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# **Experimental Studies of Cultural Evolution**

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#### Abstract

This chapter reviews how experiments have played a growing role in the study of cultural evolution recently. Experiments occupy a middle ground between formal models and real-world observational and historical studies. Like models, they offer the advantages of control and manipulation in order to determine causal relations between variables. Like real-world studies, they involve actual human behaviour, albeit constrained within artificial boundaries. When interpreted within the context of this trade-off between external and internal validity, experiments can provide valuable insights into the processes and dynamics of cultural evolution. Given the centrality of social learning in theories of cultural evolution, experiments typically involve participants learning from at least one other participant. Various experimental designs have been employed including dyadic interactions, linear transmission chains, closed groups, replacement or migration methods, and economic games. Key findings relate to content and inductive biases that describe how the content of cultural traits affects their transmission and evolution; context biases concerning from whom traits are copied; studies probing the socio-cognitive and demographic factors that underpin cumulative cultural evolution; the burgeoning experimental study of non-human culture; and variation in learning strategies over the lifetime and across cultures. The chapter ends with some recommendations for future experimental research, including an awareness of the proper function and limitations of experimental methods; the need for closer links between experiments, theory, and real-world data; and the necessity for experiments to be both replicable and reproducible via open science practices, to ensure that new generations of scientists can build on reliable knowledge.

**Keywords:** cultural evolution, cultural transmission, cumulative culture, experiments, iterated learning, open science, social learning, transmission chains

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## Introduction

The foundation for modern cultural evolution theory was laid in the 1970s and 1980s with population genetics inspired mathematical models of cultural change (Boyd & Richerson, 1985; Cavalli–Sforza & Feldman, 1973, 1981). While this work drew on prior experimental research, such as Asch's (1951) social psychology studies of conformity, this prior work was not designed to test the specificities of cultural evolution theories. Indeed, the first original tests were ethnographic surveys (Hewlett & Cavalli–Sforza, 1986) rather than experiments. In the 1990s, cultural evolution research extended to comparative phylogenetic analyses of ethnographic and archaeological real world data (Holden & Mace, 1997; Mace & Pagel, 1994). It was not until the 2000s that experimental methods were used to test the assumptions and predictions of the cultural evolution models, and provide insights into the real–world patterns, that had emerged in the preceding decades.

Experiments inhabit a valuable middle ground between theoretical models and real-world (e.g. ethnographic, archaeological, historical) data. Experiments allow us to control and minimize extraneous background variables, isolate and manipulate key variables to determine causal effects, randomly assign individuals to different conditions, and directly record and access full behavioural data. In contrast, real-world data are often biased, incomplete, and messy, with many potential confounding factors. We cannot randomly assign members of a community to live their lives under different conditions, or rerun history to see whether effects are meaningful or due to chance. And unlike models, experiments feature real human (or non-human) behaviour, cognition, perception, attention, and decision-making, rather than a modeller's assumptions or intuitions about how these work. Naturally, experiments also have limitations: their artificiality of setting and limited timescale means that experiments can never directly capture the complexities of the real world, while the constraint of having to recruit, compensate, and test participants limits the number and scope of manipulations that are possible compared to theoretical models.

As illustrated in the preceding paragraph, there is no single 'perfect' method. Models possess high internal validity (control over variables and conditions in order to determine causal effects) and low external validity (generalizability and relevance to the real world), while real-world archaeological, historical, and ethnographic methods offer high external validity but low internal validity. Experiments lie somewhere in between. To understand a phenomenon in full we often need to use multiple methods simultaneously. Indeed, the use of multiple methods is a hallmark and benefit of cultural evolution research. Unlike traditional disciplines like psychology, which is largely experimental and seldom employs formal models or fieldwork, or socio-cultural anthropology, which almost exclusively uses fieldwork methods and views experiments and formal models with suspicion, cultural evolutionists have employed models, experiments, ethnographic fieldwork, and archaeological-historical methods to try to understand cultural change and diversity. This is perhaps due to an overarching, synthetic evolutionary framework borrowed from evolutionary biology which similarly uses multiple methods to understand genetic evolutionary change and diversity (Mesoudi, Whiten, & Laland, 2006).

