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Research Report

Social Learning Mechanisms and Cumulative Cultural Evolution

Is Imitation Necessary?

Christine A. Caldwell and Ailsa E. Millen

University of Stirling

ABSTRACT—*Cumulative cultural evolution has been suggested to account for key cognitive and behavioral attributes that distinguish modern humans from their anatomically similar ancestors, but researchers have yet to establish which cognitive mechanisms are responsible for this kind of learning and whether they are unique to humans. Here, we show 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 70 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 condition was independently sufficient for participants to show cumulative learning. Because 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 that other factors may be involved.*

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, 2008b). Tomasello (1999) and Tomasello, Kruger, and Ratner (1993) called this the "ratchet effect." Similarly, Boyd and Richerson (1994) drew attention to the particular adaptive value of social learning that permits "learned improvements to accumulate from one generation to the next" (p. 134).

Address correspondence to Christine Caldwell, Department of Psychology, University of Stirling, Stirling FK9 4LA, United Kingdom, e-mail: c.a.caldwell@stir.ac.uk.

Such cumulative learning has allowed humans to develop advanced technologies and symbolic systems (such as writing and mathematical notations) and to 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 have 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) among nonhuman animals. Speculation about reasons for the apparent rarity of this kind of learning among species other than humans has centered on the learning mechanisms involved and the possibility that these may be unique to humans. Boyd and Richerson (1996) have argued that imitation, or—as Thorndike (1998) described it (as cited in Whiten & Ham, 1992)—"learning to do an act from seeing it done" (Whiten & Ham, 1992, p. 240), may be necessary for cumulative cultural evolution. Tomasello (1999) and Tomasello et al. (1993) proposed that both imitation and teaching provide the foundations of cumulative cultural evolution. Such interpretations are consistent with findings indicating that 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, 2008a) developed methods to test hypotheses about cumulative cultural evolution under

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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 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, 2008a).

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, 2008a), the task presented to participants involved building a paper airplane so that it would fly as far as possible. Participants carried out this task as a member of a chain of 10 individuals, each of whom completed the task one after the other. In the current study, we used seven different experimental conditions to manipulate the availability of different kinds of social information about the task. We divided social information into information about actions (A—i.e., opportunities to observe actual building of paper airplanes, allowing for imitation); information about results (R—i.e., opportunities to inspect completed planes and observe their flight distances, allowing for emulation); and information in the form of teaching (T—i.e., opportunities to communicate verbally with other participants, including those who had already completed the task).

METHOD

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 stipend and a research-participation credit. Seven hundred participants took part (10 chains of 10 individuals for each of the seven conditions). Their mean age was 21.37 years (SD = 5.17; youngest = 17, oldest = 68); 57% (397) of the sample were women, and 43% (303) were men. Ethical approval for this research was granted by the Ethics Committee of the Department of Psychology, University of Stirling. The procedure was explained to all participants in advance, and they each gave written consent to participate.

Procedure

The procedure for the full-information condition (ART) is described next. For the other six conditions, each of which restricted access to one or more of these sources of information, modifications were made to this basic procedure. The modifications are detailed at the end of this description. Full procedural details for each condition are in the Supporting Information available on-line (see p. 1483). Figure 1 contains diagrams of the experimental setup for each condition.

Prior to each trial, the 10 participants who would comprise the chain were assembled. 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 1 and 10 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.

When participants joined the test group, they were provided with written instructions detailing the aim of the task (to build a paper airplane, which would fly as far as possible) and their time restrictions (5 min of observation time followed by 5 min in which to build their airplane). They were informed that their participation fee would be increased proportionally with their performance on the task (10p 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 5 min, in the role of "teacher," in order to help others in the test group. Figure 2 shows the membership of the test group, and the role of each participant, at any given time during an ART trial. Participants 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. Whereas participants were encouraged to give and receive advice, to observe others' actions, and to allow others to observe their actions, they were expressly forbidden from building another individual's plane. Each participant was provided with a single sheet of size A4 paper with which to create the airplane.

Within the test group, participants were kept aware of their current role (observing, building, or teaching), and the elapsed time, by a computer display and reminders from the experimenter. Once an individual's 5-min building period was up, his or her plane was evaluated. This involved the participant throwing the plane three times, with the experimenter recording the best of the three measurements (to allow for misthrows). Members of the test group could see planes being thrown. Participants then returned to the test group in the teacher role for 5 min. 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 5 min, 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 that had been on view the longest. Participants left the testing area once their 5 min of teaching time had elapsed.

