Introduction. Cultural transmission and the evolution of human behaviour

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The articles in this theme issue seek to understand the evolutionary bases of social learning and the consequences of cultural transmission for the evolution of human behaviour. In this introductory article, we provide a summary of these articles (seven articles on the experimental exploration of cultural transmission and three articles on the role of gene–culture coevolution in shaping human behaviour) and a personal view of some promising lines of development suggested by the work summarized here.

Keywords: social learning; cultural transmission; cultural evolution; human evolution; evolutionary psychology; diffusion chain

1. INTRODUCTION

Humans learn from other humans in a wide variety of domains. Consequently, systems of knowledge and behaviour are culturally transmitted in human populations. The articles in this theme issue seek to understand the evolutionary bases and consequences of cultural transmission: how widespread is cultural transmission in the animal kingdom; how does cultural transmission work in human populations; what products does cultural evolution deliver; and how has culture interacted with biological evolution to shape our species?

Rather than outline our own research on cultural transmission and human behaviour (which is presented at length in the papers by Griffiths *et al.* (2008) and Smith & Kirby (2008)), our aim in this paper is to summarize the content of the articles in the of this issue, identify common themes and offer a personal view on the directions in which this research programme should be developed.

The articles in this issue fall into two groups. The first seven papers deal with experimental approaches to studying cultural transmission and cultural evolution— these contributions are sketched out in §2. The second group of articles (the final three articles in this issue, described in §3) deal with the interactions between biological and cultural evolution and, in particular, the relationship between coevolutionary theories and theories that seek to explain human behaviour purely or primarily in terms of biological evolution (the Evolutionary Psychology approach).

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2. AN EXPERIMENTAL APPROACH TO CULTURE

Inquiry into the evolutionary bases and consequences of cultural transmission is of course not a new endeavour: evolutionary approaches to culture have a distinguished history (e.g. Darwin 1879/2004, pp. 112–114, draws direct parallels between biological evolution and the cultural evolution of words and languages), and the study of cultural transmission and cultural evolution is a vibrant and growing research area (see Mesoudi *et al.* (2006*b*) for a programmatic review). Much of this research has been theoretical or observational in nature, based on formal models of evolutionary processes (e.g. Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Richerson & Boyd 2005) or observational study of real-world cultural phenomena (e.g. Durham 1991; Rogers 1995).

While these remain important tools for studying cultural evolution, they are not the only ones available. A further possibility is to adopt an experimental approach to explore the mechanisms and dynamics of cultural transmission—experimental study offers a potential bridge between the generality and control of the formal model and the naturalism of observation of real behaviour in real cultural environments. A powerful experimental approach, with a long history but undergoing a renaissance in recent years, is to investigate cultural evolution directly in simple laboratory populations under controlled conditions, in order to establish what actually happens when people learn from other people (or, indeed, when non-humans learn from non-humans). This theme issue brings together, for the first time, a recent and growing body of work that applies these experimental techniques (sometimes called *diffusion chains* or *transmission chains*) to investigate cultural evolution.

The experimental body of this issue can be further subdivided into three sections, discussed in turn below. The first section consists of two papers by Mesoudi & Whiten (2008) and Whiten & Mesoudi (2008), which review the methodologies and early findings from experimental studies of cultural transmission and evolution (see §2*a*). The second section (§2*b*), which consists of papers by Griffiths *et al.* (2008) and McElreath *et al.* (2008), looks in more detail at two key issues in the experimental study of cultural transmission: what do culturally transmitted systems adapt to and who do we learn from when learning socially? The final set of experimental papers from Caldwell & Millen (2008), Fay *et al.* (2008) and Flynn (2008), summarized in §2*c*, consider the functionality of the products of cultural evolution: to what extent do culturally transmitted behaviours accumulate modifications over time to produce complex and well-adapted behaviours?

