

Review

The multiple roles of cultural transmission experiments in understanding human cultural evolution

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In this paper, we explore how experimental studies of cultural transmission in adult humans can address general questions regarding the ‘who, what, when and how’ of human cultural transmission, and consequently inform a theory of human cultural evolution. Three methods are discussed. The transmission chain method, in which information is passed along linear chains of participants, has been used to identify content biases in cultural transmission. These concern the kind of information that is transmitted. Several such candidate content biases have now emerged from the experimental literature. The replacement method, in which participants in groups are gradually replaced or moved across groups, has been used to study phenomena such as cumulative cultural evolution, cultural group selection and cultural innovation. The closed-group method, in which participants learn in groups with no replacement, has been used to explore issues such as who people choose to learn from and when they learn culturally as opposed to individually. A number of the studies reviewed here have received relatively little attention within their own disciplines, but we suggest that these, and future experimental studies of cultural transmission that build on them, can play an important role in a broader science of cultural evolution.

Keywords: cultural evolution; cultural transmission; laboratory experiments; diffusion experiments; social learning

1. CULTURAL TRANSMISSION: MORE QUESTIONS THAN ANSWERS

Cultural transmission is the process by which information is passed from individual to individual via social learning mechanisms such as imitation, teaching or language. This can be contrasted with the acquisition of information via genetic inheritance from biological parents, and with individual learning, where there is no influence from conspecifics. A great deal is known about both genetic inheritance and individual learning, in no small part through extensive laboratory experiments conducted respectively by population geneticists (Hartl & Clark 1997) and experimental psychologists (Mackintosh 1983). Far less experimental research has examined cultural transmission. While there has been some experimental research into social learning within social psychology (e.g. Bandura 1977), these studies have usually been restricted to a single model and a single learner, with few studies examining the

persistence of socially learned information in chains or groups that involve larger numbers of individuals. Yet such multiple-individual or multigenerational experimental designs would appear to be essential to test hypotheses concerning broader cultural patterns and trends that are inherently group-level phenomena. Encouragingly, this situation is changing, and, in the last few years, there has been a surge of interest in the experimental study of cultural transmission in adults, children and non-human species. In this paper, we review recent and past experimental studies of cultural transmission in adult humans, complementing related reviews concerning non-humans (Whiten & Mesoudi 2008) and children (Flynn 2008).

Questions regarding cultural transmission can be broadly summarized in terms of ‘what, who, when and how’ (following Laland 2004): *what* is copied? (i.e. what kind of information is most easily remembered and most often transmitted?); *who* is copied? (i.e. the identity of the model(s) from whom information is acquired); *when* do individuals copy? (e.g. is copying more likely when the task at hand is easy or difficult, or when the environment is constant or changing?); and *how* do individuals copy? (e.g. using imitation, emulation, or spoken or written language?). Various experimental studies in the past several decades have addressed all four of these types of question, and used

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various methods in doing so. However, 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. Our aim here is to make links between these disparate studies, which have often emerged in isolated fringes of different disciplines, such as psychology, sociology, anthropology and economics, and draw them to the attention of a wider audience. We also think that a cultural evolutionary framework offers the best prospect for such a cross-disciplinary synthesis, an argument which is elaborated in §2.

2. CULTURAL TRANSMISSION AND CULTURAL EVOLUTION

We believe that experimental studies of cultural transmission will be most valuable if they are pursued within a framework of cultural evolution. This body of theory contends that human culture evolves according to basic Darwinian principles, in important respects similar to those by which biological species evolve (Campbell 1974; Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Plotkin 1994; Mesoudi *et al.* 2004; Richerson & Boyd 2005; Mesoudi *et al.* 2006b). These Darwinian principles are *variation*, *differential fitness* and *inheritance*, and just as Darwin (1859/1968) showed these basic principles to characterize the evolution of biological organisms, they can also be observed in human culture (Mesoudi *et al.* 2004): (i) cultural traits (beliefs, attitudes, skills, knowledge, etc.) vary across and within individuals and groups; (ii) not all cultural traits are equally likely to be preserved and copied due to competition for expression, attention or memory space, some ideas are more memorable or attractive than others, and some models are more likely to be copied; and (iii) cultural traits are inherited or transmitted from model(s) to learner(s) via social learning.

As indicated in point (iii), cultural transmission is a fundamental component of cultural evolution. Without transmission there can be no evolution, and the form that this transmission takes can significantly influence the evolutionary dynamics of culture. As such, the cultural evolution literature already contains definitions, classifications and rigorous mathematical analyses of many aspects of cultural transmission. For example, Cavalli-Sforza & Feldman (1981) modelled vertical (from biological parent to offspring), oblique (from parental generation to offspring generation excluding kin) and horizontal (within-generational) cultural transmission, while Boyd & Richerson (1985) modelled conformist transmission (preferentially copying the most popular variant) and prestige/indirect bias (preferentially copying the cultural trait of the most prestigious or successful member of the group). All these analyses address 'who' should be copied and the consequences of doing so. Other models have addressed 'when' cultural transmission should be favoured over individual learning and/or genetic evolution (Rogers 1988; Boyd & Richerson 1995; Aoki *et al.* 2005), generally concluding that cultural transmission should be favoured when (i) environments change too rapidly for genes to track them effectively, but not so rapidly that

the behaviour of a potential model becomes outdated, and/or (ii) individual learning is particularly costly or difficult. In the literature review below, we highlight experimental studies that have addressed these distinctions and findings.

A second advantage of adopting a cultural evolutionary approach to cultural transmission is that it encourages links to be made between small-scale transmission processes that can be observed in a restricted number of individuals, as typically studied in experiments, and population-level patterns generated by people in real-life situations over longer time periods. This population-level thinking is inherent in Darwinian evolutionary theory, and ever since the evolutionary synthesis of the 1930s and 1940s (Mayr & Provine 1980), evolutionary biologists have made links between small-scale microevolutionary processes, such as natural selection, sexual selection, mutation and drift (often studied experimentally), and population-level macroevolutionary patterns in time or space (as studied by palaeobiologists and biogeographers), with the latter patterns understood to be generated in part by the former. The same population thinking can be applied to cultural evolution (Richerson & Boyd 2005), and placing cultural transmission within an evolutionary framework potentially allows a similar interdisciplinary evolutionary synthesis for the cultural sciences (Mesoudi 2008a). Thus, the forces and biases of cultural transmission studied experimentally in the laboratory can be seen as at least partly generating the population-level patterns of cultural change documented by socio-cultural anthropologists, archaeologists, sociologists and other social scientists. This gives cultural transmission experiments added significance: cultural transmission should not only be studied for its own sake (i.e. in order to better understand cultural transmission itself), but also in order to explain broader cultural patterns and trends, all as part of a unified science of cultural evolution (Mesoudi *et al.* 2006b).

