Chapter 4

STUDYING CULTURAL TRANSMISSION WITHIN AN INTERDISCIPLINARY CULTURAL EVOLUTIONARY FRAMEWORK

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Introduction

Cultural transmission is the process by which knowledge, beliefs, skills, practices, norms, values and other forms of non-genetic information are passed from individual to individual via social learning mechanisms such as imitation and teaching. This surely places cultural transmission at the heart of pretty much every social science discipline, not just anthropology but also psychology, sociology, linguistics, history, political science and economics. Yet cultural transmission is surprisingly under-appreciated in many of these disciplines. Often, cultural influences on human behaviour are ignored or downplayed in favour of explanations in terms of individual responses to non-social stimuli, with no explicit consideration of social influence. Within anthropology, for example, cultural ecologists (Steward 1955), cultural materialists (M. Harris 1989) and human behavioural ecologists (Winterhalder and Smith 2000) all tend to explain human behaviour in terms of individual adaptation to local environmental conditions rather than as the result of cultural transmission. Similarly, cognitive psychologists typically study how single individuals understand and learn about the world largely independently from other people, while economists of the 'rational choice

theory' school assume that people individually calculate the costs and benefits of different behaviours with little cultural influence (see Gintis 2007). Other disciplines stress the role of genetic rather than cultural inheritance, such as some evolutionary psychologists' assertion that much variation in human behaviour is generated by evoked genetic responses to different environmental conditions ('evoked culture') rather than resulting from cultural transmission (Tooby and Cosmides 1992; Gangestad, Haselton and Buss 2006). None of these popular and reputable approaches to the study of human behaviour place much importance on cultural transmission.

In certain respects this unwillingness to explain human behaviour in cultural terms is understandable given the often vague and unscientific way in which cultural transmission is conceptualized in the social sciences, including social anthropology. It is often assumed that people somehow absorb the cultural beliefs, values, norms and such like of the previous generation by some mysterious, almost magical process of 'enculturation', 'acculturation' or 'socialization'. It is, for example, argued that 'acculturation occurs through a process of constant immersion of each person in a sea of cultural phenomena, smells, tastes, postures, the appearance of buildings, the rise and fall of spoken utterances' (Fracchia and Lewontin 1999: 73) or 'what each generation contributes to the next are ... the specific circumstances under which successors, growing up in a social world, can develop their own embodied skills and dispositions, and their powers of awareness and response' (Ingold 2000: 237-38). Such vague statements are far from conducive to the generation of specific, testable, refutable hypotheses (how does one quantify and attempt to measure the consequences of a 'sea of postures', for example?), and it is little wonder that psychologists and economists reject cultural explanations for human behaviour on these very grounds (see for example Tooby and Cosmides 1992: 41; Guiso, Sapienza and Zingales 2006: 23). There is little attempt in the social sciences to explain the population-level, intergenerational persistence of ideas and beliefs in terms of specific and measurable individual-level processes - who is copying what idea or belief from whom, and when. In large part this stems from the move within the social sciences towards social constructionist, interpretivist and hermeneutic stances, and the associated anti-reductionist unwillingness to explain cultural and social phenomena in terms of lower-level causes (see Slingerland 2008).

Yet this is not to say that there is no robust scientific evidence for the influence of cultural transmission on human behaviour. On the contrary, there is a growing body of rigorous and fully scientific crosscultural research showing substantial cultural influence on various aspects of human behaviour, albeit often coming from experimental psychology and economics rather than anthropology (Heine and Norenzayan 2006; Henrich, Heine and Norenzayan 2010). Significant cross-cultural variation has been demonstrated in levels of aggression (Cohen et al. 1996), vulnerability to perceptual illusions (Segall, Campbell and Herskovits 1963), categorization of, and memory for, objects (Nisbett et al. 2001), self identity (Heine et al. 1999) and cooperation in economic games (Henrich et al. 2005), amongst other fundamental psychological and behavioural phenomena. This variation cannot be explained by individual adaptation, given that it seldom corresponds to local ecological conditions (Hewlett, De Silvestri and Guglielmino 2002), and cannot be explained in terms of genetic differences given evidence that immigrants adopt the norms of the local society in just one or two generations, too fast for genetic adaptation to have occurred (Heine and Norenzayan 2006). In sum, there is robust evidence that numerous aspects of human behaviour and cognition are significantly shaped by cultural transmission.

