CHAPTER 38

Dual-inheritance theory: the evolution of human cultural capacities and cultural evolution

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38.1. Introduction

In the early 1930's Wintrop and Luella Kellogg (1933) began co-rearing their 10.5-month-old son, Donald, with a 7.5-month-old female chimpanzee named Gua. The Kelloggs expected that Gua, with the chimpanzee's popular reputation for aping, would acquire numerous behaviors and practices via imitation from both Donald and themselves. Unexpectedly, however, while Gua did finally acquire a few human patterns (e.g. combing his hair), Donald was the one who began to imitate the chimpanzee in some dramatic ways. Following Gua, Donald acquired the habits of knuckle walking (which he continued well after achieving full bipedality), chewing on shoes, scraping his teeth against interior walls, and hard biting. Donald even adopted some stereotypical chimpanzee food grunts, barks and hoots, using a particular bark as the word for orange. Thus, it was the human who did most of the aping.

People in many small-scale societies believe that a human fetus is formed by many repeated ejaculations of sperm into the womb. This belief means that a child can have multiple fathers, who share paternity according to the number of times they had sex with the mother prior to birth (in anthropological parlance, 'partible paternity'). In response to this cultural belief, women in many of these societies actively seek out extra-marital copulations, often to provide their child with extra fathers. And, while male jealously from the husband is sometimes a problem, it is regarded as socially inappropriate and thus suppressed. Detailed statistical analyses from two such societies, the Barí of Venezuela (Beckerman *et al.*, 2002) and Aché of Paraguay (Hill and Hurtado, 1996), show that the optimal number of fathers for a child's survival is more than one. These 'other fathers' (non-husbands of mom) provide resources, in the form of fish and meat, to their offspring and the mothers, both during pregnancy and while the child is growing up. Interestingly, since much of the sex associated with 'extra fathers' occurs after conception, many of these social fathers cannot be the genetic fathers. Culturally transmitted beliefs in partible paternity have been recorded in various linguistically unrelated societies across lowland

South America, as well as in New Guinea, by multiple researchers over the last 75 years (Beckerman and Valentine, 2002).

These examples illustrate two key points about humans. First, while chimpanzees do show some capacities for imitative learning (Horner and Whiten, 2005; Whiten *et al.*, 2005), their cultural transmission shows substantially lower degrees of fidelity, frequency and internal motivation. Compared to chimpanzees, humans are "imitation machines" (Tomasello, 1999). More generally, while only limited social learning abilities are found elsewhere in nature, social learning in our species is high fidelity, frequent, internally motivated, often unconscious, and broadly applicable. Humans learn, via observation of others, everything from motor patterns to goals and affective responses, in domains ranging from tool-making and food preferences to altruism and suicide. We will refer to this form of social learning, which may be particular to humans, as cultural learning.

The combination of both the high fidelity and frequency of social learning in our lineage has generated *cumulative cultural evolution*, which may exist to any significant degree only in our lineage: this is the process through which learning builds a body of culturally transmitted information (behaviour, practices, beliefs, etc.) in a population in such a way that locally adaptive aspects aggregate over time, with the accumulation of successful additions and modifications. Cumulative cultural evolution builds adaptive practices, tools, technique, and bodies of knowledge (about animal behaviour, medicinal plants, etc.) that *no single individual could figure out* in their lifetime, and that can only be understood as products of cultural evolutionary processes. Paleoarchaeology suggests that substantial cumulative cultural evolution has likely been occurring for at least the last 280 000 years (McBrearty and Brooks, 2000), and is thus a key element in understanding human genetic evolution.

Our second point is illustrated by societies with partible paternity: culturally acquired beliefs can shape how we understand the world in ways that influence decisions, including decisions arising from essential aspects of our evolved cognition. To invest in their offspring, for example, males need to figure out which offspring are theirs. Evidence indicates that we use a variety of cues to identify our kin, including phenotypic similarity and scent (DeBruine, 2002; Thornhill *et al.*, 2003), but humans also apparently use their culturally transmitted beliefs about kinship and reproduction. More generally, there is also evidence that culture influences our spatial cognition, perception of visual illusions (Segall *et al.*, 1966), judgement (Nisbett, 2003), risk preferences (Henrich and McElreath, 2002), and notions of fairness or preferences for equity (Henrich *et al.*, 2004).

Given all this, we think that a proper evolutionary framework for studying human psychology and behaviour needs to reckon with our species' heavy reliance on cultural learning and cultural evolved adaptations. In providing such a framework, *dual-inheritance theory* (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; for similar approaches also see Durham, 1991; Laland *et al.*, 2000) aims to incorporate these and other aspects of human culture under the Darwinian umbrella by focusing on three key concepts:

1. *Cultural capacities as adaptations.* Culture, cultural learning and cultural evolution arise from genetically evolved psychological adaptations for acquiring ideas, beliefs, values, practices, mental models, and strategies from other individuals by observation and inference. Thus, the first step is to use the logic of natural selection to theorize about the evolution and operation of our cultural learning capacities.