(a) *Review of experimental methods*
The primary methodology for the experimental study of cultural transmission (the diffusion chain experiment) dates back at least to Bartlett's (1932) serial reproduction experiments. In common with dyadic studies of social learning (e.g. Bandura 1977), diffusion chain experiments are based around a pairwise learning interaction, whereby one individual produces a behaviour for observation by another individual, who attempts to learn or reproduce that behaviour. The novelty of the diffusion chain method is that the second individual is then used as the model, producing behaviour for a third individual and so on—a mini-culture is created in the laboratory. Despite its venerability, the diffusion chain has been something of a fringe paradigm, used by a small number of researchers in a wide range of disciplines (most notably, comparative biology and psychology) to address a fairly eclectic set of research questions. This situation has recently undergone a dramatic shift, as methodological advances have seen an increase in the use of the diffusion chain method and an increasing awareness across disciplinary boundaries of the techniques in use and the questions addressed. The contributions from Mesoudi & Whiten (2008) and Whiten & Mesoudi (2008) review these developments, outlining the diversity of diffusion chain methodologies available (the 'linear chain' method outlined above is but one of several) and their application to the questions of animal culture and the determinants of cultural evolution in human populations.

One of the fundamental questions in understanding the human capacity for culture is to identify its evolutionary origins: is this a recent ability, or an ancient one which simply appears in an unusual form in our species? Whiten & Mesoudi review the literature on diffusion studies in non-human animals, focusing on the range of experimental methodologies employed and their ability to distinguish social learning and cultural transmission from other mechanisms capable of producing similar group-level behaviours (e.g. individual learning). The achievements in this area have been impressive: there is clear evidence for cultural transmission in a number of non-human species (primates, but also rodents, birds and fishes). Furthermore, transmission is seen under a range of experimental regimes, ranging from the highly controlled linear chain design (as described above) through to the less controlled but more naturalistic open-diffusion design, where a behaviour is seeded in a population and allowed to spread through that population in a spontaneous and uncontrolled fashion.

In the process of this review, Whiten & Mesoudi also identify the limits of this literature: the range of species which have to date been studied in this fashion is fairly limited, and the range of social learning tasks is also somewhat restricted. In addition to broadening taxonomic and task coverage, Whiten & Mesoudi identify one of the major challenges facing the burgeoning animal diffusion literature as the move from studies involving captive animals to controlled studies in the wild. Such studies would serve to narrow the current divide between naturalistic but uncontrolled (and therefore often uninterpretable) studies of putative cultural behaviour in the wild and controlled but fairly artificial studies in captivity.

The material reviewed by Whiten & Mesoudi speaks to establishing the existence (or at least the capacity for supporting) culturally transmitted traditions in various species. In our species, the question is not one of the existence of culture, but the details of the cultural transmission process and the cultural evolutionary dynamic it engenders. Mesoudi & Whiten review the historical and contemporary literature on human cultural transmission experiments, with a focus on how this literature addresses four issues: (i) what kinds of information are stable over repeated episodes of cultural transmission, (ii) who do social learners chose to learn from when learning socially, (iii) when is social learning favoured over alternatives, and (iv) how, on a mechanistic level, does social learning work? To give brief examples: addressing the 'what' question, linear diffusion chain studies show that human learners bring a number of biases for particular sorts of content to social learning tasks (e.g. biases in favour of social over non-social information; Mesoudi *et al.* 2006*a*) and these biases result in more faithful transmission of information that meets the content biases of individuals; addressing the 'who' question, closed-group studies (where a group of individuals repeatedly interact; e.g. Efferson *et al.* 2008) show that at least some humans exploit frequency information when confronted with a social learning problem, preferentially copying the behaviour of the population majority.

Again, in common with the review of the non-human diffusion literature provided by Whiten & Mesoudi, this review reveals a picture of a healthy but relatively youthful discipline: an exciting proliferation of methods and promising early results, but relatively little systematic evaluation of experimental tools or integration of studies addressing each of the four issues above.

(b) *What and who*
In their paper, Griffiths *et al.* provide several case studies that seek to address Mesoudi & Whiten's 'what' question: what kinds of culturally transmitted behaviours are stable over time, and when a culturally

transmitted behaviour changes over time, what is it changing towards? Griffiths *et al*. adopt a mix of mathematical and experimental diffusion chain techniques to demonstrate that culturally transmitted behaviours adapt to fit the inductive biases of learners. Any learning process has some bias—some behaviours are easier to learn (require less data to learn) than others, due to the architecture of the learning system and the constraints inherent in it. Culturally transmitted systems repeatedly undergo filtering through these inductive biases of learners as they are passed from individual to individual.

