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Cumulative culture in the laboratory: methodological and theoretical challenges

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In the last decade, cultural transmission experiments (transmission chains, replacement, closed groups and seeded groups) have become important experimental tools in investigating cultural evolution. However, these methods face important challenges, especially regarding the operationalization of theoretical claims. In this review, we focus on the study of cumulative cultural evolution, the process by which traditions are gradually modified and, for technological traditions in particular, improved upon over time. We identify several mismatches between theoretical definitions of cumulative culture and their implementation in cultural transmission experiments. We argue that observed performance increase can be the result of participants learning faster in a group context rather than effectively leading to a cumulative effect. We also show that in laboratory experiments, participants are asked to complete quite simple tasks, which can undermine the evidential value of the diagnostic criterion traditionally used for cumulative culture (i.e. that cumulative culture is a process that produces solutions that no single individual could have invented on their own). We show that the use of unidimensional metrics of cumulativeness drastically curtail the variation that may be observed, which raises specific issues in the interpretation of the experimental evidence. We suggest several solutions to these mismatches (learning times, task complexity and variation) and develop the use of design spaces in experimentally investigating old and new questions about cumulative culture.

1. Introduction

First introduced in Bartlett's classic study of memory [1], cultural transmission experiments, or CTEs, are now being used in cognitive science, social psychology, behavioural biology and cultural evolution. Whereas psychological experiments on learning typically deal with individuals solving a task on their own, transmission experiments allow participants to learn from one another. Doing so, they make it possible to 'capture the repeated occurrences of social learning involved in cultural change, as opposed to one-off cases of individual learning' ([2], p. 2), making them powerful tools to study culture under controlled conditions. Ten years ago, Mesoudi & Whiten ([3], p. 3490) observed that 'perhaps due to the sparseness of past experimental studies and the lack of any guiding theoretical framework, these questions and methods have not been addressed in a systematic fashion, and answers to each must be said to be sketchy at best'. Since then, these valuable experiments have become increasingly popular due to their intensive use in the study of cultural evolution and now ground a productive and exciting new experimental field (cf. electronic supplementary material 1). Several recent reviews have summarized the various methods used in CTEs, the research topics typically investigated and the findings of these experiments [3–8]. In so doing, these reviews have contributed to making CTEs a scientific success.

In their ecological (i.e. real world) settings, cultural phenomena are often large-scale population-level phenomena and span over several biological generations. In contrast, laboratory experiments involve much smaller artificial groups over much shorter time periods. An intrinsic challenge faced by CTEs consists in dealing with this asymmetry: how can these experiments retain the relevant features of actual cultural populations so as to serve as proper models? In this review, we address these challenges in the context of the study of cumulative cultural evolution, i.e. the gradual improvement of traditions over time.

In §2, we review the use of CTEs in the study of cumulative culture and detail the specific methods employed to do so. In §3, we identify two issues raised by the implementation of CTEs, which challenge the interpretation of their results. We suggest solutions to these issues so as to get the most out of these experiments. In §4, we argue that CTEs often fail to take full advantage of the information they collect. We show how the use of design spaces would make it possible to exploit this latent information, thus expanding the range of hypotheses about cumulative cultural evolution that CTEs could be used to test.

2. Cultural transmission experiments and cumulative culture

Cumulative cultural evolution refers to the process by which traditions are gradually modified and, for technological traditions in particular, improved upon over time. The repeated modification and transmission of culture is commonly described as a form of descent with modification characterized by a 'ratchet effect' (e.g. [9–11]). The ratchet effect is a mechanical metaphor that stresses the role of social transmission in 'locking in' novel modifications of socially transmitted traits in a population's cultural repertoire. As modified traits are transmitted, further modifications can in turn be made and transmitted. With time, it is expected that populations will build up increasingly complex cultural traits that no single individual could have invented on its own. A capacity for cumulative culture would be adaptive by allowing populations to collectively reach solutions that are beyond the problem-solving capacities of the individual [12] (or beyond the species' existing cognitive repertoire, i.e. their zone of latent solutions [10]). It would also allow the distribution of efforts, risks and time costs of invention by trial and error over several generations [13,14].