2. *Cultural evolution.* Our cultural learning mechanisms give rise to a robust second system of inheritance (cultural evolution) that operates by different transmission rules than genetic inheritance, and can thus produce phenomena not observed in other, less cultural, species. Theorizing about this process requires taking what we know about human cultural learning and human cognition, embedding these into evolutionary models that included social interaction, and studying the emergent properties of these models. This approach allows researchers to cobble up from psychology and individual decision-making to sociology and population-level phenomena.

3. *Culture–gene coevolution*. The second system of inheritance created by cultural evolution can alter both the social and physical environments faced by evolving genes, leading to a process termed *culture–gene coevolution*. For example, suppose that the practice of cooking meat spread by social learning in ancestral human populations. In an environment of 'cooked meat', natural selection may favour genes that shorten our energetically costly intestines and alter our digestive chemistry. Such a reduction of digestive tissue may have freed up energy for more 'brain building'. In this way, human biology is adapting to culturally transmitted behaviour.

38.2. **Concept 1: evolved psychological mechanisms for cultural learning**

Our approach to understanding culture begins by considering what kinds of cognitive learning abilities would have allowed individuals to efficiently and effectively extract adaptive ideas, beliefs, and practices from their social worlds in the changing environments of our hunter-gatherer ancestors. This approach diverges from mainstream evolutionary psychology in its emphasis on the *costly information hypothesis* and on the evolution of specialized *social* learning mechanisms. The costly information hypothesis focuses on the evolutionary trade-offs between acquiring accurate behavioural information at high cost and gleaning less accurate information at low cost. By formally exploring how the costly information hypothesis generates trade-offs in the evolution of our social learning capacities, we can generate predictive theories about the details of human cultural psychology. When acquiring information by individual learning is costly, natural selection will favour cultural learning mechanisms that allow individuals to extract adaptive information—strategies, practices, heuristics and beliefs—from other members of their social group at a lower cost than through alternative individual mechanisms (like trial-and-error learning). Human cognition probably contains numerous heuristics, directed attentional biases, and inferential tendencies that facilitate the acquisition of useful traits from other people.

Such cultural learning mechanisms can be categorized into (i) *content biases* and (ii) *context biases*. Content biases, or what Boyd and Richerson (1985) have called *direct biases*, cause us to more readily acquire certain beliefs, ideas or behaviours *because* some aspect of their content makes them more appealing (or more likely to be inferred from observation). For example, imagine three practices involving different additives to popcorn: the first involves putting salt on popcorn, the second favours adding sugar, and the third involves sprinkling chalk dust on the kernels. Innate content biases that affect cultural transmission will guarantee that chalk dust will likely not be a popular popcorn additive in any human society. Both salt and sugar have positive innate content biases for sensible evolutionary reasons: foods with salty or sugary flavours were important sources of scarce nutrients and calories in ancestral human environments. Thus, natural selection favoured a bias to acquire a taste for salty and sweet foods so that we would be motivated to acquire and eat them. Of course, if you grew up in a society that only salts its popcorn, you may steadfastly adhere to your salting preference even when you find that sugar is the standard popcorn seasoning in other societies. Thus, human food preferences are simultaneously culturally learned and influenced by innate content biases.

Content biases may be either reliably developing products of our species-shared genetic heritage (i.e. innate) or they may be culture specific. In considering the influences of innate biases (such as those for salty or fatty foods), keep in mind that evolutionary products like human minds are likely to contain accidental by-products and latent structures that create biases for fitness-neutral behaviours, ideas, beliefs and values. Boyer (2001) details one kind of by-product content bias in his explanation for the universality of certain religious concepts (like ghosts).

On the cultural side, people may acquire beliefs, values and/or mental models that then act as content biases for other aspects of culture. That is, having acquired a particular idea via cultural transmission, a learner may be more likely to acquire another idea, because the two 'fit together' in some cognitive or psychological sense. For example, believing that a certain ritual in the spring will increase the crop harvest in the summer might favour the acquisition of a belief that a similar ritual will increase a woman's odds of conception, a healthy pregnancy, and/or of successfully delivering a robust infant.

Context biases, on the other hand, exploit cues from the 'individuals who are being learned from' (we term these individuals 'models'), rather than features of the 'thing being learned', to guide social learning. There is a great deal of adaptive information embodied in both *who* holds ideas and how *common* the ideas or practices are. For example, because information is costly to acquire, individuals will do better if they preferentially pay attention to, and learn from, people who are highly successful, particularly skilled, and/or well-respected. Social learners who selectively learn from those more likely to have adaptive skills (that lead to success) can outcompete those who do not. A large amount of mathematical modelling effort has been expended in exploring the conditions under which different context biases will evolve, how they should be constructed psychologically, and what population patterns will emerge from individuals using such learning mechanisms. Moreover, a vast amount of field and laboratory data confirms that these learning biases are indeed an important part of our cognition, that they are used by both children and adults, and that they influence economic decisions, opinions, judgements, values, and eating behaviour. Our remaining discussion of psychological mechanisms focuses on the theory and evidence for two categories of context biases in cultural learning: (i) success and prestige biases and (ii) conformity bias.