Griffiths *et al*. summarize their own mathematical work (Griffiths & Kalish 2005, 2007; Kirby *et al*. 2007), which shows that, under a fairly broad set of assumptions, cultural evolution will lead to systems that mirror the inductive biases of individuals—seen in this light, the various examples provided by Mesoudi & Whiten would then be specific instances of a more general phenomenon. Furthermore, these inductive biases can overwhelm contrary pressures from natural selection—in conditions where the learning biases of individuals favour one behaviour and natural selection favours another, inductive biases win out under a broad range of conditions. Griffiths *et al*. support this formal modelling work with a summary of their laboratory experiments (Kalish *et al*. 2007; Griffiths *et al*. 2008) in two domains where the inductive biases of individuals are already well established—function learning and categorization—and show that cultural versions of these tasks result in convergence to behaviours (functions or categories) that match the inductive biases of individuals.

We would highlight one final contribution by Griffiths *et al*., derived from formal modelling. They show an equivalence between the equilibria of cultural evolution in linear transmission chains and populations where there are multiple individuals per generation. Specifically, the stable outcome of cultural evolution (the *stationary distribution*) arrived at by each process should be the same—after cultural evolution has run its course, the probability that a particular individual in a linear chain will exhibit a particular behaviour is equal to the proportion of individuals exhibiting that behaviour in a population. In other words, studying simple linear chains of transmission potentially offers a short cut to determining the outcomes of cultural evolution in populations. This constitutes an additional justification for studying cultural evolution in simplified, manageable laboratory populations, and establishing the range of conditions under which behaviour in laboratory populations approximates behaviour of larger and more complex populations would be a worthwhile next step.

Rather than asking what inductive biases learners bring to social learning tasks, McElreath *et al*. seek to understand the extent to which humans use social information and, importantly, how multiple types of social information are integrated. Social learning is not the only way in which individuals can adapt to challenges posed by their environment (an alternative is to learn individually), and social learners face choices about who they learn from (e.g. conforming to the majority behaviour or preferentially copying more successful individuals). Furthermore, such behaviours

need not be applied exclusively—learners can learn through a combination of individual and social learning, and apply a combination of social learning strategies (e.g. by weighted or hierarchical combinations of pay-off-based and conformity-based strategies).

McElreath *et al*. use an abstract task ('crop selection', where different crops have different yields and the pay-off changes periodically) that can be solved by individual or social means—participants have access to the pay-offs associated with their own past choices but also the choices and pay-offs of several other individuals. McElreath *et al*. then use model-fitting techniques to identify which combinations of individual and social learning strategies best describe the actual choices that their experimental participants made (similarly to the approach used in, for example, Efferson *et al*. (2008)). They find that their participants combine individual and social learning, attending to a hierarchically organized combination of pay-off and frequency information when learning socially (preferentially copying high pay-off behaviours, but selecting the most frequently chosen response when the difference in yields is less marked). This use of pay-off-based social learning is predicted by McElreath *et al*.'s mathematical analysis to be the most successful strategy under a wide range of assumptions about pay-offs and environmental variability.

While this is in itself an interesting result, McElreath *et al*. see the main contribution of this approach as a means of studying social learning in the wild: while they apply their fitting technique to laboratory results, the same approach could be applied to real-world data (e.g. the diffusion of competing innovations in an open-diffusion study of the type outlined by Whiten & Mesoudi (2008)). This approach therefore offers an alternative to existing experimental approaches (dyadic or diffusion chain) to teasing apart social learning strategies—it may be that in some cases the behavioural signatures of different social learning strategies are sufficient to identify those strategies.

(c) *Cultural evolution and functionality*

One of the main motivations for understanding the human capacity for culture is that it appears to form the basis of some of humanity's most surprising achievements. Sophisticated technologies, highly developed sciences and elaborate social or religious rituals are products of a cumulative process of cultural evolution, whereby each generation builds on the achievements of their predecessors in a gradual, approximately monotonic ratcheting up of complexity and functionality (Tomasello 1999). The final three experimental articles in this issue apply the methods reviewed by Mesoudi & Whiten to an exploration of this class of phenomenon: to what extent does cultural transmission yield products that are well designed, and can we use experimental techniques to delve into the processes that produce these functional outcomes?