CTEs have been used to investigate three main questions regarding cumulative culture. The first concerns the identification of the key adaptations leading to the onset of cumulative culture in the human lineage, in contrast to other non-human species that may have cultural traditions but of a non-cumulative kind. CTEs have thus been used to identify social learning processes, such as imitation, emulation and/or teaching, that can lead to the cumulative increase of performance in functional tasks (e.g. [15–17]). The second issue concerns the impact of demography on the cumulative process. It has been investigated by means of CTEs by varying the number of participants and of models (e.g. [18–21]) or by varying the density of their interactions (or 'connectivity'; e.g. [22,23]). The third issue concerns the role of inductive biases in the emergence of new complex traits without design, for instance, in the study of linguistic structures [24,25].

When dealing with human adults as participants, CTEs of cumulative culture typically employ one of three methods: linear chains (also called diffusion chains), replacement and closed-group (or constant-group) methods [6]. In linear transmission chains, a first participant is presented with a stimulus and must later recall it. The output of this first participant serves as the input stimulus for a second participant, who has to recall it in turn. This is repeated several times until it reaches the last participant in the chain. In the replacement method, groups of participants solve some task, either once or repeatedly, either individually or collectively. At each time step, new participants replace some of the previous ones and learn from the group how to solve the task. Finally, in the closed-group method a group of participants aims at solving some task. In between two trials, the participants can learn from one another, the specific means of doing so being dependent on the experimental design.

Most of the tasks used in these experiments consist in solving problems according to some performance criteria, for instance assembling a jigsaw puzzle [20] or solving anagrams [26]. Many of these problem-solving tasks require the production of artefacts, either real ones (such as paper planes, spaghetti towers, rice baskets, weight-bearing devices or stone flakes [15–18,27–30]) or virtual ones (such as virtual totems, fishnets and arrowheads [19,22,23,31–35]), or both [21]. Other experiments consist of participants transmitting some information, with or without explicit instructions to transmit it as faithfully as possible [24,25,36–39]. These tasks can usually be solved in multiple ways, with some solutions being more rewarding or effective than others.

CTEs using children or non-human animals as participants have employed linear chains, replacement or seeded group (or seeded open diffusion). Seeded groups consist in training an individual to complete a task (e.g. how to use some apparatus) and then allowing the individual to freely engage with it. Other participants observe the individual and are in turn also free to engage with the task. Experiments with children and non-humans use a variety of tasks such as opening an artificial fruit [40–42], building or combining some tools in order to solve a foraging problem [43–45], reproducing visual patterns [46–48] or finding a way back home [49].

3. Miniaturizing culture: learning time and task complexity

According to theoretical accounts of cumulative culture [3,5,10,13,14,28,50], a diagnostic criterion for a cultural process to be properly cumulative is that it leads human cultures to 'accumulate changes over many generations, resulting in culturally transmitted behaviors that no single human individual could invent on his own' ([13], p. 80). Exactly how the diagnostic criterion is to be understood remains largely open to interpretation. Under one understanding, satisfying the criterion would mean using a task that is too complex for a single individual to solve on its own, requiring a collective of individuals, such as a tradition, to reach the solution [10,12]. Alternatively, the criterion can be interpreted to mean that a task is too complex for an individual to solve during her *limited lifetime* but that it could be solved by a tradition as it distributes the effort and time required to solve the complex task over the lifetimes of multiple individuals [51]. Under both interpretations, aiming to satisfy the diagnostic criterion would 'effectively eliminate the possibility of experimental research as participants would be incapable of completing the task' ([17], p. 7). Such experiments would additionally need to span over multiple lifetimes for any cumulative effect to be detected. These two aspects of real-life cumulative culture—complex ecological tasks and large timespans—pose serious challenges for any experimental work.

