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Social Learning Mechanisms and Cumulative Cultural Evolution: Is Imitation Necessary?

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Cumulative cultural evolution has been suggested to account for key cognitive and behavioral attributes which distinguish modern humans from our anatomically similar ancestors, but researchers have yet to establish which cognitive mechanisms are responsible for this kind of learning, and whether these are unique to humans. We have shown that human participants' cumulative learning is not always reliant on sources of social information commonly assumed to be essential. Seven hundred participants were organized into seventy microsocieties, and completed a task involving building a paper airplane. We manipulated the availability of opportunities for: imitation (reproducing actions); emulation (reproducing end results); and teaching. Each was independently sufficient for participants to show cumulative learning. Since emulative learning can elicit cumulative culture on this task, we conclude that accounts of the unusual complexity of human culture in terms of species-unique learning mechanisms do not currently provide complete explanations, and other factors may be involved.

Introduction

The term *cumulative cultural evolution* is used to describe the way that cultural change accumulates in human populations over time (Boyd & Richerson, 1996; Richerson & Boyd, 2005; Tomasello, 1999). In humans, social transmission allows for successive improvements to performance over generations of learners, generated by the accumulation of modifications to the transmitted behaviors (Caldwell & Millen, 2008a). Tomasello (Tomasello, 1999; Tomasello, Kruger & Ratner, 1993) has dubbed this the *ratchet effect*. Similarly, Boyd and Richerson (1994) have drawn attention to the particular adaptive value of social learning that permits "learned improvements to accumulate from one generation to the next" (p134).

Such cumulative learning has allowed humans to develop advanced technologies and symbolic systems (such as writing and mathematical notations) and exploit a wide range of habitats (Boyd & Richerson, 1996). Humans may be unique in exhibiting such accumulated cultural histories. Although there is evidence for behavioral inheritance via social transmission in nonhumans (i.e. rudimentary culture, Laland & Hoppitt, 2003; Whiten, 2005; Whiten et al., 1999), researchers have been keen to emphasize the contrasts between nonhuman behavioral traditions and human cultures, which seem vastly more complex (Boyd & Richerson, 1996; Galef, 1992; Laland & Hoppitt, 2003; Whiten, Horner & Marshall-Pescini, 2003; Whiten & van Schaik, 2007). Many have drawn attention to the prevalence of cumulative cultural evolution in humans, and noted that this particular feature appears to be either absent (Galef, 1992; Tomasello, 1999), or minimal at best (Boesch & Tomasello, 1998; Boyd & Richerson, 1996; Heyes, 1993; Laland & Hoppitt, 2003; Whiten et al., 2003) amongst nonhuman animals. The apparent rarity of this kind of learning amongst species other than humans has prompted much speculation about the possible reasons for its scarcity, the majority of which have concerned the probable learning mechanisms involved and the possibility that these may be unique to humans. Boyd and Richerson (1996) have argued that imitation ("learning to do an act by seeing it done", Whiten & Ham, 1992) may be necessary for cumulative cultural evolution. Tomasello (Tomasello, 1999; Tomasello et al., 1993) has proposed that both imitation and teaching provide the foundations of cumulative cultural evolution. Such interpretations are consistent with findings indicating that human children are far more precise imitators than are chimpanzees (e.g. Horner & Whiten, 2005; Nagell, Olguin & Tomasello, 1993). However, others have argued that there is no particular reason to believe that imitation is crucial to cumulative culture (Heyes, 1993; Laland & Hoppitt, 2003; Whiten et al. 2003).

Recently we (Caldwell & Millen, 2008b) developed methods to test hypotheses about cumulative cultural evolution under laboratory conditions (see Mesoudi, 2007, and Mesoudi & Whiten, 2008, for reviews of similar experimental approaches to the study of culture). We created miniaturized populations ("microsocieties", Baum, Richerson, Efferson & Paciotti, 2004, or "microcultures", Jacobs & Campbell, 1961) in which generational succession was simulated through the repeated removal and replacement of participants within small groups over short timescales. We presented participants with simple tasks to complete, and showed that their solutions to the tasks improved over "generations", with later participants in the chain being more successful than earlier ones (Caldwell & Millen, 2008b).