38.2.1. Selecting good cultural models: success and prestige biases

Once an individual is learning from others, she would be wise—in an adaptive evolutionary sense—to be selective about who she pays attention to for the purposes of learning (Henrich and Gil-White, 2001). The idea is that a learner should use cues from, or characteristics of, the individuals in their social world to figure out who is most likely to have useful ideas, beliefs, values, preferences, or strategies that might be gleaned, at least partially, through observation. For example, an aspiring farmer might imitate the strategies and practices of the most skilful, successful or prestigious farmers who live around him. Simply figuring out who obtains the biggest yields per hectare and copying them is a lot easier than doing all the trial-and-error learning for the immense variety of decisions a farmer (or anyone else) has to make. A purely individual learner would have to experiment with many types of crops, seeds, fertilizers, planting schedules, and various plowing techniques. The variety of combinations creates a combinatorial explosion of possibilities, making it virtually impossible for an individual to figure out the best farming strategy by relying entirely on experimentation. This is true of many, if not most, real-world decisions. However, along with figuring out who is the most successful or most skilled, learners should also be concerned about how the things they might learn will fit with their own abilities, the expectations of their role or gender, and their personal context. Learners should assess *certain kinds* of 'similarity'—between themselves and potential models—and weigh this alongside their assessments of 'skill' and 'success'. Following this logic, we argue below that learners might preferentially learn social norms from individuals who share their ethnic markers (e.g. their dialect, language, or dress, see McElreath *et al.*, 2003).

Figuring out who possesses the adaptive skills, strategies, preferences, and beliefs is often not straightforward. To achieve this, people rely on a range of cues related to *skill* (or *competence*), *success*, and *prestige*. For rhetorical purposes, this tripartite distinction is helpful because it captures the continuum of cues from direct observation by the learner (of skill or competence) to completely indirect assessments based on prestige (defined below). Noting someone's skill or competence, for our purposes, means that one has *directly* observed and judged their technique or performance. An apprentice might watch two craftsmen working side by side, one hitting all of his marks and gliding right along to a perfect final product (say a handmade chair) while another struggles, cuts himself twice, curses a bit, and produces something that only the bravest of his friends would venture to sit on. Direct observation indicates who the learner should pay attention to for learning to make chairs.

Cues of success are less direct and take advantage of easily observable correlates of competence (especially those that are difficult to fake), as we have defined it. Depending on the domain and society, such cues might be measured by house size, family size, number of wives and/or children, number of peer-reviewed publications, costliness of their car, number of tapirs killed, number of heads taken in raids, the size of their biggest yam, etc., each of which, in particular social contexts, is related to some domain of skill. While these cues provide only an indirect measure, they are sometimes superior to cues of competence. If performances are noisy, the observations of a small sample may lead a learner to misperceive competence. Cues of success, in contrast, often average over many performances, which can help to reduce the error in the learner's assessment of who to learn from.

The evolutionary theory underpinning this form of model-based cultural learning proposes that once the psychological machinery that makes use of competence- and success-based cues for targeted cultural learning has spread through the population, highly skilled and successful individuals will be in high demand, and social learners will need to compete for access to the most skilled and successful. This creates a new selection pressure for such learners to pay deference to those they assess as most valuable (those judged most likely to possess adaptive information) in exchange for *preferred access* and assistance in learning. Deference benefits may take many forms, including coalitional support, general assistance (helping with laborious projects), public praise, caring for the offspring of the skilled, and gifts (Gurven, 2001).

With the spread of deference for highly skilled individuals, natural selection can take advantage of the observable patterns of deference to further save on information-gathering costs. Naïve entrants (say immigrants or children), lacking detailed information about the relative skill or success of potential cultural models, may take advantage of the existing pattern of deference by using the amounts and kinds of deference different models receive as cues of underlying skill. Assessing differences in deference-received provides a best guess to the skill ranking until more information can be accumulated. Figuring out who to learn from, using the distribution of deference, is merely a way of aggregating the information (opinions) that others have already gleaned about who is a good person to learn from.

As part of these deference patterns, people unconsciously cue who they think is a good model through a series of ethological and behavioural phenomena that arise directly from efforts to imitate these individuals. These patterns relate to attention, eye gaze, verbal tones and rhythms, and behavioural postures. As learners seem keenly attuned to these subtle patterns, it appears that natural selection has favoured attention to these patterns of deference, as a means of assessing whom to pay attention to for cultural learning. As we discuss below, a mechanism like 'copy the majority' (conformist transmission) provides an effective way to aggregate the information gathered by observing and listening to others. In this case, conformist transmission can be used to figure out who to pay attention to for cultural learning.

To understand the difference between cues of *prestige*, *success* and *skill*, consider the following stylized example of an academic department. A new PhD entering a department and aiming at tenure might assess his senior colleagues in order to figure out who to learn from (with the goal of getting tenure). Initially, he can glean a measure of people's *prestige-deference* by listening to and observing how people act towards each other. If he's really serious, he might pull up everyone's CVs and count their publications (and divide by their 'years since PhD'). This would give a measure of *success*. Finally, if our fresh PhD still has not given up all hope of finding a good model, he might read everyone's papers (or at least those who rank high in 'success' and 'prestige') and watch them teach. This would give our learner a measure of skill or competence. Aggregating all these measures, he'd have a decent estimate of who to learn from.