The strategy used to circumvent these difficulties consists in 'miniaturizing' generational change to fit laboratory conditions and to use tasks that can be solved by a small number of participants in a limited amount of time. The turnover of participants in the laboratory traditions, or microsocieties, is then taken to model actual generational change in virtue of linking the participants by episodes of cultural transmission [3]. For transmission chains and replacement methods, modelling generational change is achieved by the replacement of a participant by another, with each individual representing a different generation. In closed-group experiments, generations are instantiated by the successive rounds of a given task that a same group of participants solves.[1] An experimental analogue of the diagnostic criterion could then be used to detect a genuinely cumulative process in the laboratory: showing that laboratory traditions can reach higher performance levels in solving some task than individuals doing so on their own thus offers, it is suggested, a scaled-down cultural cumulative process [5].

In order to test whether a cumulative effect has been obtained, CTEs need to systematically compare how, for a same task, individuals fare on their own in solving the task with the solutions achieved by laboratory traditions.[2] Few CTEs effectively make this comparison. Those that do include as a control a 'non-social condition' where single participants, with a limited time budget, are asked to solve a task and improve their performance on their own over repeated trials [17,22,31,32,34,35,44]. The accumulation of improvements during a run of the non-social condition is interpreted as an effect of individual learning, with the increase in performance observed in these conditions indicating that participants are getting more skilful in solving the task. In contrast, in 'social conditions', several participants are involved in solving the same task, the solution produced by one participant made available to the next participant(s). When the performance achieved in the social condition surpasses the performance achieved in the non-social condition, the difference in performance is seen as evidence of a cumulative cultural process.

Using small groups of participants over short periods of time is necessary to effectively run a CTE. However, the discrepancies between the spatio-temporal scale of the processes leading to real cultural change and those in action in the laboratory microsocieties can lead to several mismatches between the underlying causes of differences in performance. We now turn to two types of such mismatches that may undermine the evidential value of the diagnostic criterion as it is implemented in CTEs. We then suggest means to overcome these problems.

(a) Learning time

Introducing some novel terminology may prove useful at this point. We refer to the sum of all the learning and trial time invested by an individual participant in a non-social condition as the *total learning time of an individual*. We refer to the sum of the time spent learning and performing a task by all the participants of a chain or group during one run of an experiment as the *total additive learning time of a tradition*. See electronic supplementary material 2 for a synthetic comparison of the two kinds of total learning times in the CTE literature and how these time budgets are calculated.

In experiments with both non-social and social conditions and with equal total learning time (i.e. of an individual and of a tradition), traditions in the social conditions tend to produce better performance results than individual participants in the non-social ones (e.g. [33,34]). These differences in performance may suggest that the laboratory traditions produce traits that are out of reach to single individuals, and thus that a cumulative effect has occurred. We argue, however, that the control conditions currently used in CTEs are insufficient to warrant the conclusion that the observed differences in performance are the results of a genuine cumulative process.

The differences between the performance of participants in the non-social and social conditions may, in particular, be the result of laboratory traditions reaching performance levels that are well within the reach of a single participant working alone, but doing so *faster* than participants working alone. Consider first that the total additive learning time of an experimental tradition is at most a few hours (see electronic supplementary material 2-2). It is thus a possibility that what the difference in performance measures is not so much a difference in capacity between a collective and an individual as one in improvement speed. For example, it could be that participants in a social condition have their individual skill improvement facilitated by their learning in a social context [52]. If this were the case, then the observed asymmetry would not be due to a cumulative process producing traits too complex for an individual to invent alone, as demanded by the diagnostic criterion. Instead, by fixing the time allowed for participants in non-social conditions to improve their performance, the asymmetry would be the result of ending the experiment prematurely (i.e. were they given more time, the participants in non-social conditions could have reached the same solution as those in social conditions).