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# **Types of Cultural Evolution Experiments**

Experiments come in many forms, from the traditional laboratory experiments of experimental psychology to field experiments and 'lab-in-the-field' experiments increasingly employed within economics (Levitt & List, 2009). I will exclude from further discussion 'natural' experiments, as they do not involve the manipulation or control of non-natural experiments. Given the central role of social learning or cultural transmission (terms I use interchangeably) in cultural evolution research, constituting the inheritance mechanism that makes culture an evolutionary process, most cultural evolution experiments involve participants learning from at least one other participant. Note that by 'participant' here I include both human and non-human individuals, given the burgeoning literature on non-human culture (Whiten, 2021). Building on previous reviews (Mesoudi & Whiten, 2008), several specific methods have emerged within the field of cultural evolution (see Figure 1):

- 1. **Dyadic interactions**: participants are placed in pairs, or a participant is paired with an experimenter, and asked to learn from the other individual. Sometimes this occurs via a physical object such as a puzzle box that the demonstrator opens in a particular way. Dyadic interactions are often used to identify specific social learning mechanisms, such as whether an individual can imitate another's actions, or even 'over-imitate' causally irrelevant actions (Hoehl et al., 2019; Reindl et al., 2017; Schillinger et al., 2015; Whiten et al., 2009). Such social learning mechanisms have implications for the fidelity with which information is culturally transmitted, which in turn determines whether cultural traditions or cumulative culture can emerge. Two-way dyadic interactions, where both members of the dyad learn from the other, are common in the experimental study of language and communication (e.g. Fay et al. 2010).
- 2. Linear transmission chains: participants are placed in linear chains, with typically four or five participants per chain. The first participant is given a written text to read and recall, an artefact to construct, or a task to complete. Their resulting recall, artefact, or solution is given to the second participant in the chain, whose output is given to the third participant, and so on along the chain. Multiple parallel chains are run to increase the number of independent observations, given that participants within the same chain are not statistically independent. Cumulative changes in the material can be assessed as it passes through multiple individuals, revealing systematic biases in cultural transmission. This method has been used to study content biases in the repeated transmission of written texts (Bebbington et al., 2017; Eriksson & Coultas, 2014; Jiménez & Mesoudi, 2020; Mesoudi, Whiten, & Dunbar, 2006; Miton et al., 2015; Stubbersfield et al., 2015), the cumulative cultural evolution of artefacts or skills (Derex et al., 2019; Kempe et al., 2012; Lucas et al., 2020; Miton et al., 2020; Tennie et al., 2014; Thompson & Griffiths, 2021; Zwirner & Thornton, 2015), and the iterated learning of artificial languages or categorization schemes (Fay et al., 2018; Griffiths et al., 2008; Kalish et al., 2007; Kirby et al., 2008; Raviv & Arnon, 2018; Winters et al., 2015).
- 3. **Closed groups**: participants are placed in small groups with fixed membership. Each participant completes some task, such as designing an artifact or identifying which of two or more choices is optimal (e.g. a 'multi-armed bandit' task), with the option to learn from one or more other participants in their group. Often asocial control conditions are run for comparison, in which participants complete the same task but without the option to copy others. This method can be used to study whether and when participants use social learning as opposed to individual/asocial learning, the context biases (e.g. conformist, success or prestige bias) that they employ, and under what conditions they employ such biases (e.g. when facing difficult or uncertain tasks) (Brand et al., 2020; Efferson et al., 2008; Glowacki & Molleman, 2017; McElreath et al., 2008; Mesoudi, 2011; Morgan et al., 2011; Muthukrishna et al., 2016; Toyokawa et al., 2017, 2019). Experimenters can also determine whether the observed learning behaviour is adaptive given the experimental setup.