In the current study, we used these methods to test hypotheses regarding the learning mechanisms necessary for cumulative cultural evolution. As in one of our previous experiments (Caldwell & Millen, 2008b), the task presented to participants involved building a paper airplane to fly as far as possible. Participants carried out this task as a member of a chain of ten individuals, each of whom carried out the task one after the other. In the current study we ran a total of seven different experimental conditions, each manipulating the availability of different kinds of social information about the task. We divided social information into: (A) information about actions (opportunities to observe actual building of paper airplanes, allowing for imitation); (R) information about results (opportunities to inspect completed planes and observe their flight distances, allowing for emulation); and (T) information in the form of teaching (opportunities to communicate verbally with other participants, including those who have already completed the task).

Methods

Participants

Participants were recruited on campus at the University of Stirling. Non-Psychology students were given £3 in exchange for their participation. Psychology students were offered the choice between the participation fee and a research participation credit. Seven hundred participants took part (ten chains of ten individuals for each of the seven conditions). Their mean age was 21.37 years (SD = 5.17, youngest = 17, eldest = 68), and 57% of the sample were female (totals = 303 males, 397 females). Ethical approval for this research was granted by the University of Stirling Department of Psychology Ethics Committee. The procedure was explained to all participants in advance, and they each gave written consent to participation.

Table 1. Summary results for the seven experimental conditions.

Condition	Mean Flight Distance (+ *SD*) Early (1,2,3) Generations	Late (8,9,10) Generations	Evidence for cumulative culture?
A R T	547.7 (246.1)	836.5 (213.0)	Significant: $L = 3385$, $p < 0.001$
A R	544.6 (282.4)	735.9 (228.3)	Significant: $L = 3212$, $p = 0.016$
A T	612.4 (247.5)	754.6 (174.2)	Significant: $L = 3197$, $p = 0.024$
R T	443.9 (209.1)	717.9 (211.5)	Significant: $L = 3345$, $p < 0.001$
A	404.4 (203.2)	598.7 (226.3)	Significant: $L = 3170$, $p = 0.048$
R	506.8 (298.9)	701.0 (286.6)	Significant: $L = 3207$, $p = 0.018$
T	543.5 (202.8)	707.1 (308.4)	Significant: $L = 3175$, $p = 0.042$