Interestingly, the indirect nature of assessing another person's utility as a cultural model (i.e. their possession of adaptive information that could be useful to the learner) creates an important phenomenon. In a complex world, such indirect measures do not tell the learner which of the model's behaviours, ideas, practices and strategies causally contribute to his success or competence. For example, are people successful in farming because of what they plant, when they plant, how they plant, or how they make sacrifices to the spirits—or all four? Because of this ambiguity, humans may have evolved the propensity to copy successful individuals across a wide range of cultural traits, only some of which may actually relate to the individuals' success. When information is costly it turns out that this strategy will be favoured by natural selection even though it may allow neutral and even somewhat maladaptive traits to hitch-hike along with adaptive cultural traits.

38.2.1.1. Evidence of selective model-based cultural learning

Evidence for these learning mechanisms is plentiful, and comes from across the social sciences. A broad spectrum of work shows that both kids and adults will preferentially learn all kinds of things from other individuals demonstrating particular cues of competence, success and/or prestige—and there need not be any particular relationship between domains of prestige or competence and the things being learned. Unfortunately, the details don't go much beyond that. For example, we would like to know how different kinds of information are integrated. How important is observed competence compared to prestige? How important is individual information when it contradicts the behaviour of highly successful people? Having looked at a wide range of social learning evidence, it is clear that the tendency to imitate prestigious and successful people is one of the most powerful aspects of cultural learning.

In providing a taste of the evidence for success and prestige-biased cultural learning, we emphasize six main points. (i) These imitative patterns spontaneously appear in incentivized (where individual's choices influence monetary payoffs or other kinds of returns) and non-incentivized circumstances, in both non-social and social situations, including situations that involve direct competition among the learners. 'Social situations' are those in which a person's pay-offs and those of others are *jointly* influenced by their choices. (ii) The effects repeatedly emerge across a broad range of contexts, including economic decisions, opinions, food preferences and consumption, beliefs, and dialects. (iii) Consistent with theory, the amount of cultural learning observed depends critically on the degree of uncertainty found in the environment. As uncertainty increases, so does cultural learning. (iv) These learning patterns emerge even when the model's domain of competence, success or prestige is apparently unrelated to the behavioural domain in question. (v) Diverse findings from laboratory experiments in both economics and psychology, using very different experimental paradigms, consistently converge—giving us confidence in the findings' robusticity across experimental contexts. (vi) The patterns of cultural learning observed in the laboratories fit closely with field data—giving us confidence that the effects observed in the artificial context of experiments actually matter in the real world. Below, we summarize some of the laboratory findings to illustrate points (i)–(v), and then describe a few key field studies that illustrate point (vi).

Experimental evidence from Pingle (1995) confirms that people (well, university students) imitate the strategies of successful individuals when pay-offs are on the line. Using a series of computerized decision situations, participants had to repeatedly select the amount of three different inputs (e.g. 'fertilizer', 'seed' and 'labour') into a production problem for either 21 or 31 rounds, depending on the treatment. Before each decision, i.e. before setting the final amounts (x_1, x_2 and x_3) of the three inputs for a given round, subjects could pay to find out what profit they would get if they used different sets of inputs (a 'costly experiment'). In the baseline treatment, subjects could only learn from their own analyses and direct experience (i.e. what they earned each round from their chosen inputs). To calculate profit in each round, the subject's inputs were run through a pre-set production function. This function, which was unknown to players, had only one set of optima inputs (x_1^*, x_2^*, x_3^*); these inputs would make the most money. In four other treatments, opportunities for imitation were introduced in varying ways and with different costs. Participants in all treatments faced the same environment (the same production function) for rounds 1 to 11 (Block 1). At round 12, the environment shifted and again remained constant through round 21. For treatments 2–4 and the control, there was also a 'competitive' environment that commenced in round 22 with an environmental shift that lasted through 31 (Block 3). During this Block, the optimal set of inputs shifted dynamically and depended on what other players had done. This means that participants faced a new environment beginning in rounds 1, 12 and 22. Blocks 1 and 2 are non-social decisions, while Block 3 provides one type of social interaction.

The different treatments manipulated the information available for imitation: in treatment 1, during each round (starting in round 2) participants could, at a cost, look at the inputs and output of *one* other subject who had previously played *that* round. In treatment 2, participants could, at a cost, look at a list of inputs and outputs for that round for all the subjects who had gone before them. In treatment 3, before the play for each Block commenced, subjects were given the best outputs and inputs of previous players for that Block. In treatment 4, each subject watched two other subjects complete all 31 rounds before playing themselves. Each treatment used different subjects, who were paid real money according to the profit they earned, which was determined by their choices of inputs.