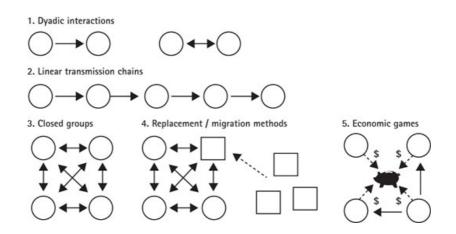
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- 4. Replacement or migration methods: participants are again in small groups, but there is some form of group turnover. In replacement designs, in each time period one or more participants are removed from the group and replaced with new, naïve participants (Baum et al., 2004; Caldwell & Millen, 2008, 2009; Chimento et al., 2021; Sasaki & Biro, 2017). In migration designs, there are multiple groups and in each time period participants are swapped across groups (Deffner et al., 2020). These designs allow the examination of demographic influences on cultural evolution, such as looking at whether, and if so how, immigrants acculturate to existing local behaviour.
- 5. Economic games: developed by economists, these involve pairs or groups of participants engaging in a strategic game, often incorporating a cooperative dilemma. Given the intersection of theories of cultural evolution and the evolution of cooperation, these have often been used to measure broad cultural influences on cooperative behaviour (Henrich et al., 2005, 2006) or more directly how players of such games may (or may not) learn cooperative behaviour from other players (Burton-Chellew et al., 2017; Lamba, 2014).

#### Figure 1



Diagrammatic illustrations of the five common cultural evolution experimental methods identified in the chapter. Circles indicate participants, and solid arrows indicate the flow of information due to social learning or cultural transmission. (1) Dyadic interactions involve one participant learning from a single other participant (or from an experimenter), or two participants learning from each other as in the case of communication tasks; (2) Linear transmission chains involve participants learning from the previous participant in their chain along a series of cultural 'generations'; (3) Closed groups involve groups of fixed membership in which each participant can learn from any other member over a series of trials (or 'generations'); (4) Replacement or migration methods involve closed groups whose membership periodically changes, such as via the introduction of new, naive participants or migrants from other groups, here indicated by squares; (5) Economic games involve strategic interactions such as in cooperative dilemmas like the Public Goods Game, where participants invest variably in a group pot which is distributed equally, thus giving the opportunity for free-riding. Participants may also have an opportunity for social learning, such as the top-right and bottom-left participants learning from the contribution behaviour of the bottom-right participant. Note that in practice, multiple dyads, chains and groups are run in each experiment.

# **Key Findings**

The following is a partial and selective sample of findings from the last few decades that have used the methods listed above.

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#### **Content Biases**

Confirming the seminal social psychological work of Bartlett (1932), modern linear transmission chain studies have shown that human cultural transmission of verbal material such as stories or other texts is *reconstructive* rather than replicative. People do not reproduce texts verbatim, rather they reproduce the gist while losing many of the details, they systematically preserve certain kinds of information omitting other kinds, and they distort material in non-random directions. In the cultural evolution literature such systematic distortions are often called content biases (Henrich & McElreath, 2003) as they concern the content of what is being transmitted, or alternatively examples of cultural attraction (Claidière & Sperber 2007; Miton, this volume; Sperber, 1996), which emphasizes the reconstructive nature of human cultural transmission. Several studies have demonstrated biases for information about social interactions and relationships over equivalent non-social information (McGuigan & Cubillo, 2013; Mesoudi, Whiten, & Dunbar, 2006; Reysen et al., 2011; Stubbersfield et al., 2015), perhaps reflecting the social evolutionary origins of human cognition (Whiten, 1999). Others have demonstrated biases for negative over positive information (Bebbington et al., 2017; Fessler et al., 2014; Moussaïd et al., 2015).

Other studies have examined where such biases operate during the transmission process, teasing apart memory biases that affect the recall of transmitted material (the 'encode and retrieve' phase) from preferences to receive certain kinds of material ('choose to receive' phase) and preferences to pass on certain kinds of material ('choose to transmit' phase). Eriksson and Coultas (2014) found a preference for disgust-eliciting information in all three phases of transmission, while Stubbersfield et al. (2015) found that encode and retrieve biases for social and survival information did not extend to the other two phases. Such differences have implications for debates over the role of selection-like versus transformational processes in cultural evolution, where encode and retrieve biases resemble biased transformation and choose to receive or choose to transmit resemble cultural selection (Mesoudi, 2021).