Conversely, cultural evolution theory can benefit greatly from more detailed empirical studies of cultural transmission. Past cultural evolution research has predominantly involved the analysis of formal mathematical models (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985), and sorely lacks empirical studies that test the assumptions and findings of those models. Experiments offer a means of performing this using actual people but retaining much of the rigour and control of mathematical models. The value of experimental tests of theoretical models can be seen in the field of experimental economics, where recent experimental findings that conflict with prior theoretical predictions (e.g. the ultimatum game, for which people universally exhibit 'non-rational', i.e. non-self-interested, behaviour; Henrich *et al.* 2005) have forced a productive reconsideration of theoretical assumptions. Below, we note several similar cases in which participants deviate significantly from theoretically derived predictions, which may force a similarly productive re-examination of the theoretical assumptions of some cultural evolutionary models.

The following sections briefly outline experimental studies concerning cultural transmission in adult

humans, focusing on their implications for the field of cultural evolution. To count as a study of cultural transmission, there must be some kind of transmission of information (knowledge or behaviour) along a chain or within a group of more than two participants. The studies are categorized according to their methodology; we discuss in turn the linear transmission chain method, the replacement method and the closed-group method. A more detailed literature review using the same classification can be found in Mesoudi (2007), and we direct readers interested in fuller descriptions of the studies mentioned here to consult that publication. For further reference, table S1 of the electronic supplementary material provides a summary of all adult human cultural transmission studies that we are aware of, listing for each one the methodology used, the participant sample, the material/behaviour that was transmitted and the study authors' main conclusions.

3. THE LINEAR TRANSMISSION CHAIN METHOD

The linear transmission (or diffusion) chain method represents perhaps the simplest experimental procedure for studying cultural transmission. Devised by Bartlett (1932), this method resembles the children's game 'Chinese whispers' or 'Telephone', wherein some material relevant to a particular hypothesis is passed along linear chains of participants (figure 1). The first participant in the chain reads or hears some material (typically text or pictures), and then attempts to recall it. This recalled information is given to the second participant, who reads it and later recalls it in a similar way; this recall is passed on to the third participant, and so on along the chain. By measuring the changes that occur within the material as it is passed along the chain, or by comparing the rates at which different kinds of material degrades, the researcher can infer the operation of systematic biases in cultural transmission.

Bartlett (1932) conducted a series of transmission chain studies using various types of material, from Native American folk tales to descriptions of sporting events. As transmission proceeded along the chains, Bartlett (1932) noted that the material became much shorter in length and lost many of the details, with only the overall gist remaining. Participants also tended to distort the material, making it more coherent and consistent with their own pre-existing knowledge. The folk tales from non-industrial societies, for example, contained many supernatural elements that were nonsensical to the English participants and were subsequently removed or replaced with more familiar events. These two processes, loss of detail and assimilation to prior knowledge, led Bartlett (1932) to propose that remembering is primarily a *reconstructive* process, and seldom a process of exact replication. Only the gist or overall impression of the material is preserved and rebuilt around pre-existing knowledge structures or schemas. Accordingly, Bartlett (1932) found that folk stories were transmitted with greater accuracy than any of the other material, which he argued was because people already possess story schemas that contain the structure of a typical folk tale, thus aiding recall.

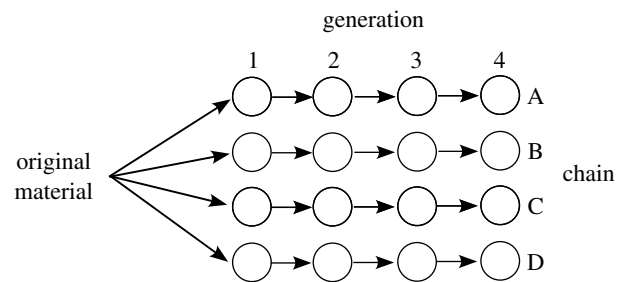


Figure 1. Design of a typical transmission chain study. The original material is passed along parallel chains of participants (represented by circles). Here, there are four chains (A–D), each comprising four generations (1–4). Adapted from Mesoudi (2007).

The two decades following Bartlett's (1932) original study saw the publication of several transmission chain studies that shared Bartlett's general methodology but varied in the material used and participants tested (Maxwell 1936; Northway 1936; Allport & Postman 1947; Ward 1949; Hall 1951). The results of these studies largely supported Bartlett's original findings of increasing generalization and assimilation to pre-existing knowledge. Although the later twentieth century saw a decline in the popularity of the transmission chain method, several recent studies have sought to reintroduce the method as a means of studying cultural change, and have updated the transmission chain method to conform to modern standards of experimental psychology (Bangerter 2000; Kashima 2000; Barrett & Nyhof 2001; Mesoudi & Whiten 2004; Mesoudi *et al.* 2006a; Kalish *et al.* 2007; Griffiths *et al.* 2008; see Mesoudi 2007). These recent studies, too, support Bartlett's (1932) conclusions. For example, Mesoudi & Whiten (2004) confirmed and updated Bartlett's (1932) notion of 'generalization' by drawing on script theories from cognitive psychology, finding that descriptions of everyday events were described at increasingly abstract levels of a hierarchically organized knowledge structure as they were passed along transmission chains. Other studies have supported Bartlett's claim of assimilation to previous knowledge, finding that transmitted information gradually converges upon pre-existing gender stereotypes (Bangerter 2000; Kashima 2000) and prior cognitive biases (Kalish *et al.* 2007; Griffiths *et al.* 2008; see Griffiths *et al.* 2008).