Caldwell & Millen provide an introduction to the area of cumulative cultural evolution: its taxonomic spread (its presence in non-humans is contentious); the mechanisms underpinning it (it remains unclear whether sophisticated imitation is required for cumulative cultural evolution, or whether more basic social

learning mechanisms will suffice); and the types of outcomes it yields (e.g. whether cumulative cultural evolution can deliver behaviours that are universal cross-culturally). The latter is a crucial issue: cross-cultural universality is often taken as a hallmark of non-cultural transmission—for example, fundamental structural similarities across diverse languages are often taken as evidence for a universal genetically specified language blueprint (Chomsky 1965). Caldwell & Millen summarize their own experimental work (Caldwell & Millen 2008) which uses a diffusion chain approach to explore the cumulative cultural evolution of technological artefacts. As well as demonstrating the phenomenon under laboratory conditions, they show convergent evolution across separate populations towards similar artefact designs, indicating that, under certain circumstances, cumulative cultural evolution can potentially offer a non-genetic explanation for cross-cultural universals.

Flynn provides a second illustration of cultural transmission delivering improved traditions, building on previous dyadic work (e.g. McGuigan *et al.* 2007) which suggests that children are prone to over-imitation—they copy both task-relevant and task-irrelevant (and therefore non- or a-functional) behaviours. Flynn presents infants (aged 2–3 years) with a box-opening ('artificial fruit') task. Diffusion chains are initialized with a mix of relevant (directed to retrieving a sticker from the box) and irrelevant (not contributing to releasing the sticker) behaviours. While task-relevant actions are faithfully transmitted down multiple generations of these chains, irrelevant actions are rapidly filtered from the populations' behavioural repertoire. The culturally transmitted patterns of behaviour in these populations therefore become more efficient over transmission events, in line with the notion of cumulative cultural evolution.

Finally, Fay *et al.* offer a detailed experimental evaluation of the optimality of the products of cultural evolution. They focus on graphical communication systems that are produced in an experimental paradigm (described in detail in Garrod *et al.* (2007)) where adult human participants negotiate communication systems through repeatedly playing a graphical communication game similar to the parlour game Pictionary. Fay *et al.* contrast the graphical communication systems that emerge through two different routes: repeated interaction between a single pair of participants (isolated pair systems) and repeated interaction within a community of multiple individuals (community systems). Both isolated pairs and communities start off with iconic systems of representation (based around relatively complex drawings that resemble the concepts they refer to) and develop more streamlined symbolic communication systems (drawings become considerably simplified and abstract). This symbolization is attributable to pressure for the participants to minimize their effort in producing graphics, while still maintaining distinct symbols for distinct concepts—in this sense both isolated pair and community systems are highly functional. Fay *et al.* show, however, that the community systems also simultaneously optimize their transmissibility (see Kirby *et al.* (2008) for a related result). In communities, the ideal communicative symbol will not only be (i) economical to produce and

(ii) distinctive, but (iii) will have some residual iconicity that allows an individual who has not seen this particular symbol before to infer its meaning—this pressure does not exist in purely pair-based systems, where both participants are privy to every symbol's iconic roots. Consequently, community-evolved symbols are optimized along this third dimension and therefore (as Fay *et al.* (2008) show) easier for naive individuals to learn.

(d) *Experimental models of cultural transmission: a summary*

The experimental study of cultural transmission is a rapidly developing and coalescing field: as the articles in the body of this issue show, the processes of developing a consensus on the appropriate experimental methodologies, the overarching theoretical predictions and the key sub-topics have begun.

However, this consensus building is at an early stage and much remains to be done. Some of this outstanding work is methodological in nature. For example, while Whiten & Mesoudi are able to compare results obtained across experimental designs, little work directed explicitly at evaluating the impact of different experimental designs has been done to date (but see Whiten *et al.* (2005), Horner *et al.* (2006) and Griffiths *et al.* (2008), which show that some results can be replicated with different diffusion chain designs). Furthermore, there remains little agreement on the validity of the different available methods for addressing particular questions. To take an example touched upon in this issue: while there is a general agreement that cumulative cultural evolution is an important sub-topic to address, there is less agreement on the best method to explore it. While Flynn uses a linear diffusion chain to study cumulative cultural evolution, Caldwell & Millen are somewhat critical of the suitability of this experimental design for investigating this phenomenon. One of the challenges for the future is to explore more fully the methodological space and address these issues head-on—as experimentalists, we should be prepared to subject our methodologies to experimental test, in particular testing for consistency across different diffusion chain designs.