Other transmission chain studies, sometimes called studies of 'iterated learning', derive from an alternative modelling framework to the aforementioned population genetic-inspired methods. This uses Bayesian inference to capture the situation where learners have prior distributions of beliefs about the world, then update their beliefs based on data, resulting in updated posterior distributions (Griffiths et al., 2008; Kalish et al., 2007). When the data come from other individuals, then Bayesian updating constitutes social learning, and we have models of cultural evolution. The prior probability distribution is seen as representing the learners' inductive biases. These inductive biases can be considered special cases of content biases where the learner is attempting to infer the probability of an event given incomplete data, an inference that is biased by the cognition, perception, attention, and emotion of the learner. Iterated learning experiments have been used to show how initially random stimuli are transformed by successive learners to become easier to learn by more closely resembling those inductive biases.

In the context of language evolution (Bailes & Cuskley, this volume), iterated learning experiments have shown how artificial languages containing arbitrary labels for stimuli evolve to become more coherently structured over successive transmission generations, exhibiting features of real languages such as compositionality (Kirby et al., 2008). Another study showed that initially random colour classification terms gradually evolve as they pass along transmission chains to reflect real world cross-culturally common colour terminologies, likely to be reflecting perceptual priors regarding how people see and learn colours (Xu et al., 2013). Inductive biases have also been shown to inhibit cumulative technological evolution, with participants converging on worse solutions in environments that do not match their inductive biases (Thompson & Griffiths, 2021). In general, iterated learning experiments provide an alternative, cognitively richer way of studying cultural evolution in the lab via the use of formal Bayesian models of computation commonly employed in cognitive science.

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## **Context Biases**

The closed group method has been used to test basic predictions from evolutionary models about when participants should employ social learning relative to asocial learning, and if the former, from whom people should learn, known as 'context biases' (Henrich & McElreath, 2003). Several studies have shown that participants are more likely to copy others when asocial learning is manipulated to be more inaccurate (McElreath et al., 2005; Morgan et al., 2011; Toelch et al., 2014; Toyokawa et al., 2019) or more costly (Kameda & Nakanishi, 2002; Mesoudi & O'Brien, 2008; Morgan et al., 2011), and when environments are more stable over time (McElreath et al., 2005; Toelch et al., 2009). Studies have also confirmed the presence of theoretically-predicted context biases, including conformity (Deffner et al., 2020; Efferson et al., 2008; Morgan et al., 2011; Muthukrishna et al., 2016; Toyokawa et al., 2019) and payoff bias (McElreath et al., 2008; Mesoudi, 2011; Molleman et al., 2014; Morgan et al., 2011). Some studies show a hierarchy of biases where payoff bias is tried first, and if a suitable trait to copy is not identified, then conformity is used (McElreath et al., 2008).

However, these experiments also show that participants do not all or always behave adaptively as predicted by theoretical models. Many participants employ social learning less frequently than models predict they should (Efferson et al., 2008; McElreath et al., 2005; Mesoudi, 2011; Morgan et al., 2011; Toelch et al., 2014), with extensive and unexplained individual differences in social learning use and strategy (Molleman et al., 2014; Toelch et al., 2014; Toyokawa et al., 2017). For example, Efferson et al. (2008) found that 30 per cent of participants tasked with identifying the more adaptive of two options failed to use the choices of others to employ conformity, consequently earning less money than the 70 per cent who did conform. Even more starkly, Mesoudi (2011) found that only 12.5 per cent of participants employed payoff-biased social learning on a majority of trials in an arrowhead design task, earning more money than the majority who relied mainly on asocial learning. These unexpected findings show the value of running experiments rather than relying solely on theoretical models, and the apparently maladaptive underuse of social learning plus individual variation is the subject of ongoing investigation (see below).