Cultural Evolution

The foregoing discussion presents a problem: there is increasingly robust evidence that culturally transmitted information significantly shapes various aspects of human behaviour, yet most social scientists either ignore cultural transmission entirely or conceptualize it in vague, non-scientific terms that preclude the generation and testing of refutable hypotheses. I suggest that an approach that can address these problems is that of 'cultural evolution' (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Henrich and McElreath 2003; Mesoudi 2011; Mesoudi, Whiten and Laland 2006). This approach views cultural change (i.e. changes in culturally transmitted beliefs, norms, values, etc.), as a Darwinian evolutionary process that acts in parallel to genetic/biological evolution. Before outlining the advantages of this approach, it is useful to specify exactly what is (and is not) meant by 'Darwinian evolutionary process'.

Darwin explained the diversity and complexity observed in the natural world in terms of just three simple principles (Lewontin 1970): (1) *variation*: individuals within a population vary in their characteristics; (2) *differential fitness*: due to limited resources, not all individuals are equally likely to survive and reproduce, and their likelihood of reproduction is determined at least in part by their characteristics; and (3) *inheritance*: offspring resemble their parents in their characteristics more than a randomly selected individual. Given these three empirically demonstrable principles, over time those characteristics that increase an individual's chances of survival and reproduction

increase in frequency in the population, ultimately combining with other beneficial traits to form complex adaptations such as eyes and wings, and causing different populations to diverge to generate the diversity of species we see today.

The theory of cultural evolution rests on the premise that cultural change exhibits these same Darwinian principles of variation, differential fitness and inheritance (Mesoudi, Whiten and Laland 2004). First, cultural traits, such as words, technological innovations, beliefs and attitudes, vary across individuals within a population. Second, not all traits are equally likely to persist or get passed on to other individuals - some ideas are more memorable than others, some practices more effective, some customs more socially acceptable. Third, traits are inherited from individual to individual via cultural transmission mechanisms such as imitation and teaching. Over time, those cultural traits that are better at being transmitted (the more memorable, more effective, more socially acceptable, etc.) increase in frequency in the population, ultimately combining with other beneficial traits to form complex cultural adaptations such as telescopes and aeroplanes, and causing different societies to diverge to generate the cultural diversity we see in the ethnographic and historical record.

Importantly, a Darwinian theory of cultural evolution makes no further claims about the mechanisms by which these basic principles operate, regarding how variation is generated, how it is transmitted and what causes differential fitness between variants. For example, we now know that biological inheritance is particulate, that is to say it involves the transmission of discrete packages of information, genes, in an all-or-nothing fashion. Yet this is not a necessary requirement of Darwinian evolution. Indeed, Darwin himself knew nothing of genes, and believed (incorrectly, for the biological case) that continuous, non-discrete biological traits blended when transmitted. In many cases there is good evidence that the mechanisms underlying biological and cultural change are quite different. Particularity of variation is a good example of this: whereas genetic inheritance is particulate, cultural transmission in many cases appears to be non-particulate. These differences are explicitly incorporated into cultural evolution models, as is discussed below.

It is also important to note that cultural evolutionary theory is not simply an extension of sociobiology, evolutionary psychology or other disciplines seeking to explain human behaviour primarily in terms of genetic evolution, as is sometimes claimed – for example, Ingold's grouping of the cultural evolutionary approach taken by Mesoudi et al. (2006) with 'neo-Darwinian "evolutionary biology" ... evolutionary psychology and memetics' (Ingold 2007: 14). Although some theoretical analyses of gene-culture co-evolution seek to explain the origin of cultural transmission dynamics in terms of genetic evolution (e.g. Boyd and Richerson 1989), many other analyses focus solely on the cultural transmission dynamics themselves. Indeed, theoretical analyses suggest that the very reason why cultural transmission is genetically adaptive is because it allows genes to forego direct control over behaviour, and permits organisms to acquire adaptive behaviour culturally instead of genetically, given that cultural learning can better respond to rapid environmental change than genetic evolution (Boyd and Richerson 1995; Aoki, Wakano and Feldman 2005). Moreover, because of this uncoupling of genetic and cultural evolution, the latter can often lead to the spread of genetically maladaptive cultural traits (Boyd and Richerson 1985). Cultural evolution is therefore explicitly *not* genetically reductionist (Plotkin 1995).

