolution. It was important that we chose a task that could show measurable improvements in performance over generations, based on the accumulation of modifications. A task with a clear aim and an objective measure of success was therefore crucial, as we needed to be able to show that participants' scores were, on average, better the further they were down the chain (therefore showing that the skills and knowledge had accumulated over the learner generations). It was also important for our design to choose tasks which were simple and easy enough for participants to complete in a short space of time, in order to make these feasible laboratory methods. However, the tasks also needed to be sufficiently difficult and complex that definite benefits could be obtained from opportunities for social learning, and that the accumulation of modifications could be documented.

We have so far used two different tasks in our laboratory studies of cumulative cultural evolution (Caldwell & Millen 2008). In one of our tasks, participants are asked to build a paper aeroplane, the goal being to build one that will fly as far as possible. In the other task, participants are asked to build a tower out of spaghetti and modelling clay. The goal for this task is to build a tower that is as high as possible. Hence we have our objective measures of the success of each participant, in relation to the goals they have been given. Furthermore, the tasks we have selected show similarities with certain examples of early human material culture, such as projectile point shaping, and shelter construction. From our point of view, this is also helpful given the types of questions we would like to address with these methods (see Section 1 above). The tasks therefore have much in common, but there are also important differences between them. Firstly, whilst many people have some prior experience of having built a paper aeroplane, the spaghetti tower task is far more novel and participants have few preconceived ideas about how to approach the task. Secondly, whilst feedback on performance on the spaghetti tower task is continual during construction (participants can of course see exactly how high their tower currently is), feedback on performance on the paper aeroplane task is delayed until construction is complete.

4.2. The design

We used a replacement method, with each chain totalling ten individuals. For each task, we ran ten replicates of these chains of ten participants. Figure 1 shows a schematic of the replacement design, indicating which participants were present in the test group at what point during each trial. Participants were randomly assigned to the positions 1 to 10 in each chain. In order to simulate generational succession, the participants' start times were staggered, such that every two and a half minutes a new person entered the group. While they were in the test group, each participant had five minutes of observation time, during which they could watch the previous participants building their artefact, followed by five minutes of building time, during which they had to construct their own artefact. Once their time was up, they left the test group. The staggered start and finish times had the effect that, at any given time (except at the very start and very end of any given chain) there were four individuals together in the group, two of whom were observing, and two of whom were actually engaged in the task (see Figure 1). So, for example, a chain would begin with participant 1 building their artefact, with participants 2 and 3 observing. Then, two and a half minutes in, participant 2 would also start building, and participant 4 would join the group as an observer. The aim was to simulate a miniaturised society, in which one generation would have the opportunity to interact with and observe individuals from the previous two generations, but not those further back. However, we did retain all artefacts for inspection by later participants, to reflect the more permanent record generated by material culture. The experimenter wrote down the relevant measurements next to each, so that this information was also available. Participants left the testing area once their artefact had been evaluated.

time minutes	participants present in test group
00.00	**1** 2 3
02.30	**1 2** 3 4
05.00	**2 3** 4 5
07.30	**3 4** 5 6
10.00	**4 5** 6 7
12.30	**5 6** 7 8
15.00	**6 7** 8 9
17.30	**7 8** 9 10
20.00	**8 9** 10
22.30	**9 10**
25.00	**10**

Figure 1. Group composition over time in the microsociety design. Generational succession is simulated through the repeated removal of experienced participants and introduction of naive participants. Each row of the table shows the group composition at any given time, made up of observing participants (grey) and participants actually engaged in the task (black). Participants were randomly assigned the positions 1–10.