How can the transmission chain method, and the findings of transmission chain studies, inform research into cultural evolution? The transmission chain method, as it has been used predominantly to date, seems most suited to identifying what Richerson & Boyd (2005) have called 'content-based' or 'direct' biases, in which transmission is determined by the content of the information being transmitted (i.e. 'what' is transmitted). However, content-based biases have received relatively little attention from mathematical modellers such as Cavalli-Sforza & Feldman (1981) and Boyd & Richerson (1985), who focus more on model-based biases ('who' is copied; see §§5 and 6c). Content-based biases have received much more attention from cognitively minded anthropologists such as Boyer (1994), Sperber (1996, 2000) and Atran (1998, 2001). Content-biased cultural

transmission resembles what Sperber (1996) has called 'cultural attraction', where culturally acquired representations are transformed or distorted to become more similar to a particular form, or 'attractor', that is favoured by pre-existing cognitive biases (which are often argued to be genetically specified products of natural selection). The findings from the transmission chain experiments that cultural transmission is reconstructive strongly support Sperber's (1996) argument that content biases will readily operate to distort cultural information in particular directions. To give a specific example, Barrett & Nyhof (2001) found that descriptions of living things, physical objects and intentional agents that are 'minimally counter-intuitive', i.e. contain a small number of features that violate some common intuitions of folk biology, folk physics and folk psychology, were passed along transmission chains with significantly higher fidelity than items that were either intuitive (did not violate folk knowledge) or bizarre (were highly unusual but did not violate folk knowledge). In another study, Mesoudi *et al.* (2006a) found that information concerning third-party social interactions was transmitted with higher fidelity than equivalent non-social information, in line with the hypothesis that primate intelligence evolved particularly to solve complex social problems (Byrne & Whiten 1988; Dunbar 2003), suggesting the operation of a 'social bias' in cultural transmission. When we add the counter-intuitive bias (Barrett & Nyhof 2001) and the social bias (Mesoudi *et al.* 2006a) to the hierarchical bias (Mesoudi & Whiten 2004) and gender-stereotype bias (Bangerter 2000; Kashima 2000) noted earlier, we can begin to see a provisional list of content biases emerging from the experimental literature.

In §2 we noted that cultural evolutionary population thinking encourages the extrapolation of individual-level biases to explain population-level patterns in actual cultural datasets. Sperber & Hirschfeld (2004) have attempted just this for some of the cognitive biases noted above. They argue that certain patterns of human cultural diversity and stability can be explained by cultural attraction towards the domains of pre-existing cognitive modules. For example, the rich and similarly structured ecological knowledge shown by a large number of otherwise dissimilar hunter-gatherer societies worldwide can be explained by the operation of a universal folk-biology module, which favours the acquisition of similarly structured biological knowledge (Atran 1998). Cultural diversity, meanwhile, can be explained in part because the proper domain of a cognitive module (the domain it evolved to deal with, e.g. for a face recognition module, human faces) may not always correspond to its actual domain (the set of environmental stimuli that activate the module, e.g. diverse masks, caricatures and portraits) due to errors in perception or exploitation by others. Finally, supernatural concepts may spread because they activate more than one domain. For example, ghosts have human-like intentions (a folk psychology module) but in being able to pass through solid objects violate another (a folk-physics module). The aforementioned study by Barrett & Nyhof (2001) supports this claim, with population-level consequences of this bias seen in the widespread popularity of supernatural or religious

beliefs across the world (Boyer 1994) and the persistence of minimally counter-intuitive folk tales through history (Norenzayan *et al.* 2006).

What of the other experimental findings noted above? A cognitive hierarchy bias (Bartlett 1932; Mesoudi & Whiten 2004) might lead to the prediction that information that has persisted for many generations should have a gist-like form that can easily be reconstructed. Accordingly, Rubin (1995) showed that many orally transmitted folk tales have been preserved over many generations precisely owing to their abstract, schema-like content. However, this should be qualified with Barrett & Nyhof's (2001) finding that minimally counter-intuitive items, which by definition do not conform to a generalized schema, are favoured during transmission. Perhaps these two findings are not so contradictory, however: a counter-intuitive belief cannot spread unless people already possess the folk schemas that it violates, making these two biases mutually reinforcing. Moreover, Norenzayan *et al.* (2006) found that too many counter-intuitive elements decrease the memorability of narratives, suggesting a trade-off between counter-intuitive and schematic properties. Operation of the gender-stereotype bias (Kashima 2000; Bangerter 2000) might be observed in everyday language, which tends to contain more male-favourable terms than female-favourable terms (e.g. 'chairman'), possible evidence of gender stereotypes influencing cultural transmission of grammar and vocabulary (Lakoff 1975). Finally, a social bias (Mesoudi *et al.* 2006a) might be partially responsible for the fact that socially oriented magazines and newspapers tend to have circulations orders of magnitude higher than non-social or factual publications (A. Mesoudi 2005, unpublished PhD thesis). Some of these claims remain quite tentative, however, and there is much opportunity here to more formally link small-scale cultural transmission experiments with actual cultural datasets from sociology and anthropology.

The experimental finding that cultural transmission resembles reconstruction rather than replication has been used by some (e.g. Sperber 2000; Atran 2001) to argue against memetic models of cultural change, in which cultural evolution proceeds through the differential selection of high-fidelity cultural replicators or memes (Blackmore 1999). However, while this criticism may be valid when directed towards certain versions of memetics, the broader cultural evolution literature has long recognized that cultural transmission can be imperfect, vulnerable to distortion by content biases, and based on continuous rather than discrete (meme-like) traits (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). Models that make these assumptions are just as useful as models that assume high-fidelity particulate inheritance (Henrich & Boyd 2002). Similarly, while certain patterns of cultural variation might be explained by the operation of cognitive attractors, as argued by Sperber & Hirschfeld (2004), this should not preclude the possibility that cultural variation can be influenced by other cultural transmission biases too (e.g. conformity, see §5), as acknowledged by Claidiere & Sperber (2007). Or perhaps both model-based and content-based biases operate simultaneously but at different levels: for example, content biases might favour

the transmission of minimally counter-intuitive concepts in general, but which specific minimally counter-intuitive concept a person adopts is determined by model-based biases such as conformity.