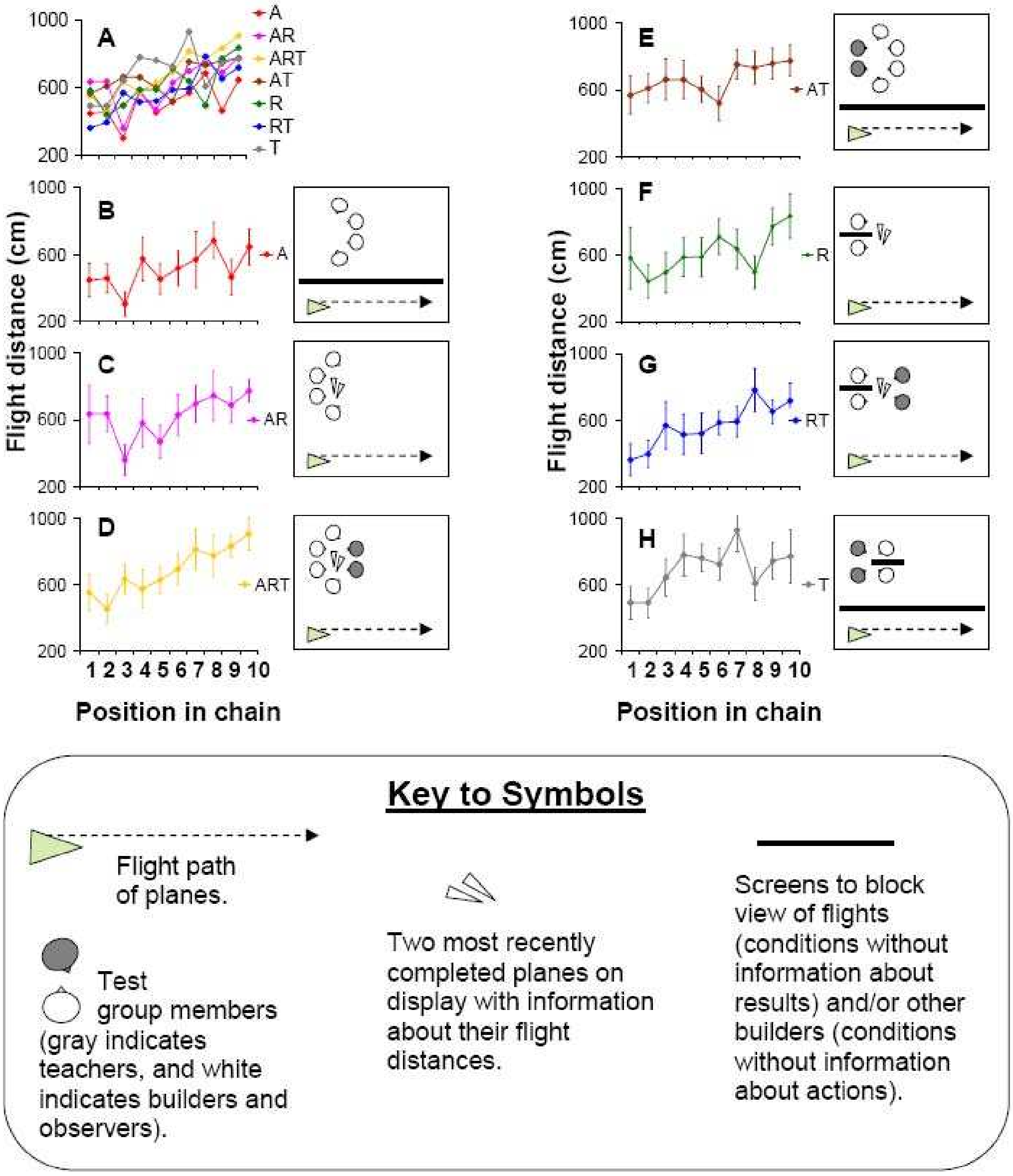
Note. The statistical information provides the results of Page's L Trend test, testing for improvement in scores over the course of the chain ($k = 10$, $n = 10$ for all tests). For conditions in which information was available in the form of actions, participants joined the test group for a five minute observation period before starting the task, and could observe others building. For conditions in which information was available in the form of results, the previous two planes were placed on display for the test group, along with flight distance information, and the test group participants could also observe flying of planes. For conditions in which information was available in the form of teaching, verbal communication was permitted between members of the test group, and following task completion participants returned to the test group for five minutes in the role of "teacher".

Procedure: ART condition (actions, results and teaching)

Table 1 offers a summary of the seven experimental conditions. The procedure for the full information condition (ART) is described below. For the other conditions, each of which involved restricting access to one or more of these sources of information, modifications were made to this basic procedure, which are detailed at the end of this description. Full procedural details for each condition are provided as supporting information (Methodological Details). Figure 1 offers diagrams of the experimental set-up for each condition.

The group of ten participants was assembled prior to the trial beginning. They were informed that they were about to take part in a team challenge, and that they would be called in turn to engage in the task. Participants were randomly assigned a number between one and ten to indicate their position in the chain. They completed consent forms and waited their turn to join the group in the test area. The test area could not be seen by waiting participants.

Figure 1. Flight distances of the paper airplanes produced by participants in positions 1-10 of the chains. Panel *A* shows the means for all seven conditions. Panels *B-H* show means plus standard error (error bars indicate +/- *SEM*) for each condition individually. Panel *B* shows condition A (actions only), panel *C* shows condition AR (actions and results), panel *D* shows condition ART (actions, results and teaching), panel *E* shows condition AT (actions and teaching), panel *F* shows condition R (results only), panel *G* shows condition RT (results and teaching), and panel *H* shows condition T (teaching only). Schematics of the testing set-up for each of the conditions are also shown alongside the corresponding graph.