There is a straightforward way to ascertain whether participants in a social condition increase their performance not just faster but also beyond the reach of participants in a non-social condition and thus to determine whether a genuine cumulative process is implemented in a CTE. To begin with, all CTEs should systematically include a baseline non-social condition in which a single participant solves the same task over multiple trials. Only about a third of CTEs testing for cumulative culture have such non-social control conditions (see electronic supplementary material 2). The non-social condition should minimally involve as many individual trials as there are generations in the social condition, with equal learning times for each individual trials and social generations. In other words, the total learning time of an individual should be equal to the total additive learning time of the tradition to which it is compared—a measure so far only implemented in [17]. This would allow a consistent comparison of the results in social and non-social conditions; it could confirm that, across tasks, traditions perform better than individuals working alone. The total additive learning time of traditions should also be of the same duration across different social conditions (e.g. when comparing the effect of different transmission mechanisms; see electronic supplementary material 2). These suggested controls participate to a more stringent criterion for the detection of cumulative culture in experimental settings. By doing so, they allow distinguishing between confounding factors and thus eliminate some risks of erroneously concluding to a cumulative effect when there is none (type 1 errors). Additionally, by equalling the time budgets between the relevant conditions, we can compare rates of learning and how they impact the emergence of cumulative culture.

(b) Task complexity

Miniaturizing cultural phenomena to fit experimental settings has further consequences for the validity of the results obtained through CTEs. CTEs demand that the experimental tasks presented to the participant be *rapidly* solvable—relatively to the time available to individual learners and to traditions in ecological conditions—if only because CTEs require a much reduced timescale for their implementation in contrast to real intergenerational cultural processes. In order to deal with this time constraint, CTEs typically include tasks that are easier and more straightforward to solve relative to the real, complex ecological problems solved by human cultures. However, scaling down the complexity of a task risks trivializing the results of any CTE. Indeed, cumulative culture is a process that is supposed to allow collectives of individuals to solve complex problems, problems that no single individual could have solved on their own during their lifetime. Instead, most tasks used in CTEs are simple enough that they do not require the collective effort of a group of individuals to be solved (e.g. solving a jigsaw puzzle, building spaghetti towers), thus casting doubt on their ecological validity [32].

Coping with the constraints of the reduced spatio-temporal scale of laboratory experiments by using simpler problems can be both misconceived and misleading. Simpler problems and their associated solutions are *not* miniaturized, scaled-down versions of complex problems and solutions because complexity is not a scalable property of a system (e.g. building a nanorobot does not mean making a smaller, simpler version of a complex, human-sized robot). Simplicity is not complexity at a smaller spatio-temporal scale. Consequently, dealing with simple tasks in CTEs can lead to results that are in fact not representative of cumulative culture at all.

For instance, in most CTEs used to investigate cumulative culture, we observe a nearly systematic improvement of the traditions at each laboratory generation (e.g. [18]). In other words, in a laboratory setting, most individual (adult) participants can and often do improve upon the tradition they inherit from the other participants. This general result among CTEs leads to a tension with both theory and fieldwork observations.

From a theoretical point of view, it is often assumed that inventions contributing to cumulative culture are uncommon, either because they are hard to achieve or because they are costly to acquire [13]. 'It is the selective transmission of *lucky errors* and *occasional experiments* that drives much of the evolution of adaptive technology, skills, beliefs, and practices' ([53], p. 202; emphasis added). Hence the alleged importance of high-fidelity transmission mechanisms to preserve these rare and precious innovations whenever they appear (securing the so-called 'ratchet effect'; [11,54]). However, taking the results of CTEs at face value, it seems that even if cultural transmission had low fidelity, the individual capacity to successfully improve upon traditions is so common and systematic that it could easily compensate for the repeated loss of most improvements.

These results also clash with fieldwork observations, especially in regard to technological traditions. Participants in CTEs are rarely, if ever, experts in the task they are asked to solve. CTEs typically demand relatively simple tasks that neophytes can readily improve upon and do so in a very limited amount of time. In contrast, in naturally occurring cultures, it seems that most innovations originate in some rare creative individuals, or lead users [55], often experts in their field [53,56–58]. This expertise is itself acquired through repeated, deliberate practice, and over many years [59–61]. Yet, CTE results seem to indicate that most participants are adept inventors, capable of innovating in a matter of minutes. These results thus conflict with what we know about actual cumulative change, which suggests that the tasks used in CTEs are not a simplified version of cultural technical traditions but a kind of practice too different from these traditions, too devoid of ecological validity to allow confident extrapolation.

