

1 Christine A. Caldwell
2 Behaviour and Evolution Research Group
3 Psychology, School of Natural Sciences
4 University of Stirling
5 Stirling
6 FK9 4LA
7 United Kingdom
8
9 Phone: +44 (0)1786 467677
10 Email: c.a.caldwell@stir.ac.uk
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Experimental approaches to studying cumulative cultural evolution

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Christine A. Caldwell¹

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Mark Atkinson

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Elizabeth Renner

20

21

University of Stirling

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28 Abstract

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30 In humans, cultural traditions often change in ways which increase efficiency and
31 functionality. This process, widely referred to as cumulative cultural evolution, sees
32 beneficial traits preferentially retained, and it is so pervasive that we may be inclined to take
33 it for granted. However, directional change of this kind appears to distinguish human cultural
34 traditions from behavioural traditions that have been documented in other animals.

35 Cumulative culture is therefore attracting an increasing amount of attention within
36 psychology, and researchers have begun to develop methods of studying this phenomenon
37 under controlled conditions. These studies have now addressed a number of different
38 questions, including which learning mechanisms may be implicated, and how the resulting
39 behaviours may be influenced by factors such as population structure. The current article
40 provides a synopsis of some of these studies, and highlights some of the unresolved issues in
41 this field.

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43 **Keywords:** cumulative culture; cultural evolution; imitation; microsocieties; ratchet effect

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46 Cumulative cultural evolution is a process by which a series of social transmission events
47 results in successive improvements in performance, arising due to an accumulation of
48 modifications to the transmitted behaviours. The human capacity for cumulative culture
49 therefore allows us to capitalise on the accumulated knowledge and experience of previous
50 generations, such that we routinely make use of inventions and discoveries which would be
51 unlikely or impossible for us to have achieved by ourselves (e.g. every time we make a phone
52 call, or heat food in a microwave oven). Furthermore, techniques and technologies are often
53 developed further based on existing knowledge, and such accomplishments are within reach
54 of any typical individual. In this respect, human culture has been very aptly described by
55 Tomasello (e.g. Tomasello, Kruger & Ratner, 1993) as exhibiting a “ratchet effect”:
56 beneficial modifications and improvements tend to be preserved such that skills and
57 technology increase in efficiency and functionality over successive generations, with little
58 backwards slippage.

59

60 The phenomenon of cumulative culture is so ubiquitous within human societies that we may
61 be tempted to dismiss this capacity as relatively unremarkable. Similarly, it is easy to
62 underappreciate the significance of its impact on human behaviour, for the simple reason that
63 it is difficult to imagine any human society without it. However, a comparative perspective
64 readily prompts a very different view, which makes it quite apparent that the capacity for
65 cumulative culture is neither trivial nor inconsequential. Despite the universality of
66 cumulative culture across human societies, there is currently little evidence of it in any
67 nonhuman species (Dean, Vale, Laland, Flynn & Kendal, 2014). Although social learning has
68 been identified in many animals (broadly defined as learning that is facilitated by contact
69 with experienced individuals, or the physical traces left by experienced individuals, c.f.
70 Heyes, 1994), evidence of anything akin to the ratchet effect remains elusive. Even the most

71 complex socially learned behaviours of nonhuman primates are generally acknowledged to be
72 no more complex than the trial-and-error achievements of some individuals (Tennie, Call &
73 Tomasello, 2009). This evolutionary anomaly therefore presents something of a puzzle. The
74 capacity for cumulative culture has allowed modern humans to dominate the planet (Boyd,
75 Richerson & Henrich, 2011), so it may represent a uniquely powerful mechanism for
76 adapting to novel and changing environments. Its apparent absence in other species therefore
77 merits serious consideration.

78

79 Appreciation of the significance of cumulative culture prompts a number of fairly
80 fundamental questions for behavioural scientists. One such question concerns the cognitive
81 capacities that are required to generate this process, the answer to which may help us to
82 understand why we do not see it in other species. Related to this, and making a reasonable
83 assumption of evolutionary continuity, it is also of interest to determine the extent to which
84 similar processes may be present in other species, particularly those closely related to us. In
85 addition, given that many examples of complex human behaviour are likely to be
86 consequences of cumulative cultural evolution, this prompts the question of whether this
87 process places its own constraints on the behaviours that are likely to emerge. Does repeated
88 social transmission create unique pressures not present in individual trial-and-error learning
89 or genetic evolution, such that behaviours tend to be shaped and filtered in particular (and
90 possibly predictable) ways? Extending this logic, can the form (or indeed presence or
91 absence) of certain behaviours within specific populations potentially be explained as a
92 consequence of peculiarities of the transmission process within that population? These
93 questions touch on fundamental issues within psychology, such as understanding cross-
94 cultural similarities and differences, and tracing the evolutionary origins of complex human
95 cognition.