4.3. The ratchet effect

Our results showed clear evidence for improvement in performance over the course of the chains (Caldwell & Millen 2008). Figure 2 shows these results for both the paper aeroplanes and the spaghetti towers. The leftmost graphs show the results for each of the ten chains separately, so each differently coloured line represents a different chain. As is clear from these figures, performance overall can be extremely variable. However, when we (Caldwell & Millen 2008) analysed the trends over generations we found a strong effect of improvement in terms of the goal measures (of plane flight distance and tower height). The rightmost graphs displayed in Figure 2 show the average score for the participants in each position in the chain, and illustrate the steady improvement much more clearly. Thus, skills and knowledge do indeed appear to accumulate in the chains, independent of individual membership, consistent with predictions assuming cumulative cultural evolution. Furthermore, similar patterns were found for both of the tasks, in spite of the differences between them, suggesting that we are tapping in to a fairly general phenomenon.

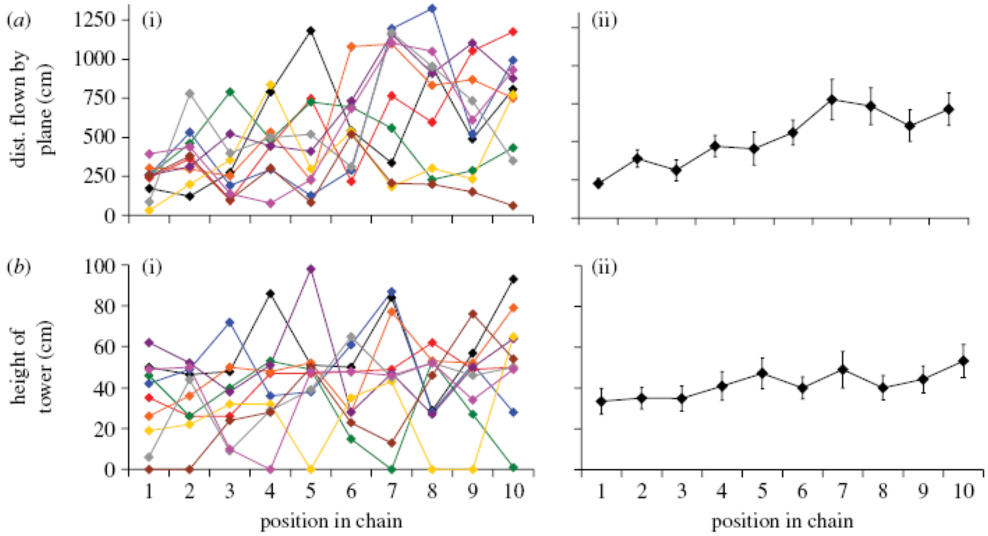

Figure 2. Measures of success over generations. (a(i)) The data for the 10 chains of paper aeroplanes, with (a(ii)) showing the mean distance flown for each position in the chains (error bars indicate ±s.e.m.). (b(i)) The data for the 10 chains of spaghetti towers, with (b(ii)) showing the mean height for each position in the chains (error bars indicate ±s.e.m.). Redrawn from Caldwell & Millen (2008).

4.4. Accumulation of modifications

As well as looking for improvement in performance over generations, we were also interested in investigating the inheritance of modifications. We predicted that designs would be more similar within chains than they were across chains (indicating cultural variation), and also that designs that were close together in the chain would be more similar to one another than those that were far apart (indicating descent with modification). For this reason we took photographs of all of the artefacts that had been created by participants, and we were able to use these to test predictions regarding the similarity of designs. The photographs were rated by naïve coders, each of whom was given one of the photographs from the set and asked to rate it in comparison to all of the others. The coders were provided with a seven point scale, which they were to refer to in making their ratings. For full details of the methods used to obtain and analyse these ratings, see Caldwell and Millen (2008). As predicted, artefacts from the same chain were rated as more similar than those from different chains, for both the paper aeroplanes and the spaghetti towers. Designs from positions close together in the chains were also more similar than those from positions far apart in chains, demonstrating that the improvement in performance was associated with the accumulation of modifications.