A comparison of the findings from across the treatments highlights several important points about imitation, all of which have been anticipated by cultural evolutionary models (Boyd and Richerson, 1985, 1988, 1995; Weibull, 1995):

1. In non-social situations, participants use imitation, often to a substantial degree, even when decisions are financially motivated and cost-benefit analysis is possible (but costly). The pattern of results across all four experiments, *vis-à-vis* the non-imitation control, shows the strength of our propensity for imitation: in round 2 of treatments 1 and 2, which can be compared directly to round 2 in the no-imitation control, people imitated 87% and 57% of the time, respectively.
2. Imitation tendencies remain strong even in competitive social environments. About 43% of subjects imitated in round 22 of treatment 2.
3. People tended to imitate (the inputs) of more successful players (those who got higher outputs). The patterns in the data are only explicable if people are looking at the difference in performance and using that as a cue about who and when to imitate.
4. Uncertainty causes a substantial increase in the reliance on imitation. In rounds 2, 12, 22, when a new environment is first encountered, rates of imitation are highest.
5. The availability of imitative opportunities, even costly ones, improves the average performance of the group. As a group, subjects in imitation treatments outperformed those of the control.
6. The 'imitation environment' (treatment) affects the average performance of the group. Average performance in treatments 3 and 4 exceeds that of treatments 1 and 2. Only the informational environment of treatment 3 avoids a substantial degradation in group performance during the Block 3.

Other work by economists confirms these findings. Kroll and Levy (1992) show that individuals readily imitate the investments of successful players, and that adding the possibility of imitation improves the overall performance of the group. Offerman and Sonnemans (1998) show that, not only will people copy economic choices and investment strategies, but they will also preferentially imitate beliefs about the state of the world from successful people. Work studying competitive Cournot markets demonstrates the power of this form as imitation (Alpesteguia *et al.*, 2003).

Recent studies exemplified by the above experiment are important because the decision-making is incentivized and the available information is rigorously controlled. Qualitatively however, these findings from economics merely confirm older empirical insights from psychology. Research elsewhere in psychology has shown that individuals preferentially acquire opinions from prestigious sources, especially in ambiguous, uncertain, or difficult situations, and even when these opinions are not connected to the model's domain of expertise. See Henrich and Gil-White (2001) for a review of this evidence. Not only do these cultural learning mechanisms operate in incentivized decision-making, but they also appear in non-incentivized situations in which behaviour, opinions and preferences shift spontaneously and unconsciously.

The same evolved cultural learning mechanisms emerge outside the laboratory, across a wide range of behavioural domains, including two areas that we mention here: (i) the diffusion of innovation and (ii) the epidemiology of suicide. In his massive review of the literature on the *Diffusion of Innovations*, Rogers (1995, p. 18) summarizes some of the lessons from 50 years of research as follows:

> Instead, most people depend mainly upon a subjective evaluation of an innovation that is conveyed to them from other individuals like themselves who have previously adopted the innovation. This dependence on the experience of near peers suggests that the heart of the diffusion process consists of the modelling and imitation by potential adopters of their network partners who have adopted previously.

Rogers devotes an entire chapter to explaining how the diffusion of new ideas, technologies, and practices is strongly influenced by 'local opinion leaders'. Compiling findings from many diffusion studies, Rogers describes these individuals as: (i) locally high in social status (e.g. high status within the village or village cluster); (ii) well respected (indicating prestige); (iii) widely connected; and (iv) effective social models for others. Rogers' insights are particularly important here because they confirm that success and prestige-biased cultural learning are important for the spread of novel technologies and practices.

The theory derived from the logic of selective model-based cultural learning even illuminates some of the robust patterns observed in studies of suicide. Data from industrialized societies show that committing suicide, including the methods (poisoning, gun, hanging, burning, etc.), are imitated according to prestige and self-similarity (Wasserman *et al.*, 1994; Stack, 1996). For prestige, many studies in the USA, Japan and Germany show that suicide rates spike more after celebrity suicides than non-celebrity suicides (Stack, 1987; Kessler *et al.*, 1988), even once media coverage is controlled for (Stack, 1990, 1996; Jonas, 1992). For similarity, the results show that the individuals who kill themselves after celebrity suicides tend to match their models on age, sex and ethnicity. Finally, the time trends of these suicides do not show regression to the mean during the subsequent month, indicating that these were not individuals who would have committed suicide in the near future.

Because suicide is strongly influenced by imitation, it can spread in epidemic fashion, showing patterns similar to those observed for diseases, novel cultural practices, and innovations. In Micronesia (Rubinstein, 1983), beginning in 1960 and lasting for at least 25 years, a suicide epidemic spread through certain island populations. This case is particularly stark because the suicides are geographically patterned and distinctively stereotyped. The typical victim was a young male between 15 and 24 (modal age of 18) years who still lived at home with his parents. After a disagreement with his parents or girlfriend, the victim was visited in a vision by past suicide victims who 'called him to them' (we know this from parasuicides). Heeding the call, the victim performed a 'lean hanging' from either a standing or sitting position, usually in an abandoned house, until he died of anoxia, or was accidentally discovered. In 75% of the cases there was no prior hint of suicide or depression. These suicides occur sporadically in local outbreaks among socially interconnected male adolescents who ethnically identify as from Truk or the Marshals (matching on sex and ethnicity), and can sometimes be traced to the precipitating suicides of prominent sons from wealthy families (associated with prestige).