96

97

LABORATORY STUDIES OF CUMULATIVE CULTURE

98

99 Despite the significant theoretical implications of the questions detailed above, finding ways
100 to investigate them is not necessarily straightforward. Cumulative cultural evolution
101 describes a property of behaviour at the level of the group, rather than the individual, and
102 therefore (in contrast to traditional psychological methods) multiple individuals are required
103 for a single experimental replicate. It also describes a dynamic process, rather than a static
104 phenomenon, characterised by directional behavioural change over time. If we aspire to
105 address some of these questions then we need to be able to demonstrate this process in action,
106 under conditions that allow us to manipulate variables of interest (Caldwell & Millen, 2008a).

107

108 Motivated by this goal, Caldwell & Millen (2008b) set out simply to establish that it was
109 possible to study this process under controlled conditions. In order to demonstrate a social
110 learning ratchet effect it must be possible to show, at a minimum, that learning from an
111 individual who has themselves had the benefit of social information must be typically more
112 valuable than learning from an individual who has had no such opportunity. Therefore we
113 aimed to devise tasks in which successive attempts, carried out by different individuals, could
114 potentially result in improved performance. The tasks also required objective measures of
115 success, and had to be achievable within experimentally-feasible periods of time.

116

117 Our initial experiments (reported in full in Caldwell & Millen, 2008b) used two different
118 tasks. In one, participants were asked to build a paper aeroplane from a single sheet of paper,
119 with success measured by the flight distance of their plane. In the other, participants were
120 asked to build a tower from raw spaghetti and a small amount of modelling clay, with success

121 measured by the height of their tower. For each task, we ran ten chains each composed of ten
122 participants, who took part in the task one after the other, with opportunities to observe
123 individuals who took part immediately before themselves. Figure 1 displays a schematic
124 illustrating the role of each of the ten participants in any given chain at any point during
125 testing. The purpose of structuring the participants' activity in this way was to create a
126 simulated, scaled-down population of learners who came into contact with members of
127 adjacent generations with overlapping experimental lifespans. Such research designs are
128 sometimes referred to as "microsocieties" (Baum, Richerson, Efferson & Paciotti, 2004) or
129 "microcultures" (Jacobs & Campbell, 1961). Further experiments using similar approaches to
130 studying cumulative culture are reviewed in Whiten, Caldwell & Mesoudi (2016).

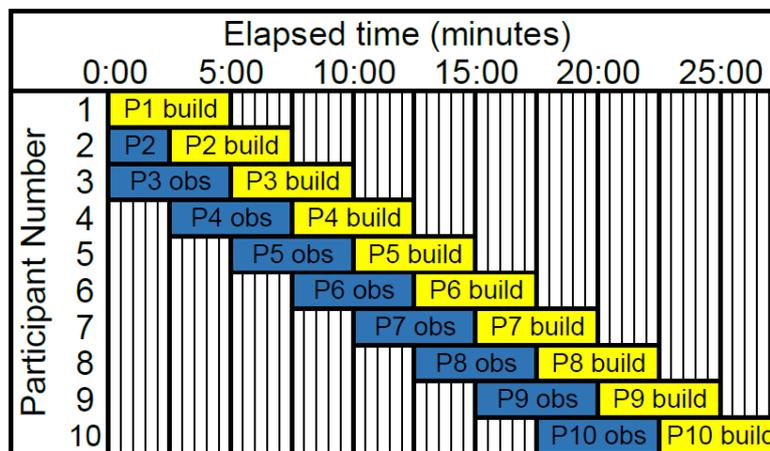
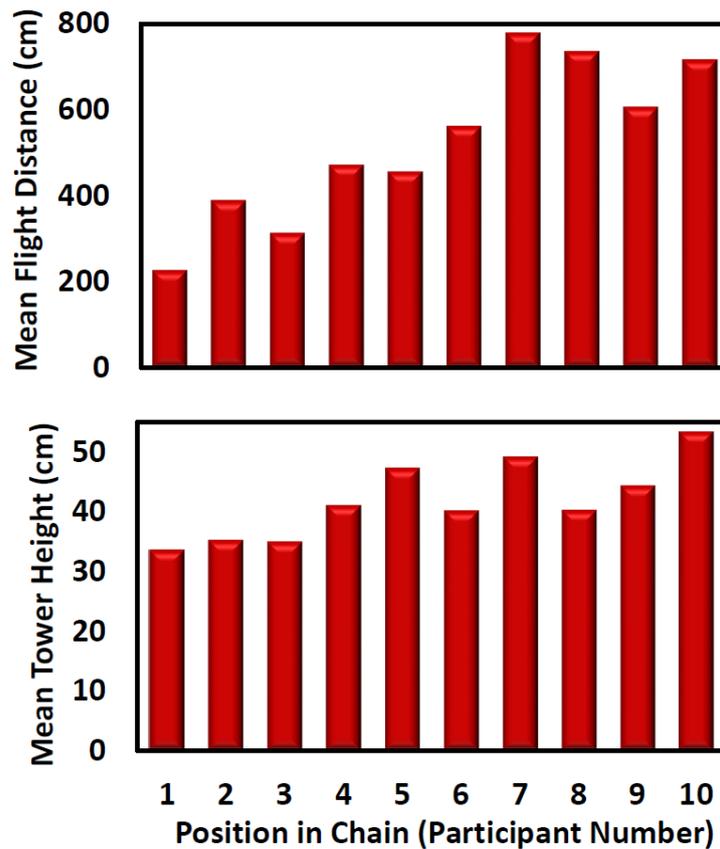
131