5. Applications of these methods

We see great potential for using these methods in order to test hypotheses about cumulative cultural evolution. In this section we discuss how some of our work to date has helped to address some of the issues raised in the introduction. We start by discussing our findings regarding cultural convergence, and explain the implications for the potential role of cumulative cultural evolution in human behavioural universals. We also discuss experiments explicitly designed to test hypotheses about learning mechanisms involved in cumulative cultural evolution. This work has obvious implications for the debate surrounding the cognitive precursors of cumulative cultural evolution, but is also relevant to the debate regarding the uniqueness (or otherwise) of this phenomenon to humans.

5.1. Convergence in cumulative cultural evolution

As mentioned in Section 1, questions about the possible role of cumulative cultural evolution in complex human behavioural universals essentially centre on the issue of whether separate cultures are likely to independently invent and retain similar behaviours. We have already been able to investigate this issue, based on the same dataset already discussed (Caldwell & Millen 2008).

In biological evolution, convergent evolution refers to a process by which species which are only distantly related independently evolve analogous adaptations in response to similar environmental pressures. Convergent cultural evolution therefore refers to situations in which different populations independently develop similar socially transmitted behaviours despite different ancestral histories (Caldwell in press). In evolutionary biology, distinctions are therefore also drawn between traits which are homologous and those which are analogous. Homology refers to the “relationship of two characters that have descended, usually with divergence, from a common ancestral character” (Fitch 2000, p227). In contrast analogy “is distinguished from homology in that its characters, although similar, have descended convergently from unrelated ancestral characters.” (Fitch 2000, p227).

Likewise, it is an important question when studying cross-cultural similarities, whether those similarities are the result of common cultural descent, or convergence from contrasting ancestral forms. In our experiments it is possible to study the extent to which convergence occurs, since we can control the contact that different microcultures have with one another. As noted in the previous section, we had all of our photographs of participants’ planes and towers rated for their similarity to one another. As well as using these ratings to look into the accumulation of modifications, we were also able to use the ratings to test for convergent cultural evolution (i.e. increasing similarity between the different chains, over generations). This would be predicted because successful designs are liable to have features in common, so the later designs ought to be rated as more similar to one another, compared with earlier designs, due to the fact that they have in effect been shaped by similar selection pressures. In order to analyse this, we took the similarity ratings for all pairs of photographs which were in the same position across chains. Positive correlations were found between the position in the chain and the mean similarity ratings, for both tasks. These results are displayed in Figure 3.