Prestige bias also appears in studies of linguistic change (Labov, 1972, 1980), the transmission of managerial styles (Weiss, 1977; Weiss *et al.*, 1999) and in naturalistic studies of jaywalking manipulation (Mullen *et al.*, 1990). It also been repeatedly observed by ethnographers in an immense variety of contexts (Berreman, 1972, p. 141; Dove, 1993; Boyd, 2001; Rao, 2001).

38.2.3. Conformist transmission

As an adaptive learner, what do you do when any observable differences in skill, success, and prestige among individuals do not covary with the observable differences in behaviour, beliefs, practices, or values? For example, suppose everyone in your village uses blowguns for hunting, except one regular guy who uses a bow and arrow, and obtains fairly average hunting returns. Do you adopt the bow or the blowgun? One solution for dealing with such information-poor dilemmas is to copy the behaviours, beliefs and strategies of the majority (Boyd and Richerson, 1985; Henrich and Boyd, 1998). Termed *conformist transmission*, this mechanism allows individuals to aggregate information over the behaviour of many individuals. Because these behaviours implicitly contain the effects of each individual's own experience and learning efforts, conformist transmission can be the best route to adaptation in information-poor environments. To see this, suppose every individual is given a noisy signal (a piece of information) from the environment about what the best practice is in the current circumstances. This information, for any one individual, might give them a 60% chance of noticing that blowguns bring back slightly larger returns than bows. Thus, using individual learning alone, learners will adopt the more efficient hunting practice with probability 0.60. But, if an individual samples the behaviour of 10 other individuals, and simply adopts the majority behaviour, his chances of adopting the superior blowgun technology increase to 75%.

The same logic can be applied to aggregate and improve the imperfect information about the relative success of others, who may be useful as cultural models. Some individuals may obtain accurate information that allows them effectively to select and copy the most successful individuals, while others may receive noisy (inaccurate) information about relative success, which prevents them from effectively distinguishing differences. This second group can still take advantage of the more accurate information received by the first group by adopting the traits adopted by the majority. To see this more clearly, imagine a group of 200 individuals, wherein 100 are experienced hunters and 100 are novices who need to figure out which technology to invest in learning. Of the 100 experienced individuals, suppose that 40 used bows and 60 use blowguns for hunting. In their current environment (which recently changed), however, bows obtain a more efficient return, although the difference is small and hunting returns in general are highly variable. Nevertheless, using the returns of the experienced hunters, 40 of the 100 novices selected a bow hunter to learn from, 50 were left confused, and 10 picked a blowgun hunter to learn from (they got bad information due to the noise in hunting returns). In their confusion, the 50 decide to use conformist transmission, where now 80 hunters use bows (40 + 40) and 70 use blowguns. This will result in *more than* 53.3% of the 'confused' individuals adopting bows. For example, of the confused 50, 40 might adopt bows, while 10 still decide to go with blowguns. After all of the transmission this generation, 120 hunters will use the more adaptive bow, while only 80 use blowguns. If the older ('experienced') generation dies, 80% of the new generation will use bows (compared to only 40% of the now dead cohort).

This kind of verbal reasoning has been rigorously tested in both analytical models (Boyd and Richerson 1985, Chapter 7) and extended to more complex environments using evolutionary simulations (Henrich and Boyd, 1998; Kameda and Nakanishi, 2002). In their computer simulation, Henrich and Boyd investigated the interaction and coevolution of vertical transmission (parent–offspring transmission), individual learning, and conformist transmission in spatially and temporally varying environments. The results confirm that conformist transmission is likely to evolve under a very wide range of conditions. In fact, these results show that the range of conditions that favour conformist transmission are *broader* than those for vertical transmission alone—suggesting that if true imitation (via parent–child transmission) evolves at all, we should also expect to observe a substantial conformist component. Taken together, this work leads to several specific predictions about human psychology. First, this model predicts that learners will prefer conformist transmission over vertical transmission, assuming it is possible to access a range of cultural models at low cost (which is often but not always the case). While a direct test of this prediction is lacking, we note that a substantial amount of research in behavioural genetics indicates that parents actually transmit very little culturally to their offspring—once genetic transmission is accounted for, vertical cultural transmission often accounts for less than 5% of the variation among individuals (Harris, 1995, 1998; Plomin *et al.*, 2000). Those familiar with earlier work on cultural transmission might recall high correlations between parents and offspring, suggesting an important role for vertical cultural transmission (e.g. Cavalli-Sforza *et al.*, 1982). This work neglected the similarity between parents and offspring created by genetic transmission. Once the influence of genetic transmission is accounted for, the effect of vertical cultural transmission in creating parent–offspring correlations largely evaporates. Certainly there may be cases in which parents are the only viable models, and so have a large role, such as in early language acquisition or family recipes. But that does not indicate that people prefer to imitate their parents, nor that parents have a large effect in general. Second, the model predicts that as the accuracy of information acquired through individual learning decreases, a learner's reliance on conformist transmission (over individual learning) will increase. Third, as the proportion of models—in the learner's sample of models—displaying a trait increases, the strength of the conformist effect should increase non-linearly as well. We address the second and third predictions below.