The Advantages of Analysing Cultural Transmission as an Evolutionary Process

That both biological and cultural change exhibit the same basic principles is not simply an academic curiosity of interest to philosophers of science. Viewing cultural change as a Darwinian process means that culture can be analysed using similar evolutionary methods to those used by biologists to understand biological/genetic change, suitably modified to incorporate the differences between biological and cultural change. In many cases these evolutionary methods result in significantly improved understanding of cultural phenomena than traditional, non-evolutionary social science methods. Perhaps the most important conceptual tool is what Mayr (1982) has called 'population thinking'. In the biological case this is where population-level 'macroevolutionary' change, such as speciation and adaptation, is explained in terms of individual-level 'microevolutionary' processes, such as different forms of selection (e.g. directional, stabilizing, sexual), genetic drift, mutation, recombination, migration and so on. In the early part of the twentieth century, population geneticists such as Fisher, Haldane and Wright constructed formal mathematical models that explicitly linked microevolutionary processes to specific macroevolutionary patterns. In a typical model of this kind, a hypothetical population of individuals is specified, with these individuals varying in their genetic traits. The modeller then specifies a set of quantifiable microevolutionary processes, such as selection or drift, that act to change the genetic variation in the population over successive time periods. Mathematical techniques are used to determine the long-term, population-level dynamics of different microevolutionary processes, such as whether a particular process increases or decreases genetic variation over time. Back in the 1920s and 1930s, these formal analyses resolved outstanding problems or misunderstandings that had hitherto hindered progress in biology. One such was Fisher's (1930) mathematical demonstration that the existence of discrete traits that are transmitted in an all-or-nothing fashion (i.e. genes), as had been demonstrated earlier by experimental geneticists such as Gregor Mendel, was nevertheless consistent with continuous phenotypic variation (e.g. in height or fur colour) because these phenotypic traits were determined by multiple discrete genes rather than a single gene. In other words, the model linked microevolutionary processes discovered experimentally in the lab (particulate non-blending inheritance) to macroevolutionary phenomena observed in the world by naturalists (continuous variation in a trait in the population as a whole).

In the 1980s, Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) used similar mathematical modelling techniques to analyse cultural evolution. These models typically specify a population of individuals, with each individual varying in their cultural traits, and specifies quantifiable cultural selection and cultural transmission processes that act to change that variation over successive periods of time. Mathematical techniques or computer simulations are used to determine the long-term, population-level dynamics, such as whether a particular trait will go to fixation or coexist with other traits at equilibrium, or the diffusion dynamics of different transmission processes. As in biology, these models have two key benefits: (1) they force the researcher to specify in precise and quantitative terms exactly how a particular cultural transmission process acts to change the frequency of some cultural trait over time, in contrast to the vague notion of 'acculturation' or 'socialization' encountered above, and (2) they allow the researcher to explore the long-term, population-level consequences of different cultural transmission processes with a precision that is simply not possible with purely verbal, informal reasoning.