Of course, the points of dispute are not merely methodological. Again, to take an example from this issue: while some theoretical accounts of cumulative cultural evolution (e.g. Tomasello 1999) emphasize the importance of a cultural ratchet, such that functional modifications are preserved and not lost (the ratchet prevents the evolving behaviour slipping backwards towards non-functionality), the chain-by-chain results of cultural evolution presented by Caldwell & Millen (2008, fig. 2 in their paper) look anything but ratcheted—performance of the evolving artefacts frequently decreases from generation to generation, although the overall trend is upwards. While this could be explained as a consequence of a slightly noisy mapping from quality of design to measured functionality in this particular experiment (even the best designed spaghetti tower will collapse if constructed from substandard ingredients), this explanation works less well in the case of highly non-functional innovations in Flynn's diffusion chains (while the

general trend is to eliminate irrelevant actions, one child introduced multiple unnecessary movements of the box door). Ideally, these kinds of experimental phenomenon should be fed back into a refined theory (in this case, can our theory tolerate a slippy ratchet?), generating new predictions to be tested experimentally (e.g. how slippy can the ratchet be if we are still to see cumulative cultural evolution in the laboratory?), and perhaps touching upon the sort of methodological questions outlined above (e.g. do certain transmission dynamics, such as linearity, lead to less of a ratchet effect and reduced cumulativity?).

3. THE RELATIONSHIP BETWEEN GENES AND CULTURE

The final three articles in this issue move beyond the experimental study of cultural transmission to consider the wider issue of how cultural evolution interacts with that other source of adaptive behaviour in the natural world, biological evolution. The deeply cultural nature of human cognition must ultimately be rooted in our biology: it has, for example, been attributed to uniquely human social learning mechanisms (e.g. Tomasello (1999) and discussion in the paper by Whiten & Mesoudi (2008) and references therein). Culture also influences biology: for example, it is often argued that our cognitive capacities have been massively adapted to work in conjunction with the human cultural inheritance (Sperber 1996). Furthermore, culture provides a second inheritance system for human behaviour (Boyd & Richerson 1985; Whiten 2005; Mesoudi *et al.* 2006*b*). The appearance of design in human behaviour therefore has at least two possible causes, biological or cultural evolution, and explaining the origins of complex and adaptive human behaviours requires us to understand which inheritance systems carry and shape which behaviours, as well as understanding how these two inheritance systems interact.

The articles in this section address these issues of interactions between biology and culture. Furthermore, all three are explicitly concerned with addressing the relationship between explanations of human behaviour involving cultural evolution and the popular Evolutionary Psychology approach (henceforth EP; e.g. Cosmides & Tooby 1987; Pinker 1997). Unlike cultural accounts, the EP school of thought is widespread in the psychological community and, indeed, in the popular consciousness. As such, pinning down the relationship between cultural and EP accounts is an important issue for proponents of cultural or coevolutionary explanations of human behaviour, both on a practical level (to assist in the promulgation of these theories) and from a scientific standpoint (to determine which theory has greater explanatory power).

The classic EP account sees human behaviour as governed by a set of hard-wired, task-specific mental modules evolved to deal with specific ecological challenges posed by the ancestral human environment. As pointed out by Wheeler & Clark in their contribution here, the EP explanatory approach seems fundamentally at odds with two alternative and powerful explanations of human behaviour: cultural evolution and embodied cognition. Cultural evolutionary accounts allow for a role for extra-genetic transmission and adaptation. Embodied accounts of cognition emphasize the reciprocal relationship between an organism and its environment, such that the environment is exploited to reduce the cognitive burden on the brain and structure in the environment in turn impacts on the way in which the brain seeks to solve problems. Both emphasize the capacity for non-genetic factors to influence behaviour and highlight the self-constructing and bootstrapping nature of an organism's or population's interaction with its environment.