When participants joined the test group they were provided with written instructions detailing the aim of the task (to build a paper airplane to fly as far as possible) and their time restrictions (five minutes of observation time followed by five minutes in which to build their own plane). They were informed that their participation fee would be increased proportionally with their performance on the task (ten pence extra for each meter of flight). They were also informed that participants who had completed the task and flown their plane would return to the group for a further five minutes, in the role of "teacher" in order to help others in the test group. Figure 2 indicates the membership of the test group, and the role of each participant, at any given time during an ART trial. They were told that they were permitted to communicate with other members of the group regarding the task, including the teachers, and that they were allowed to observe and learn from others. Whilst participants were encouraged to give and receive advice, and to observe others' actions, and allow others to observe theirs, they were expressly forbidden from building another individual's plane for them. Each participant was provided with a single sheet of A4 paper with which to create their airplane.

Figure 2. The microsociety design. This shows the membership of the test group at any one time during a trial, for the conditions involving action information and teaching (conditions ART and AT). Shading indicates the role of the participant: black indicates observing, gray indicates building, and white indicates teaching. Conditions without action information (conditions R, RT and T) included no observation period, and conditions without teaching (conditions A, AR and R) included no teaching period.

Time (minutes)	Participants present in test group									
0:00–2:30	1	2	3							
2:30–5:00	1	2	3	4						
5:00–7:30	1	2	3	4	5					
7:30–10:00	1	2	3	4	5	6				
10:00–12:30		2	3	4	5	6	7			
12:30–15:00			3	4	5	6	7	8		
15:00–17:30				4	5	6	7	8	9	
17:30–20:00					5	6	7	8	9	10
20:00–22:30						6	7	8	9	10
22:30–25:00							7	8	9	10
25:00–27:30								8	9	10

Within the test group, participants were kept aware of their current role (observing, building, teaching), and the time elapsed, by a computer display and reminders from the experimenter. Once an individual's five minute building period was up, their plane was evaluated. This involved the participant throwing their plane three times, with the experimenter recording the best of the three measurements (to allow for mis-throws). Members of the test group could see planes being thrown. Participants then returned to the test group in the role of "teacher" for a further five minutes. Once a plane's flight distance had been recorded, it was placed on display in the test area. The experimenter wrote down the distance measurement next to each, so that this information was also available. Each plane was held on display for five minutes such that at any time (with the exception of the very start of the chain) the two most recently completed planes were visible. When a new plane was displayed in the test area it replaced the plane which had been on view for the longest. Participants left the testing area once their five minutes of teaching time had elapsed.

The other experimental conditions followed the same procedure with the following exceptions. Conditions without action information (RT, R and T conditions) did not include a five minute observation period prior to their building time. Participants were instead called from the waiting area roughly one minute before their building time began in order to read their instructions. They were informed that they were not permitted to watch other members of the test group building their planes, and they were screened from other participants who were simultaneously engaged in building (see diagrams in Figure 1).

In conditions without results information (AT, A and T conditions), no planes were placed on display in the test group, and no information was provided by the experimenter about flight distances (although teachers were permitted to pass on this information if they were present). Participants in the test group could not see planes being flown as this was carried out behind a screen (see diagrams in Figure 1).

In conditions without information from teaching (AR, A and R conditions) participants left the test group as soon as they had completed and thrown their plane. They did not return to the group in the role of "teacher". Furthermore, members of the test group were instructed that they were not permitted to communicate verbally about the task.

Results

The results for the seven conditions are displayed Figure 1 and Table 1. In each condition we tested for cumulative cultural evolution by using Pages *L* trend test (Page, 1963). The Page test predicts the ordering of conditions in a repeated measures sample. Each of our chains was therefore treated as a single replicate, within which it was predicted that participant 10 would have a higher score than participant 9, and participant 9 higher than participant 8 and so on. The results of the trend tests are reported in Table 1. In every one of the seven conditions there was a significant trend towards improvement further along the chain, demonstrating cumulative culture.