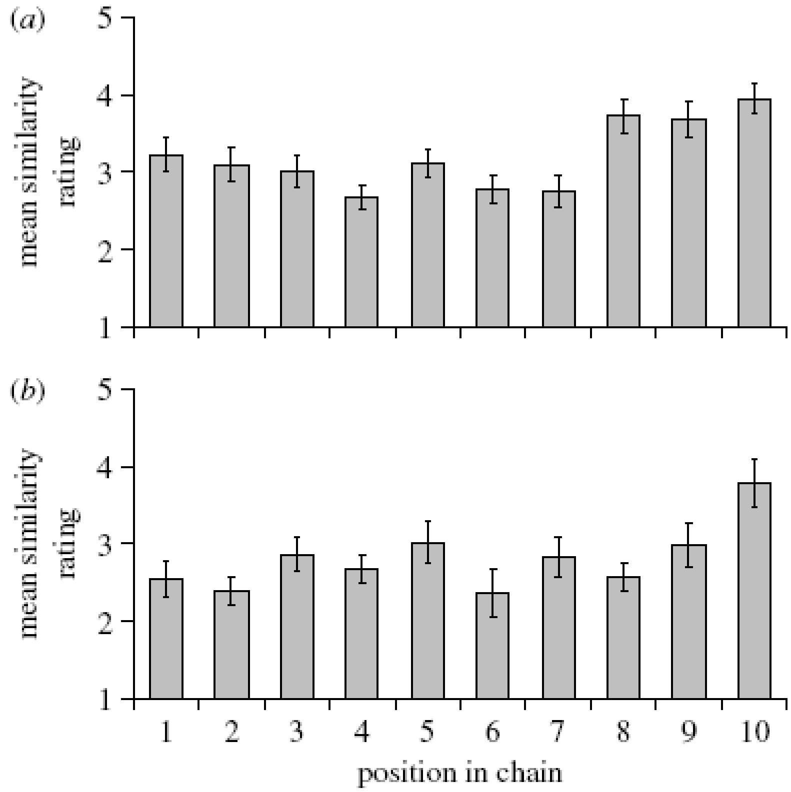

Figure 3. Ratings of similarity for pairs of artefacts in the same position across chains. The data for (*a*) paper aeroplanes and (*b*) spaghetti towers. Error bars indicate ±s.e.m. Redrawn from Caldwell & Millen (2008).

We are by no means the first to show that "iterated learning", i.e. each generation learning from data generated by the previous one, can result in convergence across different microsocieties. Kalish et al. (2007), for example, have illustrated well that learners' biases interfere with transmitted information in consistent ways, resulting in different chains of learners – who have often been provided with quite different information to start with – passing on very similar data (see also Griffiths et al this volume). However such findings, albeit fascinating, may not contribute greatly to the question of whether cumulative cultural evolution could present an alternative account of the existence of complex human behaviours. As noted in Section 1, Tomasello (1999) has argued that cumulative cultural evolution could explain why human behaviour is so different from that of the other great apes. In effect the suggestion is that these behaviours are the result of the accrued learning of many generations, rather than the result of natural selection. The finding that cultural transmission degrades information in the general direction of learners' innate biases therefore does not add much to this particular issue.

In contrast, our results show that increasing cultural similarity can go hand-in-hand with increasing adaptive complexity. Although universality in complex human behaviour is often attributed to specialised innate predispositions, our results imply that similar behaviours may well be independently discovered and passed on within different populations. It is in fact examples such as ours, which show cumulative cultural evolution being shaped by feedback from multiple attempts, which serve to emphasise just what is so useful about cumulative cultural evolution (e.g. Henrich & McElreath 2003). It is a means by which information is gained, and then retained, within populations. The extended learning period afforded allows us to make discoveries which would not have been possible within a single lifetime. Whilst our experiments are so simple, small-scale and short-term, as to somewhat trivialise this point, our findings are nonetheless illustrative of phenomena that we believe to be operating over much longer timescales, in many realms of behaviour.

5.2. Learning mechanisms

In our ongoing work, we are using the methods that we have developed to test hypotheses about the learning mechanisms that may be involved in cumulative cultural evolution. It has been proposed that cumulative cultural evolution may depend on a capacity for imitation, and that this may be the reason for its apparent rarity in nonhumans. Consequently we have run experiments (Caldwell & Millen unpublished data) designed to test whether restricting opportunities for imitation, and indeed other forms of social learning, influences the trends that we find towards improvement over generations of learners.

Using our paper aeroplane task detailed previously, we have run a variety of different experimental conditions, in which certain sources of social information are either available or unavailable. Whilst in our previous experiment (Caldwell & Millen 2008) participants could observe the two previous participants in the chain, and discuss the task with them, as well as see the results of their efforts in the form of the completed plane and information about its flight distance, in this study we separated these sources of information. In a series of different experimental conditions, participants had access to information in the form of either: actions only; results only; teaching only; actions plus results; actions plus teaching; results plus teaching; or actions, results and teaching. If imitation (in terms of "learning to do an act by seeing it done", e.g. Whiten & Ham 1992) is indeed crucial to cumulative cultural evolution, then conditions in which this not possible (i.e. those with no information from actions) ought to show much weaker trends towards improvement over generations.

6. Conclusion

In summing up, we believe that the experimental methods that we have developed will prove to be extremely useful tools in helping to understand the phenomenon of cumulative cultural evolution, and that it will be possible to make important contributions to some of the debates which surround this field. We hope that our current findings help to illustrate how scaled-down laboratory tests can be used to investigate fundamental cultural processes.

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