There are several possible ways to avoid reducing the complexity of the task without increasing the duration of the experiment beyond reason. A first possibility is to recruit participants that are already experts in the type of tasks used in the experiment, or that have already acquired some skills that would help them in succeeding at the experimental task (for experiments involving experts, see [62–64]). To the best of our knowledge, no CTEs have reported using participants with previous experience in the type of task they had to solve (or evaluated their initial expertise in such tasks), in contrast with fieldwork experiments and observations dealing with the acquisition of complex skills [65,66]. A second possibility would be to train participants until they reach a given level of proficiency in the task used in the CTE (or a similar task recruiting the same set of skills) before they take part in the actual experiment. The level of proficiency could be set as reaching some performance score or reaching a degree of improvement of performance between runs of the training task that becomes small enough. Several experiments on language evolution have opted for this latter solution and include a training phase in their design [24,25]. Both solutions would ensure that observed increases in performance would not be due to an initial learning phase where the participants acquire initial skills but rather to the emergence of cumulative effects.

4. Using design spaces to study variation

In the previous section we have examined some issues arising from the necessary miniaturization of cultural phenomena and have suggested solutions and improvements in addressing them. We now turn to the measurement of variation in laboratory traditions. Just as the conservation of innovations is a key condition for cumulative processes, so is the production of the variation to be retained and passed on from one generation to the next. Two aspects of CTEs, namely the collapsing of each cultural generation into single individual participants and the use of unidimensional metrics of cumulativeness, drastically curtail the variation that may be observed, which raises specific issues in the interpretation of the experimental evidence. We suggest means to make information about this variation available and exploit it. By examining in more detail the role of variation in the production of cultural traditions, CTEs might provide, we suggest, better insights about cumulative culture than they currently do.

(a) Accessing information about variation in cultural transmission experiments

Most CTEs do pay some attention to the relationship between cumulative culture and cultural variation. These experiments, however, either aggregate data about variation *between traditions* at each generation or *between generations* of a same tradition, but never measure variation *within* generations (i.e. between participants of a same generation of a same tradition). For many CTEs, specifically those using linear transmission chains and replacement paradigms, the micro-societies used often reduce a whole cultural generation, which, in real life, typically involve many interacting individuals, to a single participant.[3] This precludes interactions between within-generation variability and the cumulative process, interactions that are likely to be important to understand the cumulative process. Does, for instance, cumulative culture depend on highly homogeneous populations, with little variance in their cultural traits, or does it depend on a population with a larger, richer cultural repertoire, one that would promote the recombination of existing solutions into better performing ones (e.g. [67,68])? How do novel or improved traits diffuse throughout a population (a process known as innovation [69])? Which individuals are more receptive to innovations (e.g. venture, early, or laggard adopters [69])? What kind of individuals tend to improve upon traditions (e.g. by comparing the innovative capacities of experts and non-experts)? Without intragenerational variability, we cannot address these questions.

We thus suggest that, for more informative experiments with greater ecological validity, CTEs should as much as possible have several participants at each generation instead of representing each generation by a single participant. Actually, multi-participant generations have already been used, and with great success, especially in research concerned with the evolutionary impact of the number of models one learns from and on the effect of group size on the cumulative process [20,21,70], although again with little if any detailed investigation of within-generation variation.

A second problematic aspect of CTEs is that cumulative change is typically measured strictly in terms of performance or complexity. Indeed, in many CTEs dealing with the creation of real [15–18,21,27–29] or virtual artefacts [19,21–23,31–35], the effects of cumulative culture are usually reported as some simple quantitative score—either a performance score or a measure of complexity—where traditions with higher scores are understood to have undergone more cumulation. Cashing the effects of the cumulative process into a unidimensional score passes over relevant information about the relation between variation and the cumulative process. How do the properties of each specific solution (e.g. the size and shape of some artefact) vary from one tradition to another? This is generally left unreported. Some experiments have used similarity ratings, but since the metrics were based on the intuitions of naive coders, they throw little light on the variability of the solutions devised by participants (e.g. [28]).