## **Cumulative Culture**

Cumulative culture, or cumulative cultural evolution (CCE) (Caldwell, this volume; Dean et al., 2014; Mesoudi & Thornton, 2018; Tennie et al., 2009), refers to the improvement over time of cultural traits due to repeated innovation and social learning, such that they typically exceed what any single individual could invent alone. CCE is often claimed to be unique to humans and underpin our ecological dominance (Hill et al., 2009; Tennie et al., 2009). This though simply begs the question of why only humans exhibit CCE. Suggestions include our greater social learning fidelity allowing traits to be faithfully preserved and accumulate (Lewis & Laland, 2012) and our larger or more suitably interconnected populations (Henrich, 2004; Powell et al., 2009). While archaeological and ethnographic data have been used to test these potential explanations, results are mixed (Collard et al., 2013). Lab experiments offer an additional line of inquiry: while they can never definitively prove whether a particular factor is responsible for CCE, they can lend plausibility to specific explanations and help refine their predictions.

One line of studies has used the transmission chain method with physical tasks such as constructing paper aeroplanes, weight-holding baskets, stone handaxes, or wheels that descend sloping tracks. In each case there is some criterion of performance (e.g. aeroplane flight distance or weight held by basket), and CCE is demonstrated when this criterion increases over successive participant generations. Contrary to early claims (e.g. Tomasello, 1999) that CCE requires imitation (copying motor actions) rather than emulation (copying end products or goals), experiments have shown that performance cumulatively improves via both imitation and emulation (Caldwell & Millen, 2009; Lucas et al., 2020; Reindl & Tennie, 2018; Zwirner & Thornton, 2015). However, this may be due to the simplicity of the tasks compared to real-world human

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technologies (e.g. paper aeroplanes versus real aeroplanes) (Miton & Charbonneau, 2018). Indeed, when causally opaque and unfamiliar tasks are used, imitation but not emulation supports CCE (Wasielewski, 2014), and when more complex tasks are used then even higher fidelity teaching is more effective than imitation and emulation (Lucas et al., 2020; Zwirner & Thornton, 2015). The most real-world-relevant task used to date, handaxe knapping, only accumulated with teaching, with imitation and emulation insufficient to generate CCE (Morgan et al., 2015). Finally, Derex et al. (2019) showed that CCE occurs in the absence of the transmission of causal theories about how the task works, again emphasizing the importance of high fidelity transmission over individual cognition in explaining complex technologies. In sum, these studies indicate that high fidelity transmission mechanisms such as imitation and teaching are at least highly conducive to, if not required for, the CCE of complex technologies.

Other experiments have tested the claim that large or sufficiently interconnected populations are necessary for CCE. Some studies have found no effect of group size on CCE (Caldwell & Millen, 2010; Fay et al., 2019), although again this may be due to overly simple tasks. Studies with more challenging tasks have shown that CCE occurs only, or is faster, in larger groups of participants (Derex et al., 2013; Kempe & Mesoudi, 2014; Muthukrishna et al., 2014; Raviv et al., 2019). Further studies have used tasks requiring the recombination of accumulated traits from different trait lineages, showing that partially connected groups exhibit superior CCE than fully connected groups (Derex & Boyd, 2016). This is because partially connected groups can explore all cultural trait lineages better than fully connected groups, which prematurely converge on one lineage. Other studies have explored the effect of different social network structures on language evolution, suggesting that small world networks generate more variation in linguistic structure than other networks (Raviv et al., 2020). These results suggest that population structure is just as important as population size in facilitating CCE.

#### **Non-human Culture**

While culture was in the past considered, or even defined, as specific to humans, recent decades have seen an explosion of research on how diverse species exhibit social learning and between-group cultural traditions (Whiten, 2021). Accompanying field observations of such phenomena (Whiten et al., 1999), extensive experimental work has tested the social learning mechanisms underlying these cultural dynamics. These experiments are often more elaborate and powerful than equivalent experiments with humans, partly due to the greater ability to manipulate non-human animal societies. It is also more feasible to run field experiments, taking advantage of automated tracking technologies that would be too invasive for human societies (although see Migliano et al., 2017).