Importantly, Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) recognized in these models that the details of cultural microevolution may be very different to those of biological microevolution. In many cases they drew on existing research in social psychology, social anthropology, sociology and sociolinguistics when constructing their modified models. First, whereas biologists have established that genetic inheritance is of high fidelity and involves the all-or-nothing transmission of discrete units of inheritance (i.e. genes), Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) instead modelled cultural transmission as potentially being of much lower fidelity. This is consistent with experimental findings from social psychology that cultural transmission is a process of lowfidelity transformation rather than high-fidelity replication (Bartlett 1932), and in some cases involves the blending of continuously varying cultural traits rather than discrete gene-like units, as observed by sociolinguists for dialect change (Lehmann 1992). Second, whereas biologists model genetic inheritance as strictly non-Lamarckian, with acquired characteristics never directly inherited by offspring, Boyd and Richerson (1985) modelled the Lamarckian-like cultural process of 'guided variation', where people systematically transform culturally acquired representations towards a pre-existing favoured form, and then transmit this modified form to another person. Third, whereas genetic inheritance is largely parent-to-offspring, or 'vertical', in vertebrate species (although horizontal gene transfer is common in plants and bacteria), Cavalli-Sforza and Feldman (1981) modelled not only vertical cultural transmission (from parents) but also oblique (from unrelated members of the parental generation) and horizontal (from unrelated members of the same generation) cultural transmission, consistent with evidence that much human cultural transmission is non-vertical (J. Harris 1995). Moreover, obligue and horizontal transmission was modelled as either one-to-one, representing direct faceto-face instruction, or one-to-many, as in teaching or the mass media (Cavalli-Sforza and Feldman 1981). Fourth, Boyd and Richerson (1985) modelled three types of cultural transmission: (1) content-biased cultural transmission, where certain traits are intrinsically more attractive or memorable than others for psychological reasons, as has been proposed by cognitive anthropologists (Sperber and Hirschfeld 2004); (2) conformist and anti-conformist cultural transmission, where people preferentially adopt the most or least common trait in the population as has been observed by social psychologists (Jacobs and Campbell 1961; Moscovici, Lage and Naffrechoux 1969); and (3) prestige-biased cultural transmission, where people preferentially adopt the traits exhibited by particularly successful or prestigious individuals, consistent with research in social psychology (Bandura, Ross and Ross 1963), socio-linguistics (Labov 1972) and sociology (Rogers 1995). Finally, Cavalli-Sforza and Feldman (1981) modelled the cultural analogue of genetic drift, where cultural traits are copied entirely at random with no intrinsic differences between traits, and of migration, where people move across social group boundaries and take their traits with them.

Just as population geneticists determined the population-level consequences of biological microevolutionary processes, Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) modelled the population-level macroevolutionary consequences of these cultural microevolutionary processes. In other words, Darwinian population thinking and formal mathematical models that treat cultural change as a Darwinian evolutionary process allow links to be made between the micro- and the macro-levels in the social/behavioural sciences – the former studied by experimental psychologists and economists in the lab or ethnographers in the field concerned with the details of who learns what from whom, and the latter studied by ethnologists, archaeologists, sociologists, historians and historical linguists concerned with long-term cultural change or between-society cultural variation. This micro-macro divide has been a perennial problem in the social sciences, and previous attempts to bridge the gap (e.g. Schwartz and Mead 1961) have been informal and consequently ultimately unfruitful. The formal evolutionary models of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) allow the micro-macro divide to be bridged more effectively and potentially to synthesize these various macro and micro branches of the social sciences (Mesoudi, Whiten and Laland 2006; Mesoudi 2007, 2011).

Case Study: Prehistoric Projectile Point Evolution in the Great Basin

To illustrate the value of decomposing population-level macroevolutionary patterns of cultural variation down into underlying microevolutionary cultural transmission biases, I will discuss a case study involving projectile points - stone artefacts such as arrowheads and dart tips. The points in question are from the Great Basin region of the south-western United States and date to around ad 300-600. Archaeologists Bettinger and Eerkens (1999) documented systematic differences in the variation in the points found across two sites in this region. Points found at a site in present-day central Nevada were found to exhibit little variation in their attributes, such as length, width, thickness and shape, such that only a few combinations of attribute values occurred. For example, points that were corner-notched (i.e. had hook-like notches in their base that prevented them from coming loose when embedded in flesh) were almost always thin and light: in other words, the two attributes shape and thickness were linked. In contrast, points from another site in eastern California featured no systematic linkage between attributes; points that were cornernotched were no more likely to be thick than thin, for example. This generated far more within-site diversity in California than in Nevada.