Wheeler & Clark argue that this apparent incompatibility between EP, embodied cognition and culture can be resolved by a more nuanced view of how an evolved mental module might interact with its (self- and culturally constructed) environment. For example, the initial disposition of the cognitive system (potentially a component of our evolved mind) interacts with the environment (which may be constructed and exploited by the individual and/or their cultural predecessors) via an incremental bootstrapping process, such that the brain develops along the route primed by the genes but shaped through interaction with the environment. Under the most extreme interactionist version of this argument 'what is special about human brains... may be precisely their ability (…) to enter into deep, complex and ultimately architecture-determining relationships with an open-ended variety of culturally transmitted practices, endowments, and non-biological constructs, props and aids' (Wheeler & Clark 2008). At the other end of the spectrum lies something resembling the classic EP position, where interaction with the environment is downplayed. Wheeler & Clark see the challenge facing an integrated, embodied cultural EP as identifying where on this spectrum from heavy genetic influence to emergent mind each aspect of human cognition resides.

Laland offers three case studies on the intimate coevolutionary relationship between culture and genes in shaping human behaviour. While adopting a far less conciliatory tone towards EP, Laland's (2008) conclusion is broadly similar to that of Wheeler & Clark: 'human minds and human environments have engaged in a long-standing, intimate exchange of information... leaving each beautifully fashioned in the other's image'.

Laland's first case study (Laland *et al.* 1995) deals with explaining variation in handedness in human populations. While purely genetic accounts of handedness are highly influential, Laland shows that the best fit to the observed data on human handedness is obtained by a model where genes and culture (in the form of parental shaping of offspring handedness) interact: no purely genetic account fits the data on heritability and cross-cultural variation. In other words, EP-style accounts that ignore cultural influences on behaviour (such as handedness) risk falling at the first hurdle of explaining observed human behaviour.

The second and third case studies deal with situations where culturally transmitted traits (mate preferences in the second case study and niche-constructing capacity in the third) impact on or change the course of biological evolution. Preferences for sexual partners (one of the core areas of EP; e.g. Buss 1994; Miller 2001) can be influenced by the observed

preferences of others (Jones *et al.* 2007), and Laland's (1994) formal modelling work shows that such socially learned mate preferences can generate selection acting on biological evolution that takes the preferred trait to fixation in the opposite sex. Culturally transmitted niche-constructing behaviours can generate selection pressures that drive evolution in directions differing from those that would be favoured by the unmodified environment (Laland *et al.* 2001), suggesting that heavy niche constructors (such as humans) should be less responsive to selection pressures arising from changes in the environment, because they can modify that environment to attenuate those pressures. As Laland points out, this is at odds with the tenet of EP that humans are operating with a set of mental modules adapted for our ancestral environment and possibly maladapted to our current environment—to a large extent, we construct our environment to suit ourselves.

The final article by Smith & Kirby (2008) similarly tackles gene–culture interactions and the EP approach to explaining human behaviour, with a specific focus on language. Language underpins many culturally transmitted human behaviours, but is itself a culturally transmitted system: we learn the language we hear around us as we grow up. Despite this fairly obvious contribution from culture, explanations of language design (why does human language have the particular characteristics it does?) have typically been biological rather than cultural: following the classic EP model, the argument is that language looks the way it does because the mental module dedicated to language, the language faculty, evolved to build in those features, primarily because they are useful for communication (e.g. Pinker & Bloom 1990).

Smith & Kirby argue against the necessity of this strong EP position on language in two ways. First, they review a body of computational work, developed over the past 10 years, which shows that cultural evolution can explain certain aspects of language design. Specifically, a language, like any other cultural system, can only survive repeated transmission if it can be reliably learned, and certain design features of language can be seen as cultural adaptations to these learnability constraints. Second, they show that cultural transmission has the potential to fundamentally alter the sorts of language faculty that natural selection favours—under certain scenarios, selection acting on the language faculty pushes evolution into regions of design space where the language faculty only weakly constrains the structure of language. In other words, not only does cultural evolution potentially offer an alternative explanation for some aspects of language design, but it also potentially changes the extent to which biological evolutionary accounts work at all.