The final study we discuss in this section used the transmission chain method to address not *what* people copy but *how* they copy, and comes not from psychology or anthropology but from experimental economics. Schotter & Sopher (2003) had successive pairs of participants play the 'Battle of the Sexes' game, in which two players must choose one of two options with no communication. If the players choose different options, then neither player gets any pay-off; if both players choose the same option, then they both get a pay-off. This rule encourages cooperation. However, the two options differ in their pay-offs to the two players: if both players choose the first option, then player 1 gets a larger pay-off than player 2; and if both players choose the second option, then player 2 gets a larger pay-off. This rule encourages competition. Two modes of transmission between successive generations were allowed: either (i) a behavioural history of the choices (option 1 or 2) made by pairs of players in every previous generation and their associated pay-offs, or (ii) explicit verbal advice given by the previous generation as to which option the present generation should choose and why. Verbal advice was found to generate stable conventions, i.e. long periods during which both players agreed on which option to choose, punctuated with brief periods of rapid change. Viewing behavioural history without verbal advice, on the other hand, did not generate stable conventions, resulting instead in continuous fluctuation. This study nicely demonstrates how the transmission chain method can be used to test the effect of different transmission mechanisms and that these mechanisms can have striking effects on the rate and form of cultural change.

4. THE REPLACEMENT METHOD

The replacement method, originally proposed by Gerard *et al.* (1956), involves groups of participants repeatedly engaging in a task or game that is designed to capture some aspect of actual cultural change. One by one, the participants in the groups are replaced with new participants, with each replacement representing a single 'cultural generation' (figure 2). Researchers can then examine how group performance changes over successive generations, and how the socialization of each new participant into the group affects this change. In some replacement studies, a norm or bias is artificially introduced into the first generation of participants, either by explicitly training the participants to follow this norm or by using confederates to introduce the norm surreptitiously. The extent to which this artificially introduced norm remains in the group during successive generations then represents a measure of its transmission to the new members. Generally, the replacement method is useful for simulating cultural change that occurs with changing group membership, as is found, for example, in business organizations with frequent staff turnover or traditional hunter-gatherer societies in which small groups maintain stable traditions despite continual population replacement via births, deaths and migration.

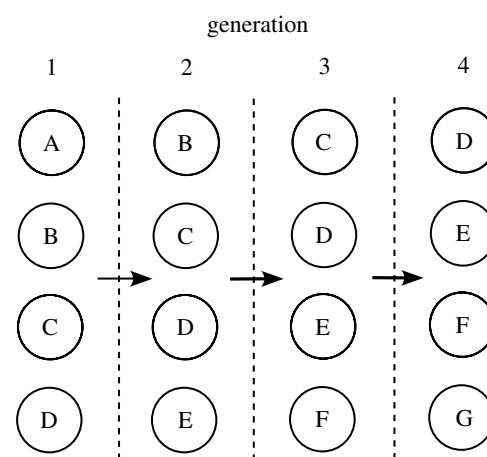


Figure 2. Design of a typical replacement study. Four participants (A–D) engage in a learning task, and in each generation one member of the group is replaced with a new participant. Adapted from Mesoudi (2007).

As an illustrative example, Jacobs & Campbell (1961) used the replacement method to study the conformist transmission of artificially exaggerated judgements of an ambiguous perceptual illusion. In an earlier study by Sherif (1936), participants responded to a perceptual illusion in which a stationary point of light in an otherwise pitch-black room is perceived as constantly moving by a few centimetres. The participants were asked to publicly estimate the distance which the light moved after several other participants, actually confederates of the experimenter, had given unrealistically exaggerated judgements. Sherif's (1936) now-classic finding was that the majority of participants gave similar estimates to the confederates despite that estimate being patently false, illustrating the powerful effect of conformity in group settings. Jacobs & Campbell (1961) repeated Sherif's (1936) experiment with the additional step that, after the group had made their estimates, one group member was replaced with a new naive participant and the new group estimated again. Significant evidence of the artificially introduced norm remained for about four or five generations following the replacement of all of the confederates, after which the perceptual judgement tended to return to that exhibited by naive control groups. This finding indicates some degree of conformist transmission but no long-term persistence.

Several other studies have used the replacement method with various tasks and tested various hypotheses (Rose & Felton 1955; Zucker 1977; Insko *et al.* 1980, 1983; Baum *et al.* 2004; Caldwell & Millen 2008a; see Mesoudi 2007). Here, we highlight the implications that these studies have had or potentially could have on three areas of cultural evolution research in particular: cultural group selection; cumulative cultural evolution; and cultural innovation.

Cultural group selection has been proposed by Richerson & Boyd (2005) to explain the widespread non-kin and non-reciprocal altruism that is observed in human societies. This theory holds that, during human evolutionary history, more-cooperative and more-cohesive groups tied together by conformity and policed by the punishment of non-cooperators would

have out-competed less-cooperative and less-cohesive groups, resulting in the evolution of 'tribal social instincts', which motivate cooperation with ingroup members and hostility towards outgroup members. Although they did not directly address this theory, two replacement studies lend support to this cultural group selection hypothesis. First, Zucker (1977) repeated Jacobs & Campbell's (1961) study but with the addition that participants were given instructions emphasizing membership of an institution or organization, and found that transmission of the arbitrary norm significantly increased in fidelity. This suggests that conformist transmission is particularly effective when it operates explicitly within groups, possibly indicating evidence of the aforementioned tribal social instincts. Second, Insko *et al.* (1983) used the replacement method to simulate between- and within-group cooperation in the trading of goods. Groups of participants were taught to produce different types of paper models, with pay-offs increased when paper models from different groups were combined. In a 'voluntaristic' condition, groups could voluntarily trade their goods. In a 'coercive' condition, one group could forcibly confiscate the goods produced by other groups. Periodically, one member of each group was replaced, in order to simulate the continual group turnover of actual societies. It was found that voluntaristic societies were significantly more productive and earned significantly more money than coercive societies, due to sabotages, strikes and slowdowns in the latter. Although Insko *et al.* (1983) did not explicitly frame their study as a simulation of cultural group selection, we might infer from their results that societies composed of mutually cooperative subgroups would have out-competed more competitive, less-cohesive societies, potentially favouring the spread of cooperative norms via cultural group selection.

Future studies might explicitly test cultural group selection theories, perhaps by allowing groups to compete more directly and allowing unsuccessful groups to go extinct either by removal from the experiment or by switching to a different group norm. This may require the modification of the replacement method along the lines of a recent study conducted by Gurerk *et al.* (2006), in which participants playing a public goods game could choose whether to participate in a sanctioning society, in which free-riders could be punished, or a non-sanctioning society, in which punishment was not possible. By the end of the experiment, virtually every participant had migrated to the sanctioning society, providing experimental support for the theoretical finding that moralistic punishment is one way of facilitating the cultural group selection of cooperative norms (Boyd *et al.* 2003). An important point to note from Gurerk *et al.*'s (2006) study is that initially only approximately one-third of the participants chose the sanctioning societies, indicating an *a priori* aversion (or at best indifference) to the use of punishment. Despite this initial preference, eventually, all participants migrated to the sanctioning societies. This initial variability and subsequent flexibility in participant behaviour suggests that cooperative norms for strong reciprocity may not be genetically hard-wired 'instincts' as sometimes

suggested; rather, people are diverse and flexible in their behaviour, and cooperative group norms may be an entirely cultural invention (given broad, genetically specified capacities for social learning, individual recognition, etc.).