Having ruled out potential explanations for these differences in point variation across the two sites in terms of raw material or prey, Bettinger and Eerkens (1999) turned to an explanation in terms of the aforementioned cultural transmission biases. Specifically, they argued that point designs in California originally spread via guided variation, where people acquire a design from another person but then modify that design according to their own idiosyncratic individual learning styles. This latter individual learning would have eliminated any links between attributes, as different people modified different attributes separately. In the Nevadan site, on the other hand, Bettinger and Eerkens proposed that point designs were copied via prestige-biased (or more generally 'indirect') cultural transmission, where people acquire a design from a single successful or prestigious individual with no further modification of that design (Boyd and Richerson 1985). If everyone in a group is copying the same successful model, then soon everyone will have the same point design and attributes will be linked in the way documented in Nevada. In sum, Bettinger and Eerkens had explained population-level cultural variation (linked vs. unlinked point attributes) in terms of individual-level cultural transmission biases (prestige bias vs. guided variation).

Michael O'Brien and I have extended Bettinger and Eerkens' (1999) work by simulating their proposed cultural transmission scenario both experimentally in the psychology lab and theoretically using agent-based simulations (Mesoudi and O'Brien 2008a, 2008b). The value of theoretical simulations is that they allow us to check formally Bettinger and Eerkens' intuitions regarding the population-level consequences of their proposed transmission biases in this specific case, while the value of experimental simulations is that they can tell us whether people can and do engage in these proposed transmission biases. Barring the invention of a time machine, neither of these is possible with purely archaeological/historical methods.

In the lab experiments (Mesoudi and O'Brien 2008a), participants were faced with the task of designing a 'virtual arrowhead' via a computer programme by entering values for its attributes (length, width, thickness, shape and colour). They could then test their design by going on a series of 'virtual hunts' during which they got feedback on its effectiveness in the form of calories obtained. Participants were placed in groups of five or six, and different phases simulated the different transmission biases proposed by Bettinger and Eerkens (1999). An initial 'prestige bias' phase allowed the participants to copy the arrowhead design of one of a group of previous players of the game, having been given information about the previous players' success. The vast majority of participants during this phase did indeed choose to copy the most successful hunter, confirming previous social psychological findings that people prefer to copy prestigious or successful individuals. A subsequent 'guided variation' phase comprised a series of hunts, during which there was no opportunity to copy other group members, relying instead solely on individual trial-and-error learning. As Bettinger and Eerkens had predicted, arrowhead designs during the prestige bias phase featured significantly lower attribute variation than arrowhead designs following the guided variation phase, supporting their proposed transmission scenario.

However, the experiments (Mesoudi 2008; Mesoudi and O'Brien 2008a) and theoretical models (Mesoudi and O'Brien 2008b) revealed an important limitation on Bettinger and Eerkens' (1999) hypothesized scenario. In designing our experiments we were forced to specify fitness functions for the virtual arrowheads – that is to say, mathematical expressions that translate attribute dimensions into calorific payoffs. One possibility is a simple linear, unimodal set of functions such that there is a single optimal arrowhead design that gives the highest payoff, with payoffs declining steadily the further the design gets from this optimum. Agent-based simulations (Mesoudi and O'Brien 2008b) revealed a problem with this assumption, in that during the 'guided variation' phase each isolated individual learner eventually converged on the same single optimal arrowhead design through individual trial-and-error learning. This resulted in low cultural variation in the guided variation phase, exactly the same end result as in the prestige bias phase, and counter to Bettinger and Eerkens' proposed scenario. Instead, we assumed in the experiments multimodal fitness functions. To borrow a biological concept introduced by Wright (1932), we can envisage arrowhead fitness as a landscape where the height of the landscape represents fitness and each coordinate in the landscape represents a different combination of attributes (length, width, thickness, etc.). The unimodal functions generate a single peak in this landscape with all points leading uphill to the single optimum. Multimodal functions, on the other hand, feature several peaks of different heights representing several locally optimal designs of different fitness. Assuming this multimodal adaptive landscape meant that variation was not eliminated during the guided variation phase, because individual learners became stuck on different locally optimal peaks. Any deviation from their chosen peak reduced their payoff, even though there may have been, unbeknownst to them, a higher peak (a better arrowhead design) elsewhere in the design space. Prestige bias still eliminated variation in multimodal landscapes because each member of the group copied the most successful group member, namely the one who had found the highest peak in the landscape, such that every group member converged on this same peak. In sum, Bettinger and Eerkens' hypothesis only works if one is willing to assume a multimodal adaptive landscape underlying projectile point evolution.