For example, Aplin et al. (2015) used replicate wild sub-populations of great tits to show that novel, experimentally introduced foraging behaviours spread from bird to bird via conformity within each sub-population, generating stable cultural traditions as a result. Similarly, Barrett et al. (2017) experimentally introduced a novel food item into a group of white-faced capuchin monkeys, showing instead that payoff-biased social learning, not conformity, caused its spread through the group. Similar to the human closed group experiments discussed above, Barrett et al. (2017) found individual variation in social learning, here largely structured by age, with younger capuchins more likely to employ both social and asocial learning. No doubt further field experiments will determine whether the differences between these two studies—conformity versus payoff-biased social learning—are due to differences in species, ecology, task, or some other factor.

Finally, an innovative study used the replacement method with homing pigeons to show the social learning and potential CCE of homing routes (Sasaki & Biro, 2017). Initial pigeons were trained to follow a particular route and were then paired with naive pigeons. In each timestep the more experienced of the pair was replaced with a new naive pigeon. Over successive pairs, the homing route became gradually more efficient.

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This apparent demonstration of CCE in a non-human species has sparked productive debate over the nature of CCE (Mesoudi & Thornton, 2018).

#### **Developmental Variation**

The various experimental methods described above have revealed an interesting contrast between children and adults. Whereas dyadic interaction experiments demonstrate that young children eagerly and effectively copy others' actions or solutions to tasks, sometimes even 'over-imitating' causally irrelevant actions (Hoehl et al., 2019; Whiten et al., 2009), many of the closed group experiments with adult (usually student age) participants reveal less copying than expected. Molleman, Kanngiesser, & van den Bos (2019) recently found that adolescents lie somewhere in between, suggesting a steady decline in social learning during the lifetime. This trend perhaps makes sense considering the theoretical prediction that social learning should be used in uncertain or unfamiliar environments or when asocial learning is difficult, both of which will be the case at younger ages. As we grow, we accrue skills and knowledge from others, allowing greater reliance on our own experience. Further experiments using standardized tasks (e.g. the BEAST: Molleman, Kurvers, & van den Bos, 2019) over multiple age ranges, or even longitudinally over the lifespan, and testing specific predictions deriving from life history theory (Buchsbaum & Gelpi, this volume; Deffner & McElreath, 2020), will be instructive in further elucidating developmental changes in learning strategies.

## **Cross-cultural Variation**

As well as individual variation, experiments have also revealed cross-cultural variation in the dynamics of cultural evolution. This is important because across the behavioural sciences claims are often made about human universality based solely on the behaviour of participants from Western, Educated, Industrialized, Rich, Democratic (WEIRD) societies (Henrich et al., 2010), even though non-WEIRD participants often show different behaviour. Cultural evolution experiments are no exception. For example, Berl and Hewlett (2015)'s dyadic interaction study found a lack of over-imitation in Aka forager children, in contrast to Western children, challenging notions that over-imitation is a human universal. Eriksson et al.'s (2016) transmission chain study found that a content bias for disgusting stimuli previously demonstrated in Western participants failed to replicate in an Indian sample. Closed group studies have found higher rates of social learning amongst participants from collectivistic societies such as China, compared to participants from more individualistic societies such as the United Kingdom, as well as Western-influenced populations such as Chinese participants living in the United Kingdom or Hong Kong (Mesoudi et al., 2015). Finally, economic games have revealed cross-cultural variation in cooperative behaviour, potentially influenced by culturally evolving norms (Henrich et al., 2005, 2006). Further experiments are needed to map learning strategies comprehensively, as well as other behaviours such as innovation or acculturation, across a larger number of societies, as well as across different ethno-linguistic or socio-economic groups within societies.

As well as documenting cross-cultural differences, we also need to explain them. Labels like WEIRD, or individualistic-collectivistic, are just that—labels—and simply add another layer of description. Some studies have therefore targeted societies that differ in specific ways, or members of the same society who have different lifestyles, to test specific factors. For example, Glowacki and Molleman (2017) found that Nyangatom pastoralists showed higher rates of social learning than herding members of the same ethnic group, suggesting that more interdependent means of subsistence foster greater reliance on social information than more independent means of subsistence. Further tests are needed of this subsistence theory of cultural variation in learning strategies (Talhelm et al., 2014; Uskul et al., 2008), plus other factors such as different rates of environmental change (Chang et al., 2011) or changes in kinship structures (Schulz et al., 2019). Linking to the previous section, developmental studies would be useful to test at what age cross-cultural variation emerges.