Cumulative culture (Boyd & Richerson 1996; Tomasello 1999; Caldwell & Millen 2008b) describes the capacity to accumulate cultural innovations in successive generations, with each new generation learning from and adding to the previous generations' cultural knowledge. While many species exhibit regional differences in behaviour that appear to be attributable to cultural transmission (Whiten *et al.* 1999), these behaviours, such as nut-cracking or termite-fishing in chimpanzees, do not appear to be the product of cumulative culture (Tomasello 1999). This contrasts with the products of much human culture, such as computers or quantum physics, that have accumulated over multiple generations and could not plausibly have been invented by a single individual in a single lifetime. Several replacement studies have found that the performance on the prescribed task improved over generations, plausibly indicative of cumulative cultural evolution, where each new participant acquires the existing group customs and successively improves these customs. For example, Insko *et al.* (1980, 1983) found that the voluntaristic groups of traders increased their productivity and earnings during successive replacements due to the emergence and intergenerational transmission of increasingly efficient trading tactics (e.g. soft bargaining: giving more than is received) and division of labour (e.g. seniority rules for leadership, where the longest serving member took charge). Baum *et al.* (2004) found that replacement groups faced with a choice of solving anagrams that gave either small, immediate pay-offs or larger, delayed pay-offs gradually converged on the optimal choice. This was due to the emergence of intergenerational traditions in which existing group members encouraged new members to choose the optimal choice by transmitting accurate or inaccurate information about pay-offs. Interestingly, this echoes Schotter & Sopher's (2003) finding that explicit advice is particularly effective at maintaining optimal behaviour. Finally, Caldwell & Millen 2008a found that replacement groups constructed increasingly effective artefacts across successive generations: paper aeroplanes and spaghetti towers that were constructed by later generations flew significantly further or were significantly taller, respectively, than aeroplanes and towers constructed by earlier generations, suggesting the preservation and accumulation of increasingly effective manufacturing techniques.

A note of caution, however, is that none of these studies included an individual learning control condition in which a single individual engaged in the same task for the same amount of time or trials as the replacement chains (see Whiten & Mesoudi (2008) for further discussion on the use of, and need for, control conditions in diffusion experiments). Without this control condition it is difficult to conclude with certainty that these experiments have demonstrated true cumulative culture, in which a society accumulates a cultural trait that could not have been invented by

a single individual alone; this remains a challenge for future studies.

An issue that has been seldom addressed by the cultural evolution literature is that of innovation, or the emergence and spread of novel cultural traits. In an early study, sociologists [Rose & Felton \(1955\)](#) used a modified form of the replacement method to ask under what conditions cultural innovation is likely to occur. Groups of participants discussed their interpretations of Rorschach ink blots, and over successive generations participants were systematically swapped across groups in order to see how rates of cultural innovation and transmission (in this case, of ink-blot interpretations) were affected by different forms of migration/replacement. The somewhat surprising result was that closed societies with no participant migration were significantly more innovative in generating novel interpretations than open societies in which members frequently switched groups. With hindsight, this result is somewhat intuitive: migrants into a new group could simply repeat the interpretations that they generated in previous groups, whereas the participants in closed groups were forced to come up with novel interpretations. However, as [Rose & Felton \(1955\)](#) noted, this finding contradicts the commonly held notion that cosmopolitan societies with many immigrants (e.g. large cities such as New York or London) are more creative/innovative than closed societies that prohibit migration (e.g. the Amish). Although different experimental findings might be obtained with functional rather than subjective/arbitrary cultural traits, [Rose & Felton's \(1955\)](#) study shows how experiments can be useful in challenging intuitive beliefs concerning cultural processes, and points to how the replacement method might be used to explore the effect of migration on cultural phenomena such as innovation.

5. THE CLOSED-GROUP METHOD

The closed-group (or constant-group) method involves simulating cultural transmission within small groups of participants with no replacement of members. Individuals within a group repeatedly engage in a task or game over the course of the experiment, and the experimenter can manipulate the opportunities for cultural transmission (i.e. who can view and copy other participants' behaviour and when) within the group ([figure 3](#)). This method is useful for simulating under controlled conditions the various cultural transmission biases modelled in the cultural evolution literature concerning 'who' people copy, such as conformity or prestige bias, as well as testing cultural evolutionary hypotheses regarding the conditions under which cultural transmission is predicted to be employed relative to individual learning ('when' questions). Consequently, closed-group experiments typically employ an individual learning control condition in which participants engage in the same task as the participants in groups, but with no social interaction. In practical terms, the closed-group method requires fewer participants and is less time consuming than the replacement method, which requires a steady stream of new participants to introduce into the groups. Consequently, several closed-group studies have appeared

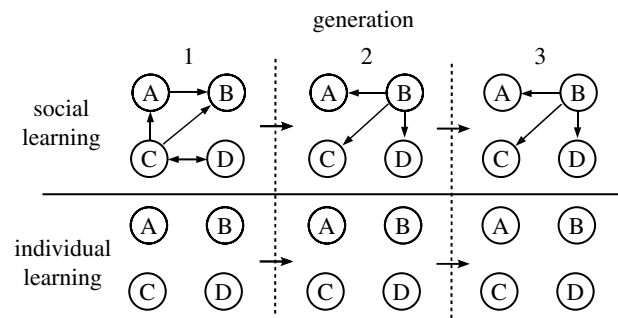


Figure 3. Design of a typical closed-group study. In the social learning condition, four participants (A–D) repeatedly engage in a learning task. Arrows indicate the flow of information via social learning, e.g. in generation 1, A learns from C, B learns from A and C, and C and D learn from each other. In generations 2 and 3, A, C and D all learn from B, who might have been recognized (or manipulated) to be particularly successful or prestigious. In the individual learning control condition, four participants engage in the same task but with no social interaction. Adapted from [Mesoudi \(2007\)](#).

in the last few years ([Kameda & Nakanishi 2002, 2003](#); [McElreath *et al.* 2005](#); [Efferson *et al.* 2007, 2008](#); [Mesoudi & O'Brien 2008](#); [Mesoudi 2008b](#); see [Mesoudi 2007](#)).