But is this assumption valid? Experimental studies conducted by Cheshier and Kelly (2006) suggest that it may be. They fired replica arrowheads into animal carcasses and measured their durability and penetrative power, finding tradeoffs between different demand characteristics. For example, long and thin arrowheads were easier to aim and more likely to penetrate the animal's skin, but created smaller wounds that would have been less likely to kill the animal. Wide and thick arrowheads, on the other hand, were more difficult to aim and fire, but when they did hit the target they created larger wounds that would have been more likely to kill the animal. This suggests the existence of at least two peaks: a 'long, thin, penetrative' peak and a 'wide, thick, wounding' peak. Further experimental and ethnographic studies might quantitatively determine the exact shape of the adaptive landscape underlying arrowhead fitness, informed by the aforementioned simulations.

In sum, this series of studies illustrates the value of (1) explaining population-level patterns such as between-site differences in artefact diversity in terms of precisely specified individual-level cultural transmission processes, and (2) using a range of methods - archaeological, experimental and theoretical modelling – to explore the validity and applicability of these individual-level explanations. The traditional fractionated state of the social sciences has frequently hindered such interdisciplinary exchange of findings, methods and concepts. However, the micro-macro bridge facilitated by Darwinian population thinking encourages such links. Both lab experiments and computer simulations, for example, have the advantage over archaeological/ historical methods of allowing us to directly observe people copying one another according to known transmission biases, to obtain complete and uninterrupted data records, and to manipulate variables (e.g. fitness functions) in order to explore the limits of the proposed explanation. Of course, what we gain in control and manipulation when conducting simulations is offset by what we lose in external validity: the people participating in experiments (typically undergraduates) are very different from the prehistoric hunters who would have made the original points, and the computer-based task employed in the lab is hugely simplified compared to the real-life task of hunting and manufacturing points. But by constantly cross-checking experimental and theoretical results with archaeological findings, and vice versa, as illustrated above, hopefully these strengths and weaknesses will complement one another.

Other Micro-Macro Links

In addition to the case study discussed above, several other studies have linked the aforementioned microevolutionary processes to real-world data regarding specific cultural phenomena (Mesoudi 2007). For example, Henrich (2001) has shown theoretically that content-biased cultural transmission, where people preferentially copy 'more-effective' traits exhibited by other people, causes novel beneficial traits to diffuse through populations in a distinct S-shaped fashion, where uptake is slow at first, then rapid, then slow again. In contrast, guided variation, where people independently modify acquired traits according to individual trial-and-error learning, generates r-shaped diffusion curves which do not exhibit the initial slow uptake. Given that sociologists have observed S-shaped diffusion curves for the vast majority of real-life cases of technological diffusion (Rogers 1995), Henrich (2001) suggests that content-biased transmission is more important in real-life technological cultural change than guided variation, in contrast to the assumptions of many economists and sociologists who emphasize individual learning over cultural transmission.

In another example, cultural drift – the copying of cultural traits entirely at random with no selection or transmission biases – has been shown theoretically to generate a distinct 'power-law' distribution of cultural traits, where a small number of traits are extremely popular and a large number of traits are very rare (Bentley, Hahn and Shennan 2004), in contrast to non-random cultural transmission biases such as conformity and anti-conformity which do not generate power laws (Mesoudi and Lycett 2009). The power-law distribution characterizes several real-life cultural datasets such as first names, dog breeds, patent and scientific article citations, and prehistoric pottery decorations, suggesting that each of these phenomena are governed by a drift-like random copying bias (Bentley, Hahn and Shennan 2004).