The other experimental conditions followed the same procedure, with these exceptions. Conditions without action information (i.e., the RT, R, and T conditions) did not include a 5-min observation period before their building time. Participants were

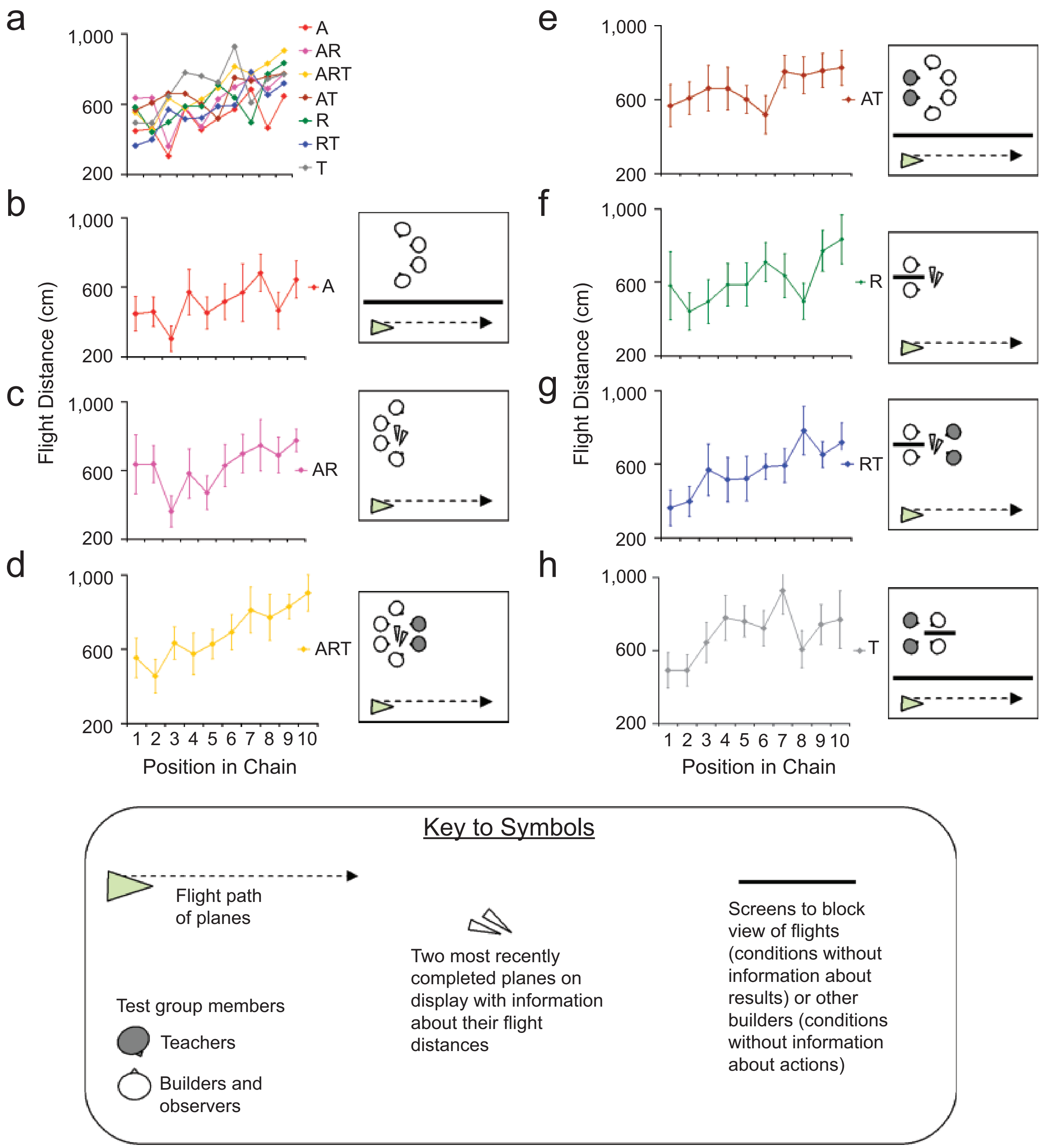

Fig. 1. Flight distances of the paper airplanes produced by participants in Positions 1 through 10 of the chains. Results for all seven conditions are presented together in (a). The other panels present results separately for (b) the actions-only condition; (c) the actions and results condition; (d) the actions, results, and teaching condition; (e) the actions and teaching condition; (f) the results-only condition; (g) the results and teaching condition; and (h) the teaching-only condition. Error bars represent ±1 *SEM*. The diagrams to the right of the graphs illustrate the experimental setup in each condition.

instead called from the waiting area roughly 1 min before their building time began, to read their instructions. Participants 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 Fig. 1).