(a) Genes and culture: a summary
The significance of gene–culture coevolutionary theory has not to date been widely grasped in the section of the research community for whom it is most relevant: psychologists concerned with evolutionary explanations of human behaviour. The more reductionist explanations of EP, focusing on biology to the exclusion of culture, hold sway in the broader consciousness, and the final three articles in this section all represent

attempts to remedy this lack of penetration, by either suggesting a synthesis (Wheeler & Clark 2008) or attacking the foundations of EP (Laland 2008; Smith & Kirby 2008). Of course, taking cultural transmission seriously does not offer instant insights into the causes of human behaviour—as highlighted by Laland (2008) and Wheeler & Clark (2008), the relationship between environment, genes and culture is rather intricate and requires us to probe deeper into how we think the various component parts of the theory work and how the component parts interact. These are tough questions and as such lack some of the appeal of clean EP explanations for human behaviour. The challenge, as met in Laland's handedness case study, is to show that coevolutionary theories provide a better fit to observed human behaviour.

4. LOOKING AHEAD
As the articles gathered in this issue show, understanding cultural transmission is key to understanding human behaviour. Many aspects of human behaviour are influenced by social learning, including some of the features that are often taken to differentiate humans from other animals (e.g. complex technologies or language), and purely biological explanations for the evolution of such behaviours, as offered by EP, are therefore deeply problematic. The explosion of interest in the experimental study of social learning and cultural transmission provides a promising and powerful tool for understanding the relationship between cognition and cultural evolution, bridging the gap between theoretical and observational approaches.

One of our goals in editing this theme issue was to provide a snapshot of the state of the field as it currently stands, as a useful reference for researchers already working in this area and a starting point for newcomers. Another was to help drive the field forward, not least by providing such a starting point. Given this second goal, it seems only fair that we should provide some personal thoughts on what we see as the potential near future of the field.

We have already offered some suggestions in the summary sections above on possible lines of development, including: more systematic exploration of the diffusion chain methodology (e.g. wider use of the methods summarized by Whiten & Mesoudi and explicit testing for convergence of results across experimental designs, greater coverage of species and social learning tasks); improving interaction between theoretical and experimental results; following Laland's lead in challenging EP on conceptual and explanatory grounds. We would highlight one further overarching objective here, which recurs throughout the articles in this issue: the desirability of a tighter coupling between the three tools of theoretical model, experimental model and real-world data.

Several of the articles here explicitly address this triumvirate of approaches. McElreath *et al.* provide a method for linking mathematical models (both evolutionary and behavioural) to real behaviour, albeit in the laboratory, and argue that this same technique can be extended further, to explore and explain cultural behaviour in the real world. Griffiths *et al.* similarly

provide integrated formal and experimental models (based at present around linear diffusion chains, although other forms of transmission could be explored), and some suggestions regarding the real-world cultural phenomena these models relate to. Working from the other end, Whiten & Mesoudi suggest that the divide between real-world and laboratory studies of cultural evolution could be bridged by running experimental techniques in the field. In the ideal world, all these techniques might be brought to bear on a given cultural behaviour of interest. For example, we might first identify the phenomenology of a real-world human behaviour which we expect involves social learning. Formal models of possible social learning strategies or inductive biases that aim to explain that behaviour would be fitted to the real-world behaviour, providing an indication of which sort of social learning strategy or bias best describes that phenomenon. Moving to experimental approaches, laboratory analogues and field experiments could provide an opportunity to examine model predictions, and therefore both potentially falsify models and also unveil added levels of detail on the social learning processes underpinning the behaviour of interest. Finally, further cultural or acultural experiments could be used to tease apart the fine details of the social learning mechanisms, before we return to the real world to establish whether the predictions of the newly developed model are consistent with the details of the real-world behaviour.

Taking this kind of multi-pronged approach to explaining human behaviour is of course extremely challenging, not least because it requires a research team with a detailed grasp of the real-world behaviour of interest, familiarity with a range of experimental methodologies and access to sophisticated mathematical modelling techniques. While we are much more interested in getting on with doing the work than agonizing over frameworks and terminology, it is a truism that one of the barriers to this kind of interdisciplinary research is the absence of common expectations and terminology. At the very least, we hope that this issue will provide the foundations for the shared vocabulary and body of knowledge required by this approach to explaining the role of cultural transmission in shaping human behaviour.

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