Thus none of our conditions resulted in a complete loss of cumulative learning. This effect was remarkably robust to manipulations of the different sources of social information. The participants were apparently able to make use of any of the sources of information, be it actions, results or teaching, in order to accumulate effective strategies within the chain. It was nonetheless of interest to determine whether certain conditions were more effective than others. In order to compare conditions, data were collapsed across the first three (positions 1, 2 and 3) and last three (8, 9 and 10) participants in each chain. Means are reported in Table 1. These values allowed us to perform a 2x7 ANOVA, with generation (early and late) as a repeated measures variable, and experimental condition as a between-subjects variable.

There was a main effect of generation [$F(1,63) = 33.245$, $p < 0.0005$, $\eta_p^2 = 0.345$], consistent with our finding that scores were higher later in the chain. However there was no main effect of condition [$F(6,63) = 1.182$, $p = 0.327$, $\eta_p^2 = 0.101$], so no condition was overall any better than any other. There was also no interaction between position and condition [$F(6,63) = 0.330$, $p = 0.919$, $\eta_p^2 = 0.030$], so the trend towards improvement later in chains was no stronger in certain conditions over others.

Discussion

Our findings have important implications for understanding cumulative cultural evolution, particularly the reasons for its rarity in nonhumans. Amongst an adult human sample, cumulative culture was possible even in the absence of opportunities for either imitation or teaching. This suggests that these learning mechanisms are not always essential for cumulative cultural evolution. Cumulative effects were apparent even when participants had opportunities only for emulation (copying the end results of behavior: Call, Carpenter & Tomasello, 2005; Nagell et al., 1993), a capacity which Tomasello and colleagues (e.g. Tomasello, 1993) have argued nonhuman primates depend upon to a much greater extent than imitation.

It should be noted that our results, generated in the context of a paper airplane-building task, may not generalize to other very different types of cultural tradition. Human traditions take a variety of forms, and imitation and teaching may be essential to the transmission and accumulation of certain behaviors. It is difficult to see how traditions that do not involve some kind of material record (such as arbitrary communicative conventions) could be transmitted in the absence of either observation or teaching. At the opposite end of the spectrum, behaviors involving very complicated instrumental actions that are difficult to reverse engineer will also be unlikely to be effectively transmitted through emulation alone. Skills such as knot-tying and knitting are generally passed on through a combination of observation, explicit demonstration, and detailed written descriptions. Indeed, it may be the case that even in the context of our task, different types of modifications could be transmitted in certain conditions but not others. In our previous research (Caldwell & Millen, 2008b) we have found clear evidence of variation in design traditions across microsocieties, and it may be that some of our conditions in the current experiment were more likely to result in traditions involving either very complex, or very subtle, design features.

All the same, a number of apparently cultural traditions in chimpanzees involve relatively simple instrumental actions involving tools (Whiten et al., 1999), and yet these show little evidence of ratcheting (Boesch & Tomasello, 1998; Whiten et al., 2003). Our results suggest that this may be attributable to factors other than just particular social learning mechanisms. Some researchers have proposed alternative explanations for the minimal evidence of cumulative culture in nonhumans. Whiten et al. (2003) have argued that chimpanzees' social learning mechanisms are in fact relatively sophisticated, allowing for some imitation of actions as well as emulation. They have therefore proposed that the comparative complexity of human behavior and cognition may account for the prevalence of cumulative culture in humans, rather than particular social learning mechanisms. More recently, Marshall-Pescini and Whiten (2008) showed that chimpanzees perseverated markedly with learned techniques even when exposed to superior ones, and suggested that this may constrain their capacity for cumulative culture. In addition, Laland (2004) has proposed that cumulative culture may depend on an ability to appraise the relative effectiveness of behavioral alternatives, and that this may be beyond the capabilities of nonhumans. We believe that alternative interpretations such as these merit further exploration.

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