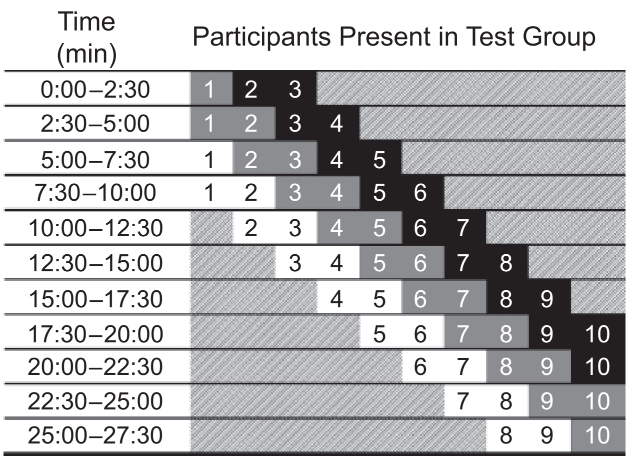

Fig. 2. The microsociety design. This diagram shows the membership of the test group at any one time during a trial, for the conditions involving action information and teaching (actions and teaching condition and actions, results, and teaching condition). Shading indicates the role of the participant: Black indicates observing, gray indicates building, and white indicates teaching. Conditions without action information (results-only condition, results and teaching condition, and teaching-only condition) included no observation period, and conditions without teaching (actions-only condition, actions and results condition, and results-only condition) included no teaching period.

In conditions without results information (i.e., 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 Fig. 1).

In conditions without information from teaching (i.e., 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 teacher role. 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 in Figure 1 and Table 1. In each condition, we tested for cumulative cultural evolution by using Page's 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, Participant 9 would have a higher score 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 toward improvement further along the chain, demonstrating cumulative culture.

TABLE 1
Summary of Results for the Seven Experimental Conditions

	Mean flight distance		Evidence for cumulative culture	
Condition	Participants 1–3	Participants 8–10	L	p
ART	547.7 (246.1)	836.5 (213.0)	3,385	.001
AR	544.6 (282.4)	735.9 (228.3)	3,212	.016
AT	612.4 (247.5)	754.6 (174.2)	3,197	.024
RT	443.9 (209.1)	717.9 (211.5)	3,345	.001
A	404.4 (203.2)	598.7 (226.3)	3,170	.048
R	506.8 (298.9)	701.0 (286.6)	3,207	.018
T	543.5 (202.8)	707.1 (308.4)	3,175	.042

Note. The condition labels indicate the nature of the information provided to participants: A = actions; R = results; T = teaching. Standard deviations are given in parentheses. L = 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).

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, to accumulate effective strategies within the chain. It was nonetheless of interest to determine whether certain conditions were more effective than others. To compare conditions, data were collapsed across the first 3 (i.e., Participants 1, 2, and 3) and last 3 (Participants 8, 9, and 10) participants in each chain. Means are reported in Table 1. These values allowed us to perform a 2 × 7 analysis of variance, 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, $F(1, 63) = 33.245$, $p < .0005$, $\eta_p^2 = .345$, in keeping with our finding that scores were higher later in the chain. However, there was no main effect of condition, $F(6, 63) = 1.182$, $p = .327$, $\eta_p^2 = .101$, so no condition was overall any better than any other. There was also no interaction between position and condition, $F(6, 63) = 0.330$, $p = .919$, $\eta_p^2 = .030$, so the trend toward improvement later in the 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. Among 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). Tomasello and colleagues (e.g., Tomasello et al., 1993) have argued that nonhuman primates depend on emulation to a much greater extent than they depend on imitation.

Note 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 in others. In our previous research (Caldwell & Millen, 2008a), 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 using 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, rather than particular social learning mechanisms, may account for the prevalence of cumulative culture in humans. More recently, Marshall-Pescini and Whiten (2008) showed that chimpanzees perseverated markedly with learned techniques, even when exposed to superior ones. Marshall-Pescini and Whiten 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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