132 Figure 1 displays the data for both the paper aeroplane task and the spaghetti tower task,
133 which supported our basic expectation of a ratchet-like effect across multiple successive
134 learners. Effectively, the learning opportunities available to participants appeared to permit
135 generational carry-over of the experience of past members of the microsociety, such that
136 learners (given exactly the same instructions, materials, and time constraints) could perform
137 better if they were placed in later generations.

138

139

140 **Figure 1.** Participants' scores on goal measures increased over generations of the
 141 microsocieties. Top panel displays flight distances of paper aeroplanes, and centre panel
 142 displays heights of towers, each based on the mean performance across ten microsocieties, as
 143 detailed in Caldwell & Millen (2008b). Bottom panel shows how each participant's
 144 observation (blue) and building (yellow) stages were staggered relative to other members of
 145 their microsociety.



146

147

148 Does Cumulative Culture Depend on Imitation?

149

150 Although Caldwell and Millen's (2008b) study showed that it was possible to capture
151 cumulative cultural evolution under laboratory conditions, it was unclear what information
152 participants were using to generate this effect. However, these methods permitted
153 manipulation of the information available to learners to address this question. Dominant
154 theoretical perspectives on cumulative culture proposed that imitation and teaching were
155 required for it to occur (e.g. Tomasello et al., 1993; Tennie et al., 2009). Although definitions
156 of imitation are widely debated within comparative psychology (Caldwell & Whiten, 2002),
157 there is general consensus that it requires observation of another's behaviour, and that it
158 should result in some detectable match between the actions of the model and those of the
159 observer. Early studies which failed to find evidence of such action copying in nonhuman
160 species (e.g. monkeys: Visalberghi & Fragaszy, 1990; apes: Tomasello, Davis-Dasilva,
161 Camak & Bard, 1987) gave credence to the view that this might provide an explanation for
162 the absence of cumulative culture in nonhumans. However, later studies which identified
163 copying of specific techniques (e.g. using "two-action" experimental designs) in a range of
164 nonhuman species (e.g. see Whiten, Horner, Litchfield & Marshall-Pescini, 2004, for a
165 review of evidence in apes) cast some doubt on the validity of this interpretation (although
166 evidence of imitation in nonhumans continues to be debated, e.g. Tennie et al., 2009).

167

168 Consistent with this, further experimental studies of cumulative culture in humans
169 demonstrated that action copying may not be strictly required. Through manipulation of the
170 information available to learners in particular microsocieties, Caldwell and Millen (2009)
171 found that participants were capable of generating cumulative culture even when information
172 about others' actions was not available. In the paper aeroplane task, when members of the

173 microsocieties received information only about results (flight distances) and end products
174 (completed planes), without opportunities to observe others building, they still showed
175 cumulative increases in performance over generations.

176

177 In this particular task performance scores were primarily determined by the physical structure
178 of the artefacts produced, and those structures were relatively easy to reproduce from
179 inspecting the finished products. For other tasks, reproduction of specific behaviours may of
180 course be necessary in order to generate improvements in performance over generations (e.g.
181 knot tying, for which it is often difficult to infer the required steps on the basis of the finished
182 product alone). And for some skills, active instruction may also be required in order to
183 correct mistakes, shape behaviour, and explain underlying principles (e.g. food preparation
184 techniques which remove undetectable toxins, whose function may be opaque to an
185 observer). Nonetheless, it seems clear that cumulative culture can occur in the absence of
186 opportunities for action copying, and so this in itself does not provide a comprehensive
187 explanation for the absence of cumulative culture in nonhumans.