Unlike many of the transmission chain and replacement method studies, these closed-group studies have often been explicitly designed to test the assumptions and findings of existing theoretical models of cultural evolution. Accordingly, it is easier to draw direct links between experiments and models (indeed, many of these studies present both theoretical models and experiments in the same paper). For example, [Kameda & Nakanishi \(2002, 2003\)](#) explored experimentally the conditions under which cultural learning is adaptive relative to individual learning. A previous theoretical model ([Rogers 1988](#)) suggested that the reason that culture is adaptive is *not*, contrary to popular belief, that cultural learning helps to avoid the costs of individual learning. This is because in a population of cultural and individual learners, the cultural learners become free-riding 'information scroungers' who copy adaptive behaviour from individual learners ('information producers') without paying the associated costs of individual learning. If the frequency of cultural learners becomes too high, however, then there are not enough individual learners to effectively track environmental change. Thus, cultural learners copy outdated, maladaptive behaviour from each other, such that cultural learners decrease in frequency and individual learners increase in frequency. [Kameda & Nakanishi \(2002\)](#) tested these predictions experimentally. Participants in groups had to choose one of two locations to search for a rabbit, one of which was correct, using either individual or cultural learning. The results confirmed that groups of learners do indeed divide themselves into cultural learners (information scroungers) and individual learners (information producers) and that both types coexist at equilibrium. The theoretical prediction that cultural learning should be more common when individual learning is costly ([Boyd & Richerson 1995](#)) was also supported: increasing the cost of individual learning increased the proportion of cultural learners. Finally, the experiment revealed that this equilibrium was polymorphic, i.e.

a proportion p of participants always learned individually and a proportion $1-p$ always learned culturally, rather than monomorphic, i.e. all participants learn individually with a fixed probability p and culturally with a fixed probability $1-p$, a distinction that could not be made using theoretical models alone.

A follow-up study by Kameda & Nakanishi (2003), by contrast, found a mismatch between the predictions of theoretical models and experimental results. Using the same task as before, Kameda & Nakanishi (2003) found that, against the prediction of Rogers' (1988) model, groups in which cultural learning was permitted significantly outperformed groups of pure individual learners, despite the presumed detrimental effect of information scroungers in the former. Further analyses suggested that the cultural group did not divide into fixed individual learners (who always engaged in individual learning) and fixed cultural learners (who always engaged in cultural learning) as assumed in Rogers' (1988) model. Rather, the participants flexibly switched between individual learning (when individual learning was accurate) and cultural learning (when individual learning was inaccurate). (A similar flexible learning strategy was observed by Mesoudi (2008b) using a different task, and similarly enhanced fitness relative to individual learning controls.) Kameda & Nakanishi (2003) presented theoretical models which confirmed that flexible cultural learners do indeed outperform the fixed cultural learners of Rogers' (1988) model (see also Boyd & Richerson 1995). Kameda & Nakanishi's (2002, 2003) work is a good example of how experiments and models can be most effective when combined: experiments can be used to test the predictions of models, and where a mismatch is found, further models can then be used to explore the reasons for this mismatch, which are then subject to further experimental tests, and so on.

Other studies have addressed 'who' is copied, or what Richerson & Boyd (2005) have called model-based and frequency-based biases. Several studies have focused on conformity (disproportionately adopting the most common trait in a population), following cultural evolutionary models which suggest that conformity is adaptive under a wide range of conditions (Boyd & Richerson 1985; Henrich & Boyd 1998). McElreath *et al.* (2005) asked participants to select one of two crops to plant, one of which gave a higher pay-off than the other. The participants could view the choices of either one randomly selected group member (allowing simple cultural learning) or all other group members (potentially allowing conformity). Substantial individual variation in learning strategies was found, with a sizeable proportion of participants not engaging in cultural learning, even where models suggested cultural learning would have given higher pay-offs. Of those who did copy, conformity was only used when the environment (i.e. which crop was optimal) changed, despite models suggesting that conformity is the most adaptive strategy under all conditions. A further study (Efferson *et al.* 2008) using a similar task also found individual variation in the use of social information: while the majority (70%) of participants who could potentially use social information engaged in conformity, resulting in significantly

higher earnings in line with theoretical expectations, a substantial minority (30%) did not, instead ignoring information about the behaviours' frequency in the group. Finally, Efferson *et al.* (2007) conducted a similar experiment with Bolivian subsistence pastoralists. One group of participants was shown the choice of the player who received the highest pay-off in the previous round (allowing a 'copy-best' strategy), while another group was shown the choices of all players from the previous round (potentially allowing conformity). Although the latter group outperformed the copy-best group and individual controls, analyses of the participants' learning strategies indicated that neither group of cultural learners actually used the social information that was presented to them, given that their learning strategies were indistinguishable from those of the individual controls. Efferson *et al.* (2007) suggested that social facilitation (improved performance due to the mere presence of conspecifics) may have contributed to the better performance of the total distribution group. In general, experimental studies of conformity (McElreath *et al.* 2005; Efferson *et al.* 2007, 2008) have found that while many participants do conform (and receive higher earnings for doing so), there is often considerable individual variation in participants' use of social information, such that sizeable numbers of participants fail to engage in conformity despite theoretical models showing it to be the optimal learning strategy.

A set of studies conducted by the first author have examined the cultural learning strategy of copying the most successful individual in a group (Mesoudi & O'Brien 2008, 2008; Mesoudi 2008b). Mesoudi & O'Brien (2008) used the closed-group method to experimentally simulate the cultural transmission of arrowhead designs, in order to test a specific hypothesis concerning actual arrowhead variation in the archaeological record (Bettinger & Eerkens 1999). Participants designed their own 'virtual arrowheads' and received pay-offs partly determined by their designs. Arrowhead designs could be improved either by trial-and-error individual learning or by copying the most successful fellow group member. As predicted, periods of individual learning resulted in increasingly diverse sets of arrowhead designs as participants followed their own idiosyncratic learning strategies, while periods during which participants could engage in copy-successful-individuals cultural learning resulted in more uniform arrowhead designs, as participants converge on the design of the most successful player. These patterns of variation match corresponding patterns of arrowhead diversity observed in the prehistoric Great Basin (Bettinger & Eerkens 1999): high diversity in prehistoric California, indicative of individual learning, and low diversity in prehistoric Nevada, indicative of copy-successful-individuals learning.