Other cultural evolution researchers have begun to use the ethnographic method to test for the presence and form of microevolutionary processes in small-scale societies. Tehrani and Collard (2009), for example, used the ethnographic method to address a long-standing issue in anthropology over whether cultural macroevolution is branching or blending. Kroeber (1948) famously argued that whereas biological macroevolution is a branching, tree-like process, because when two species diverge they stay separated, cultural macroevolution features the frequent transmission of customs, practices, words and beliefs across societal boundaries such that it better resembles a reticulated bush than a bifurcating tree. This purported difference has subsequently been used to argue against the application of phylogenetic methods to reconstruct cultural macroevolution (e.g. Moore 1994), which were originally designed by biologists to deal with branching biological datasets (although see Collard, Shennan and Tehrani 2006). Tehrani and Collard (2009) argued that this criticism actually rests on untested assumptions concerning the extent of vertical vs. horizontal transmission across social group boundaries at the microevolutionary level. Their ethnographic study of Iranian weavers found that women typically learned weaving techniques exclusively from their mothers, indicating vertical cultural transmission, and learned weaving patterns typically from other members of the community, indicating horizontal transmission. However, even in the latter case the weaving patterns were seldom learned from women from other social groups due to norms restricting the movement of women. So even with substantial horizontal cultural transmission at the individual level, a tree-like branching pattern of textile pattern macroevolution was maintained because of impermeable social group boundaries. Again, this study shows how knowledge of cultural microevolutionary cultural transmission biases can inform our understanding of cultural macroevolution.

Conclusions

Studying cultural transmission within a Darwinian evolutionary framework has several methodological advantages. Darwinian population thinking encourages researchers to think about the long-term, population-level consequences of different cultural transmission processes. Formal evolutionary methods borrowed from population genetics force researchers to quantify in precise terms exactly how cultural transmission acts to change cultural variation in a population, and to provide tools that can be used to determine the long-term, populationlevel cultural dynamics generated by different transmission processes with a precision not possible with purely verbal, informal notions of transmission. Finally, in bridging the micro-macro divide in this way, new interdisciplinary avenues open up as the transmission processes studied in the lab by psychologists and experimental economists are used to explain patterns and trends documented in the archaeological and ethnographic record by anthropologists, sociologists and historians. The consequent exchange of theories, concepts and methods across what are, traditionally, impermeable disciplinary boundaries promise to stimulate a similar 'evolutionary synthesis' to that which occurred in evolutionary biology in the 1930s and 1940s in response to similar formal evolutionary methods that bridged biological microand macro-evolution (Mesoudi 2007, 2011). Given the subsequent success of evolutionary biologists in explaining biological diversity and complexity, it is hoped that similar success will attend the study of cultural change in the coming years.

An evolutionary framework also points to potential areas in which research efforts might be most profitably directed. The biggest postsynthesis advance in biology was Watson and Crick's discovery of the structure of DNA, constituting a molecular basis for genetic inheritance. The equivalent underlying basis of cultural transmission would concern how information is represented in the brain, and how that information is transmitted from one brain to another at the neural level. Yet neuroscientists currently have little understanding of such processes. Initial findings related to 'mirror neurons', neurons that respond both to oneself performing an action and observing another person performing that same action (Rizzolatti and Craighero 2004), provide a preliminary glimpse of a potential neural mechanism for imitation (Rizzolatti et al. 2002), although this is just a very basic starting point and applies to manual skills such as tool use rather than cognitive representations such as beliefs and values.

At the other end of the spectrum, there is a need to explain the existence of large-scale cooperative cultural institutions such as business firms and nation-states. Some cultural evolution researchers have explained these institutions as products of a process of cultural group selection (Henrich 2004; Cordes et al. 2008; Boyd and Richerson 2009), whereby cultural transmission processes such as conformity generate cohesive social groups that then compete with one another, with more cooperative groups selected over less cooperative groups. This macroevolutionary process of cultural group selection may then generate novel selection pressures at the microevolutionary level, such as the spread of group-beneficial cultural practices and beliefs, in an instance of macroevolution shaping microevolution rather than vice versa as is commonly considered. Yet the precise cultural transmission processes that permit the formation of stable largescale institutions have yet to be identified. Although the challenges of explaining cultural phenomena at multiple levels, from neurons to institutions, all within a single explanatory framework, may seem insurmountable, the beginnings of such a project can be detected in the interdisciplinary research that is currently being facilitated by the synthetic cultural evolutionary framework outlined here.

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