Measures of performance and complexity are of course important. Nevertheless, measuring the effects of the cumulative process strictly in terms of a unidimensional score doesn't help us understand why and how differences in performance and complexity emerge in the first place, and the extent to which different traditions have specific evolutionary trajectories. For this reason, we believe it would be beneficial to use multidimensional metrics to study cumulative culture. We propose to do so by using what are commonly known as 'design spaces'.

(b) Using design spaces

A useful strategy to examine how the solutions found by participants vary beyond differences in performance or complexity scores is to employ design spaces. The use of design spaces is not new. They have already been exploited in evolutionary modelling (e.g. [71–73]) and in the study of specific traditions, especially in archaeology (e.g. [74]). The novel development we suggest is to exploit design spaces in the specific context of *experimental* investigations of cultural evolution.

In the context of CTEs, a design space is the set of all potential solutions to an experimental task that participants may produce. We can build a design space by identifying specific dimensions along which these solutions may vary. For instance, when dealing with spaghetti towers, one can measure not only the height of the structures (which typically serves as the measure of performance (e.g. [28,75]) but also the number and mean angles of edges, number of vertices, number of levels, amount of spaghettis and Plasticine used, the shape of each level (e.g. triangular, quadrangular, etc.), general symmetry of the structure, and so on. By measuring these different features, one can then plot each solution onto the multiple dimensions of the design space, together with the specific generation at which the solution was produced. When represented visually, specific measures are used as spatial coordinates. It is then possible to visualize how a population of solutions evolves in time by plotting the generation at which they were produced. The evolutionary trajectories of traditions and of the participants in non-social conditions can then be compared and differences in exploratory behaviours assessed.

Using design spaces enables a richer analysis of the data obtained through CTEs at minimal cost in three ways. First, it avoids losing information about the variation in the participants' solutions and allows to compare variability both within and between generations. Second, it offers finer-grained descriptions of the evolution of traditions than measures of performance and complexity. Third, design spaces can also be used to compare which aspects of the solutions are faithfully retained and which ones are modified (and how they are modified).

Moreover, design spaces can also be used to study aspects of cumulative culture that otherwise couldn't be studied through unidimensional measures of performance and complexity. We now introduce two such questions and discuss how design spaces can be profitably put to use in addressing them.

(i) What sorts of evolutionary dynamics characterize cumulative culture?

When measuring cumulative change on a single dimension (e.g. in terms of performance), the only evolutionary patterns exhibited by experimental traditions are changes over time (increases, stagnations or decreases) on this single dimension. However, this fails to capture the diversity of possible evolutionary trajectories that can lead to the same outcome (see electronic supplementary material 3). When measuring changes on the multi-dimensional properties of solutions through design spaces, on the other hand, a broader range of evolutionary dynamics can be brought to light [2]. Unlike unidimensional measures, a multidimensional design space makes it possible to distinguish and to properly describe traditions starting from different less effective solutions and converging on the same improved solution and traditions starting from the same less effective solutions but diverging towards two different but equally effective solutions. Examining whether traditions converge or diverge can help us study the conditions under which cumulative processes are more or less path dependent and which sorts of constraints act on the potential evolvability of cultural traditions [73,76,77]. See electronic supplementary material 3 for additional examples of alternative evolutionary trajectories.