A substantial amount of empirical research from psychology shows that people conform in a wide range of circumstances, particularly when problems are complex or difficult to solve on one's own. This work reveals that humans have two different types of conformity that operate in different contexts (Baron *et al.*, 1996). The first, often called *informational conformity*, matches the theoretical expectations from models of conformist transmission and is used to figure out difficult or ambiguous problems. Informational conformity results in people actually altering their private opinions and beliefs about something. The second, often called *normative conformity*, is conformity for the purposes of going along with the group to avoid appearing deviant. Under this type of conformity, people alter their superficial behaviour, but often do not change their underlying opinions, preferences or beliefs.

Experimental work shows that conformist transmission is important in individual decision-making situations (non-social circumstances). In an experimental design that parallels the aforementioned simulation constructed by Henrich *et al.* (2004), McElreath *et al.* (2005) had undergraduate subjects repeatedly face an economic choice between two options, A or B, for 20 rounds. This was posed as a 'farming decision' in which A and B were different crops with different yields and yield variances. Players did not know the mean yields or yield variances for the two crops, but were told that the local environment might fluctuate such that the mean yields of the crops change. After each round, each farmer learned the yield realized in that year for his field, and could choose to look at the decisions (crop A or B, but not the yields) of other farmers in the past year. At the end of the 20 rounds players were paid according to their total yield over the 20 seasons, making between $4 and $8. Consistent with theoretical predictions, McElreath *et al.*'s analysis confirms that (i) people increase their appetite for social information when crop variance is high and decrease it in temporally fluctuating environments, and (ii) a simple conformist learning rule (copy the majority) seems to capture an important part of decision-making in this problem, although there is quite a bit of individual heterogeneity.

A naturalistic experiment using non-incentivized behaviour further confirms these conformist effects by showing the non-linear influence of the frequency of a behaviour (Coultas, 2004) on its adoption. Here, subjects entered a computer laboratory one-by-one, not realizing they were in an experiment, and observed a 'rare behaviour' that involved placing the keyboard cover on top of the monitor. In pre-testing, the experimenters confirmed that no one, without modelling, ever put the cover on top of the monitor—so without modelling the expected frequency of placing the cover on the monitor is zero. The experimenters were able to manipulate the number of individuals placing the cover on the monitor by silently giving explicit instructions to some few through their computer monitors. Others, not receiving these instructions, were observed to see if they placed the cover on top of the monitor. Figure 38.1 summarizes the results by showing how the frequency of models performing the cover placement affected a subject's likelihood of making the same placement. The horizontal axis gives the percentage of individuals already present in the room who had their keyboard covers on top of their monitor as the subject entered. The vertical axis gives the probability that the subject would then place his keyboard cover on top of his monitor. As predicted, the likelihood of performing this behaviour, which is not otherwise performed, increases non-linearly as the percentage of models performing the behaviour rises above 50%. One problem with this experiment is that it does not carefully

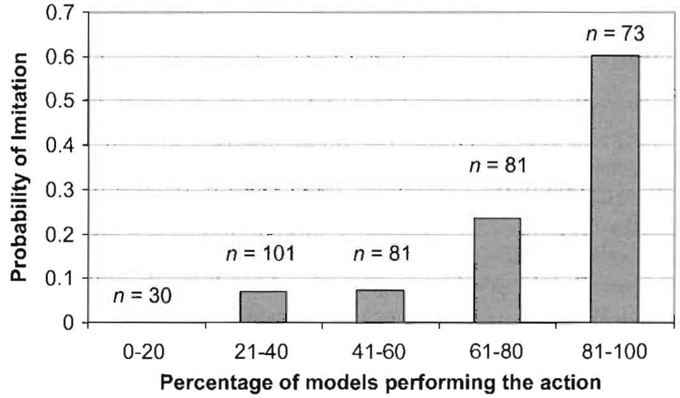

Fig. 38.1 The figure shows how the percentage of models performing the 'covers on the monitor' behavior influences the likelihood of others performing the same behavior. The *n* values above each bar gives the number of individuals observed for that bar—e.g., 73 subjects entered a room in which between 81 and 100 percent of the people in the room had their keyboard covers on their monitors; about 60% of these subjects then put their covers on the monitor.

distinguish informational from normative conformity.

As with prestige-biased transmission, conformist transmission is also important in social situations, including cooperative interactions. Conformity effects have also been observed in experimental situations involving opportunities for cooperation and punishment. Players in these games were willing to use conformist learning for acquiring cooperative behaviour, selfish behaviour, the costly punishment of non-cooperators, and even the costly punishment of those who refuse to punish non-cooperators (Carpenter, 2004; Denant-Boemont *et al.*, 2005). In general, the powerful effects of cultural learning on cooperation and altruism are empirically well-established (for summary see Henrich and Henrich in press, Chapter 2).