188

189 The question of the specific cognitive differences explaining the uniqueness of human
190 cumulative culture currently remains unresolved. However, future research will likely benefit
191 from an approach which considers particularities of the ways that human learners process and
192 use social information irrespective of source.

193

194 How Does Cultural Evolution Shape Resulting Behaviours?

195

196 In addition to clarifying the conditions necessary for cumulative cultural evolution to occur,
197 experimental approaches have also been used to investigate factors influencing the outcomes

198 of this process in terms of the resulting behaviours. It is likely that such behaviours are
199 shaped in particular ways by repeated social transmission. Experimental work has begun to
200 investigate how cultural traits tend to transform over multiple learner generations. This has
201 been demonstrated most clearly in studies of artificial language learning (e.g. Kirby, Cornish
202 & Smith, 2008; Kirby, Tamariz, Cornish and Smith, 2015). In these experiments participants
203 are trained on a set of novel labels with corresponding stimuli representing their meanings.
204 They are then tested, and this output is used as training data for the next participant. Kirby et
205 al. (2015) found that sets of labels changed to become more internally structured, i.e. each
206 label became increasingly predictable from other labels assigned to related meanings. In this
207 way, the language evolved to become more learnable over the repeated generations of
208 transmission. This only happened, however, in chains of participant pairs who learned their
209 labels from preceding pairs. It did not occur in a control condition in which communicating
210 pairs completed the same task, but did so over multiple sessions with the same partner,
211 receiving their own output from the most recent session as training for the next. In the
212 absence of new learners, the languages did not adapt to become more learnable.

213

214 Whilst the cultural evolution of language might not represent a prototypical case of
215 cumulative cultural evolution as we have defined it, it is likely that similar effects occur in
216 other contexts. We should therefore expect that pressures for learnability will shape the
217 attributes of other culturally transmitted behaviours in particular ways, which may be
218 unrelated to, or even in conflict with, other functional pressures.

219

220 Following this logic, it is also likely that differences in the transmission processes involved in
221 the ancestral histories of cultural traditions can affect the eventual forms of behaviour. So, for
222 example, differences in population size or structure may influence the level of complexity of

223 the traits which can persist, as a consequence of the availability of learning opportunities and
224 the likelihood of exposure resulting in accurate transmission. Larger and/or more densely
225 connected populations are assumed to be less vulnerable to losing complex skills which may
226 only rarely be successfully transmitted, due to the increased probability of encounters
227 between proficient individuals and potential learners (Henrich, 2004; Powell, Shennan &
228 Thomas, 2009). Hard-to-learn skills might therefore only ratchet up in well-connected
229 populations which ensure exposure to a diversity of potential models.

230

231 Muthukrishna, Shulman, Vasilescu and Henrich (2014) tested this hypothesis experimentally
232 by asking participants to use image editing software to produce a complex target image, and
233 evaluating the effectiveness of the attempts of ten generations of learners. They compared
234 conditions in which learners were exposed to information about how to complete the task
235 from either one member, or five members, of the previous generation. In line with
236 predictions, the images created by participants in the five-model condition showed
237 improvement over generations whereas those in the one-model condition did not (see also
238 Derex, Beugin, Godelle & Raymond, 2013, for an experimental test of the group size
239 hypothesis without generational replacement).

240

241

242 OUTSTANDING ISSUES

243

244 Although experimental methods have permitted significant insights into cumulative culture, a
245 number of key questions remain unanswered. For example, although there is little evidence of
246 cumulative culture occurring spontaneously in nonhumans, it remains to be seen whether it is
247 possible to find performance increases over transmission under experimental conditions

248 similar to those described previously for studies of human participants. Under favourable
249 laboratory conditions (probably involving relatively well-trained animal subjects and target
250 behaviours which are comfortably inside their performance repertoire) it may be possible to
251 elicit similar effects. If this turns out to be the case then researchers face a further question
252 regarding the barriers limiting cumulative culture in naturally occurring behaviours.

253

254 Along similar lines, questions remain over the extent to which particular transmission
255 mechanisms may be necessary depending on the behaviour in question. For example, given
256 that teaching appears to be uniquely flexible in humans, if not strictly unique (e.g. Kline,
257 2015), is it necessary for the transmission of certain behaviours? And if so, does this help us
258 to re-construct a co-evolutionary sequence of mutually reinforcing adaptive pressures
259 between the early existence of relatively complex cultural artefacts, the evolution of human
260 pedagogy, and the resulting effects on the cultural traits that could be transmitted? It is likely
261 that approaches similar to those discussed in the current article will contribute to the eventual
262 resolution of some of these important outstanding issues.

263

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265

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¹ Address correspondence to: Christine A. Caldwell, Psychology, School of Natural Sciences,
University of Stirling, Stirling, FK9 4LA, United Kingdom.

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