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## **The Function of Experiments**

A common criticism of experiments, particularly from scholars outside those disciplines that traditionally use them, is that experiments lack external validity, that is, they do not generalize to the real world due to the artificiality of lab settings, the awareness of participants that they are part of an experiment or being monitored by experimenters, the different incentives motivating participants in experiments compared to real-world incentives, etc. (Chibnik, 2005; Levitt & List, 2007). All these points are true: experiments are unrealistic in all these ways, and more. However, just like similar critiques of theoretical models (which have even lower external validity: Smaldino, 2016), these criticisms somewhat miss the point. Experiments are unrealistic by design. We use simple experimental tasks shorn of much of the complexity of the real world, and isolate and manipulate specific variables while holding all else constant, because the real world is typically too complex and contains too many interacting factors to test causal theories. An experiment that is as complex as the real world would not be much use: we would have replaced a complex real world with a complex lab world. Moreover, several measures can reduce the problems listed above, such as not revealing hypotheses to participants before the experiment to reduce demand characteristics, or tying incentives to participant performance to increase motivation.

Furthermore, as Camerer (2011) has argued in the context of experimental economics, the target of experiments is often not to generalize directly to the real world (which itself is a vague concept, as the 'real world' is diverse and constantly changing). Rather, the target is to test theories about how particular variables map to behaviour. For example, in the context of economic experiments, anonymous donations to others in the dictator game are typically around 15 per cent of the dictator's allocation, much higher than real world anonymous donations to charity of around 1 per cent of people's salaries (Camerer, 2011). Yet dictator game experiments have still revealed important insights about the factors that influence anonymous, non-reciprocal sharing, such as the extent of monitoring by third parties. Such factors may similarly affect real-world sharing, even though absolute rates of sharing are different in the lab compared to the real world.

Equivalently, cultural evolution experiments discussed above that aim to study the effect of population size and structure on CCE use participant group sizes of two to 16 individuals (Derex et al., 2013), or differently connected groups of six (Derex & Boyd, 2016). These are obviously far smaller than any real-world human society. Yet this range appears suitable to demonstrate the effects of varying group size or interconnectivity on CCE, not necessarily with the aim to make statements about real societies that contain, say, two versus 16 individuals, but rather to test general theories about the relation between demography and CCE (e.g. Henrich, 2004), and unpack the psychological plausibility of such theories. For example, Muthukrishna et al. (2014) tested Henrich's (2004) modelling assumption that people learn from a single most successful individual, finding that while participants did indeed preferentially learn from successful others, they tended to copy more than just the single best one (see also Kempe & Mesoudi, 2014, in which participants additively combined the solutions of multiple participants). Such findings can be used to inform further models.

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## Stronger Links between Experiments, Theory, and Real-world Data

Despite the points made in the previous section defending the value of experiments, there are always ways to improve their use. One is to make more specific predictions that directly derive from theory—ideally formal theoretical models—rather than loose predictions only vaguely connected to theory (Muthukrishna & Henrich 2019). For example, initial cultural evolution experiments aimed to test whether participants show conformity, specifically that they are disproportionately more likely to adopt the majority trait amongst a set of demonstrators (Efferson et al., 2007, 2008). While methodologically rigorous and providing valuable initial findings, their results were sometimes ambiguous, with conformity shown by only some participants or none at all. Recent studies have made more specific predictions that derive from formal models about when people should conform. For example, Deffner et al. (2020) showed that participants used conformist social learning when they moved into an unfamiliar group containing existing residents from whom they could adopt the locally adaptive behaviour most efficiently via conformity. Less conformity was observed following a temporal change in the environment when no-one possessed adaptive behaviour. This supports the specific prediction from formal models that conformity is adaptive when environments vary spatially rather than temporally (Nakahashi et al., 2012). Similarly, rather than testing whether people in general show prestige biased social learning, that is, preferentially copying others on the basis of indirect cues of success such as receiving attention or being copied (Henrich & Gil-White, 2001), Brand et al. (2020) tested and confirmed the specific predictions from Henrich and Gil-White (2001) that prestige bias should be used only when prestige cues are to some degree tied to success, and not when they are unconnected to success or when direct success information is available alongside the indirect prestige cues.