As well as simply recreating past patterns of cultural transmission, however, experiments can also be used to determine the adaptiveness of different learning strategies and systematically manipulate variables of interest, both of which are extremely difficult with historical data alone. Mesoudi & O'Brien (2008) found the copy-successful-individuals bias to be significantly more adaptive than individual learning, especially

when individual learning was costly, consistent with previous theoretical models (Boyd & Richerson 1995). Given that the environment in prehistoric Nevada is thought to have been harsher than the prehistoric Californian environment, this provides a potential explanation for differences between the two regions in learning strategies. Importantly, however, all of these conclusions are crucially dependent on the shape of the fitness functions underlying pay-offs of different arrowhead designs. Mesoudi & O'Brien (2008) assumed a multimodal adaptive landscape underlying arrowhead fitness, with multiple locally optimal designs ('peaks' in the landscape). Consequently, during periods of individual learning, different participants converged on different peaks in this adaptive landscape, thus maintaining within-group diversity in arrowhead designs. During periods of cultural learning, different participants converged on the high-fitness peak found by the most successful group member, thus reducing diversity and increasing overall group fitness. However, Mesoudi (2008b) showed that when the adaptive landscape is unimodal—with a single peak and a single optimal arrowhead design—then individual learners easily converge on this single peak and perform just as well as the cultural learners, thus eliminating the adaptive advantage of cultural learning. An important message here, then, is that the adaptiveness and use of a particular cultural learning strategy, e.g. copying successful individuals, critically depends on the shape of the underlying adaptive landscape (just as the shape of genetic adaptive landscapes can dramatically affect genetic evolution; Arnold *et al.* 2001).

6. DISCUSSION

At the beginning of this paper, we identified the goals of cultural transmission experiments as answering the what, who, when and how questions posed by Laland (2004): what is copied; who is copied; when do individuals copy; and how do individuals copy? These questions were motivated by the insight from theoretical models, some of which were discussed above, that indiscriminate social learning is not universally adaptive (e.g. Rogers 1988; Boyd & Richerson 1995; Henrich & Boyd 1998). These models suggest instead that individuals should use social information selectively; that is, they should be selective in who they learn from, what they copy, how they copy and when they copy. The various experiments discussed above support this prediction, and begin to provide specific answers to these 'who, what, when and how' questions regarding cultural transmission. The following sections summarize these findings and point to directions for future research.

(a) What is copied?

Transmission chain studies, in which information is passed along linear chains of participants, show that human cultural transmission can often be vulnerable to distortions and biases rather than constituting a process of high-fidelity replication. These studies have identified several candidate content biases in cultural transmission: a counter-intuitive bias (Barrett & Nyhof 2001); a hierarchical bias (Mesoudi & Whiten 2004);

a gender-stereotype bias (Bangerter 2000; Kashima 2000); and a social bias (Mesoudi *et al.* 2006a). (We qualify these as 'candidate' biases given that each is supported by one or at most two experiments; as the field expands, we anticipate future experiments to provide further support or qualifications to these initial findings.) Cognitive, evolutionary and social psychology offer a wealth of hypotheses regarding other potential content biases that might be tested formally using the transmission chain method. For example, Heath *et al.* (2001) have proposed that cultural transmission is affected by emotional reactions of disgust, and showed using historical data that rumours that elicit disgust are more likely to survive than rumours that do not. Nairne *et al.* (2008) found that words that are processed within a survival context (e.g. relating to food or predators) are recalled better than those same words presented in non-survival contexts, suggesting an 'ecological' bias in cultural transmission that might under certain conditions rival the social bias found by Mesoudi *et al.* (2006a). The transmission chain method might be used to experimentally test whether disgust, ecological or other content biases, which are currently supported only by observational evidence or single-generation memory experiments, operate in cultural transmission, i.e. to what extent they extend beyond single individuals. It would also be useful, following the example of the closed-group method, to implement individual control conditions in which a single individual repeatedly recalls their own recalled material (much similar to Bartlett's (1932) method of repeated reproduction) in order to quantify exactly how (or whether) the cumulative, cultural recall of multiple participants differs from the recall of a single participant.

(b) How is it copied?

Few diffusion studies with humans have explicitly addressed the mechanism through which cultural transmission operates. Schotter & Sopher (2003) found that explicit verbal advice or rules are more effective in generating stable behavioural conventions in an economic game than simply observing past behaviour. This is echoed by Insko *et al.*'s (1980, 1983) and Baum *et al.*'s (2004) findings that optimal traditions were maintained by explicit verbal rules. The latter studies found cumulative improvement in performance, suggesting that explicit verbal rules might maintain cumulative culture. However, apart from Schotter & Sopher's (2003) study (which did not allow cumulative improvement), there has been no formal experimental comparison of different cultural transmission mechanisms, such as imitation, emulation and stimulus enhancement (Whiten *et al.* 2004). Although such work has only just begun in the non-human animal literature (Hopper *et al.* 2007; Whiten *in press*), future studies using human adults could similarly profit from the detailed taxonomies of social learning and methods of the non-human social learning research (Want & Harris 2002; Whiten *et al.* 2004) in order to identify the cognitive mechanisms underlying particular forms of cultural transmission.

(c) Who is copied?

Recent studies have used the closed-group method to test the adaptiveness and consequences of two 'who' biases: copying the majority (conformity) and copying the most successful individual. Efferson *et al.* (2008) found that some, but not all, participants engage in conformity, and, as a result, they do better than non-conformists, consistent with theoretical expectations (Henrich & Boyd 1998). It is puzzling, then, why not all of Efferson *et al.*'s (2008) or McElreath *et al.*'s (2005) participants and none of Efferson *et al.*'s (2007) participants engaged in conformity, even though conformity would have yielded higher earnings. Establishing the reasons for this discrepancy is an important task for future experiments. Mesoudi & O'Brien (2008) and Mesoudi (2008b) simulated a copy-successful-individuals bias, and found, by contrast, that almost all participants readily discarded the artefact that they had spent several trials designing to adopt the artefact design of the most successful member of the group. (N.B. this appears to contrast with recent studies of non-human primates that showed a marked tendency to stick to a known, satisfactory technique rather than upgrade to a more productive one being used by another individual, a difference that might help explain why complex cumulative culture is such a distinctive human attribute; Marshall-Pescini & Whiten 2008). Efferson *et al.* (2007), however, found that the behaviour of the most successful group member was *not* adopted. The discrepancy between these findings and those of Mesoudi & O'Brien (2008) might be explained by differences in task and participant sample. For example, Efferson *et al.* (2007) used a simple task of choosing one of two discrete options (one of two technologies), whereas Mesoudi & O'Brien (2008) used a more complex task with multiple variables, some continuous and some discrete, some functional and some neutral, and with multimodal adaptive landscapes underlying artefact success. As shown by Mesoudi (2008b), the shape of this adaptive landscape can dramatically affect the adaptiveness of cultural learning. Further studies might look more systematically at the nature of the task set for participants and the underlying fitness functions determining task success.