Traditions and individuals may explore design spaces in different ways. A participant learning on her own tries to improve over her previous performances. Her own biases and idiosyncrasies are likely to lead her to produce new solutions that are nevertheless closely similar to her own previous efforts, effectively leading to small, incremental changes in the design space. In contrast, in a social learning context, participants have to improve solutions devised by other participants, solutions that they might not have thought of on their own. Consequently, each participant in a social condition may bring their unique contribution to the process and generate novel solutions that are further away in design space. For instance, recombinant learning can combine the innovations of others with one's own, thus effectively leading to larger jumps into design space [67,73]. Differences in the distances traversed by individuals and traditions could allow traditions to explore larger areas of design spaces, find novel solutions with greater ease, and even effectively jump from one local performance optimum to another [34,35,71–73]. Moreover, there are already some experimental results suggesting that single participants simply do not follow the same trajectories as traditions with multiple individuals. For instance, Claidière *et al*. [47] have found, in a transmission chain with baboons, a higher performance and transmission fidelity in traditions with multiple participants than in individuals presented with their own earlier outputs (but see [78]).

(ii) Do traditions using different types of social learning explore the design space differently?

Most CTEs testing for the effect of different types of social learning (e.g. emulation and imitation) generally only consider differences in the overall improvement in performance, viewed as an evolutionary signature of the learning processes (e.g. [15,16,30,32,75]). By using design spaces, on the other hand, one could examine whether traditions using different learning mechanisms evolve along the same pathways or follow different trajectories.

Some empirical work has been dedicated to identify population-level patterns (or signatures) specific to different evolutionary processes and learning mechanisms in human populations and the archaeological record [79–81]. The use of design spaces would contribute to this line of work by experimentally identifying more such signatures and adding experimental evidence in support or against already used ones. For instance, in some social learning conditions, participants may be very conservative, both exploring very few novel solutions for a task and faithfully copying the models of the previous generation. In such scenarios, a cumulative effect would be marked mostly by the faithful retention of past innovations, leading a population to slowly move through the space (gradual change) and minimizing the spread of the population over the design space. In contrast, a cumulative effect could be due to participants selectively using some information from the previous generation (e.g. understanding the physical principles behind the working of some artefact) but innovating over it with little concern to produce similar solutions. In such cases, the cumulative effect would be mainly due to individual innovations, with the population exploring larger regions of design space and at a quicker pace, leading the population to spread more easily over the design space.

5. Conclusion

Culture is a large-scale phenomenon, taking place in populations over multiple generations. In contrast, cultural transmission experiments (CTEs) have narrowly restricted spatio-temporal scales. We identified two issues induced by fitting cultural phenomena in experimental settings and offered potential solutions for each. The first issue concerns the balancing of learning times between conditions. A second issue deals with the complexity of the experimental tasks and its relation to skill acquisition. We then argued that significant information about the evolutionary behaviours of traditions are often compressed into unidimensional scores but could be expanded and better exploited through the use of design spaces.

Experimentally studying cultural transmission is both a difficult and a promising endeavour. In this review, we suggested ways in which this already successful experimental field could be further improved.

Data accessibility. This article has no additional data.

Authors' contributions. H.M. compiled the relevant literature. Both authors contributed equally to the conception and drafting the review. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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Endnotes

[1]Although such successive rounds are sometimes understood as laboratory generations (e.g. [3]), in some CTEs they are instead understood as episodes of social learning occurring during the lifetime of individuals (e.g. [34,35]).

[2]Most experiments with children and non-humans use seeded groups when testing for cumulative culture. In those cases, the performance obtained within the (seeded) group is compared with the performance obtained in individual controls (i.e. individuals who can manipulate the apparatus or engage in the task without the possibility to observe other conspecifics). However, in seeded groups,

the population is held constant and participants only take part to the task when they want to. It is thus unclear if these can be used to test for cumulative culture as there are no laboratory generations to implement the diagnostic criterion. This makes experiments using seeded groups even more susceptible to demonstrating different results between individual and social conditions not because of a cumulative effect, but for other reasons (such as social facilitation).

[3]In contrast, closed group experiments do, by including several participants in the same generation, maintain some kind of intragenerational variation, which is measured but rarely interpreted. However, here the modelling of generational change is compromised as each generation is populated by the very same participants throughout the whole experimental tradition. This has the effect of reducing the impact of interindividual differences over the cumulative process.

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