Even stronger links between experiments and theory can be made by fitting theoretically derived generative models to participants' behavioural data, rather than using generic statistical models such as linear regression. This was pioneered by McElreath et al. (2005), and used there and in more recent studies (e.g. Barrett et al., 2017; Deffner et al., 2020; Toyokawa et al., 2019) to estimate directly, say, the strength of conformity via a quantitative parameter in the generative model, rather than using a *p*-value to reject a null hypothesis that participants do not conform. While this approach sometimes places constraints on the types of experimental designs that can be employed, given that generative models must remain tractable, it yields more powerful inferences about the underlying cultural evolutionary processes affecting participants' behaviour than non-generative statistical models.

Without detracting from the point in the previous section that experiments should be viewed as tests of theories rather than exact simulations of the real world, there should nevertheless be some kind of link to real-world cultural phenomena for an experiment to be useful. Sometimes this is done explicitly, by combining experimental and non-experimental methods. For example, Miton et al. (2015) combined experimental and ethnographic analyses in their study of blood-letting, the cutting and draining of blood near sites of bodily ailment. They first used ethnographic data to establish cross-cultural regularities in the use of blood-letting. They then used experimental transmission chains to show that blood-letting is particularly likely to be preserved during cultural transmission and even spontaneously emerges from similar but mundane events like accidental cutting. This lends plausibility to their argument that bloodletting is favoured by universal cognitive mechanisms. Similarly, Xu et al.'s (2013) iterated learning study of colour terminologies showed that participant chains converged on colour terminologies that are reliably observed cross-culturally in the ethnographic record. Other studies have combined experimental methods with archaeological data, testing the psychological plausibility of hypotheses concerning changes in handaxe size (Kempe et al., 2012) or regional variation in arrowhead diversity (Mesoudi & O'Brien, 2008). Again, the interdisciplinary nature of cultural evolution research is a major benefit here, given that experimentalists, ethnographers, and archaeologists all share a common theoretical framework.

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## **Replicability and Reproducibility**

The replication crisis in social psychology has shown how many supposedly core findings in that field do not replicate (Open Science Collaboration, 2015), and are likely spurious results arising from poor methodological practices. These include the use of small sample sizes, poor statistical practices such as HARKing (Hypothesizing After Results are Known) or the use of dichotomous *p*-values rather than effect sizes, or the file drawer problem, where null results remain unpublished and do not enter the literature. Naturally, we should strive to avoid these problems in the field of cultural evolution. Prospects for this are good, given that the incentives behind poor scientific practices have been the subject of cultural evolution modelling and theorizing (Smaldino & McElreath, 2016). Hopefully more awareness of the problems will favour the adoption of better practices to reduce or eliminate those problems, such as pre-registration, using large samples to provide adequate power, publication of null findings and replications, statistical methods that acknowledge uncertainty and effect size rather than arbitrary significance thresholds, and stronger links to formal theory as discussed above. Encouragingly, several experimental findings have already been replicated, such as the social bias in cultural transmission (McGuigan & Cubillo, 2013; Mesoudi, Whiten, & Dunbar, 2006; Reysen et al., 2011; Stubbersfield et al., 2015).

A separate issue is reproducibility, which describes the ability of another researcher to recreate the findings of a study using the same data. In a recent survey directly relevant to the topic of this chapter, Minocher et al. (2021) assessed the reproducibility of experimental studies of social learning in humans and nonhumans, including many of the studies cited above. The good news from Minocher et al.'s (2021) survey was that when a study's data were accessible, either published alongside the paper as supplementary material or (less reliably) available from the author upon request, the results of a large majority (79 per cent) of the studies could be reproduced successfully. However, only a minority of studies (30 per cent) had available data. This highlights the need to make both data and analysis scripts available for others to both verify and build upon published findings. Science itself is a cumulative cultural evolutionary process (Hull, 1988), and only works when new generations of scientists can build on reliable knowledge.

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