(d) When do people copy?

Experimental studies have broadly confirmed the theoretical predictions that cultural learning should be more frequent relative to individual learning when environments do not change (McElreath *et al.* 2005) and when individual learning is inaccurate (McElreath *et al.* 2005) and/or costly (Kameda & Nakanishi 2002; Mesoudi & O'Brien 2008). However, several studies (McElreath *et al.* 2005; Efferson *et al.* 2007, 2008) have found that people engage in cultural transmission far less than would be optimal. Moreover, much individual variation has been found in these and other studies, with participants often differing widely in their tendency to learn from others. At present, the cause of this individual variation is a mystery, and points to a more general question about this and the model-based biases (§6c): what is the origin of these cultural

transmission biases and strategies? Are they genetically specified, as sometimes assumed in cultural evolution models (e.g. Boyd & Richerson 1985), or are they learned during ontogeny (a kind of 'learning of learning strategies')? Perhaps cultural learning strategies are themselves learned from others, such that conformists conform because they have copied from others a tendency to conform. Developmental studies would be valuable here in determining how individual variation in experimental behaviour might be explained by different learning opportunities during ontogeny. Recent twin studies (McEwen *et al.* 2007; Fenstermacher & Saudino 2007) have suggested that individual differences in the capacity of 2-year-olds to imitate can be partly attributed to genetic variance and partly to environmental factors, although the studies disagreed as to the relative influence of each and whether the environment is shared (e.g. interaction with parents) or non-shared (e.g. individual reinforcement histories). It should also be noted that a capacity for imitation, one particular social learning mechanism, may be unrelated to the voluntary use of cultural learning strategies (e.g. conformity or copy-successful-individuals) tested in the experiments reviewed here; future developmental and twin studies might examine these more specific cultural learning strategies as well as broader capacities such as imitation, and in children of varying ages. Cross-cultural studies might also be used to explore the cultural learning of cultural learning strategies. So far, the vast majority of cultural transmission experiments have been conducted using western (USA or UK) participants (see table S1 in the electronic supplementary material), with the exception of Kameda & Nakanishi's (2002, 2003) studies in Japan and Efferson *et al.*'s (2007) study in Bolivia. Non-transmission experiments have found that more 'collectivist' East Asian participants show higher levels of conformity than more 'individualist' western participants (Bond & Smith 1996); perhaps the low levels of conformity seen in some of the experiments reviewed above are due to the use of western participant samples. Kameda & Nakanishi (2002) found that a majority of Japanese participants engaged in conformist transmission, but whether this was systematically different from observed rates of conformity in studies that used western participant samples is unclear given differences in experimental tasks and procedures.

(e) Integrating questions

So far, we have assumed that questions regarding cultural transmission—who, what, how and when—can be considered separately. In reality, it is unlikely that cultural behaviour is neatly divided in this way. A promising avenue for future research would be to pit different biases against one another. For example, what happens when the group majority exhibits a different behaviour or belief to the most successful individual? What happens when low-prestige models pass on minimally counter-intuitive information? Perhaps certain biases will be found to dominate cultural transmission, or perhaps equilibria will be observed where different biases operate simultaneously. Inspiration might be sought from evolutionary biology, where experimental studies are used to explore the

simultaneous operation of multiple evolutionary processes in the same population (e.g. natural and sexual selection; Skroblin & Blows 2006).

7. CONCLUSIONS

Our understanding of human cultural change can greatly benefit from laboratory experiments. While mathematical models in the gene–culture coevolution/cultural evolution tradition have produced invaluable insights into the processes of cultural change, laboratory experiments are needed to test the assumptions and findings of these models with actual people. Similarly, while, historical, ethnographic and archaeological studies of cultural evolution (Basalla 1988; Hewlett *et al.* 2002; O'Brien & Lyman 2002) are invaluable in providing real-world data regarding cultural change, laboratory experiments offer a degree of control and manipulation that is impossible to achieve with naturalistic studies. Of course, laboratory experiments also have their shortcomings, most obviously deficits in external validity resulting from the simple tasks and artificial laboratory settings involved. However, when experiments are used in conjunction with other methods, as part of a unified science of cultural evolution (Mesoudi *et al.* 2006b), then a better understanding of cultural phenomena can be attained than when a single method is used alone. The studies reviewed here suggest that this interdisciplinarity is beginning to pay dividends, with studies such as Kameda & Nakanishi (2003), McElreath *et al.* (2005) and Efferson *et al.* (2008) explicitly tying experiments to mathematical models, and others (e.g. Insko *et al.* 1983; Mesoudi & O'Brien 2008) using experiments to explicitly test hypotheses from cultural anthropology and archaeology.

Much of the older work reviewed here has so far had relatively little direct impact in the fields in which they originated, typically social psychology but also sociology, economics and anthropology. For example, Jacobs & Campbell's (1961) pioneering experimental simulation of conformist cultural transmission has, in the last 47 years, only been cited between eight (Web of Knowledge, 1970–present) and ten (PsycInfo, 1961–present) times. Similarly, in the quarter-century since Insko *et al.*'s (1983) hugely innovative study was published in one of the leading social psychology journals (the *Journal of Personality and Social Psychology*), that paper has been cited only eight times according to Web of Knowledge, while PsycInfo records no citations for it at all. For whatever reasons, social psychologists have not considered cultural transmission to be worthy of study in this way, and cultural anthropologists have not considered experiments to be particularly relevant to their work. By drawing such studies to the attention of a wider body of researchers in the cultural evolution tradition, and linking them to each other and to formal cultural evolution theory, we hope to offer added value and renew interest in experimental studies of cultural transmission.

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