38.3. **Concepts 2 and 3: cultural evolution and culture–gene coevolution**

By combining these kinds of working hypotheses about the nature of our evolved individual-level adaptive learning mechanisms (e.g. prestige-biased and conformist-biased transmission) with formal models of *population processes* (see McElreath and Henrich, this volume, Chapter 39) dual-inheritance theory can generate a wide range of higher-level theories about the cultural evolutionary and culture-gene coevolutionary origins of sociological phenomena (e.g. ethnic groups). Instead of arguing that unidirectional causation exists at either the individual or society level, dual-inheritance theory *explicitly* models individuals with evolved or evolving psychologies in interactions with other individuals to understand more precisely how cultural learning mechanisms give rise to cultural evolution, and how this might feed back on genetic evolution (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). Here we discuss theory, rooted in formal modelling efforts, applied to the following questions: (i) why do cultural evolutionary rates and degrees of adaptation vary among populations (Shennan, 2001; Henrich, 2004) and how might this have influenced the basic cognitive abilities of different human groups and (ii) why do ethnically-marked groups emerge and how did our 'ethnic psychology' develop (Gil-White, 2001; McElreath *et al.*, 2003). Other work in this area examines how adaptive cultural learning can sometimes give rise to the otherwise puzzling patterns of maladaptive cultural practices, such as the demographic transition (Richerson and Boyd, 2005), cooperation as well as uniquely human forms psychology (McElreath and Henrich, this volume, Chapter 39).

38.3.1. Demography and cultural evolutionary rates

In the last 10 000 years, the rate of cumulative cultural adaptation has accelerated many times over, but the distribution in rates has been very uneven across the continents (Diamond, 1997). While much of this variation is likely to be explained by historical particulars, we suspect several important general processes are also at work (Turchin, 2003). While difference between continents is probably the most significant pattern in human history, evolutionary approaches, at least those devoid of an explicit appreciation of cultural transmission, have remarkably little to say about it. To illustrate, we briefly discuss one cultural evolutionary model that explores the interaction between demographic conditions and cultural evolutionary rates of adaptation (e.g. in technology, skills, knowledge) that may help explain *both* variable rates of cultural adaptation in different places and peculiar cases of maladaptive cultural and technological losses.

As the most extreme and archaeologically best-documented case of maladaptive technological loss, Tasmania provides an intriguing puzzle, and good point of departure for an inquiry. Humans first arrived in Tasmania about 34 000 years ago and were subsequently cut off from mainland Australia between 12 000 and 10 000 years ago by rising seas that filled the 200 km stretch of land linking Tasmania to Victoria. At the time of European discovery, Tasmania had the simplest technology of any population ever encountered. A combination of ethno-historical and archaeological data suggests that, over the 10 000 year period after being cut off from mainland Australia, Tasmanians likely lost, or never evolved, the ability to make bone tools, fitted cold-weather clothing, hafted tools, fishing spears, barbed spears, nets, and boomerangs. Bone sewing needles, of the kind used ethnographically by Australian aboriginals to make fitted clothing, are clearly present in Tasmania before the seas rose. To hunt and fight, Tasmanian men used only one-piece spears, rocks and throwing clubs. In all, the entire Tasmanian toolkit consisted of only about 24 items, and contrasts starkly with both their contemporary aboriginal cousins just across the Bass Strait in southern Australia and other cold-climate foragers such as the Ona and Yahgan of Tierra del Fuego. The Australian mainlanders possessed the entire Tasmanian toolkit plus hundreds of additional specialized tools including multi-pronged fish spears, spear throwers, boomerangs, mounted adzes, sewn bark canoes, ground edge axes, string bags, composite tools, and a variety of nets for birds, fish and wallabies (Henrich, 2004).

With this puzzle in mind, Henrich (2004) constructed a model in which individuals preferentially imitate highly skilled individuals. Unlike previous models, however, Henrich's model left open the possibility that transmission was both noisy (highly variable) and negatively biased (copies are usually worse than the originals)—both plausible assumptions, especially for complex technological skills and areas of knowledge. The analytical results show two things worthy of note: (i) the rate of adaptive evolution depends on the natural logarithm of the *effective* population size (effective population size incorporates absolute size and degree of interconnectedness: the size of the pool of interacting social learners); and (ii) if a well-adapted large population suddenly shrank, it could enter a regime of gradual maladaptive deterioration, as it moved towards a new, less-well-adapted, *equilibrium*. Empirically, the intervening time-period between the two equilibria would show a gradual loss of complex skills and knowledge (easy-to-learn skills would not be affected). Effective population size influences the evolutionary rate by making 'positive' errors—those that result in a more adaptive practice—more likely. This, along with a few other nuances in the archaeological record, indicates that the Tasmania pattern of deterioration may have been ignited by the interaction between the dynamics of cultural transmission and the sudden drop in effective population size created when rising oceans severed the link to the social learning networks of southern Australia. Overall, besides revealing the possibility of maladaptive deteriorations when networked populations are cut off, this simple model also shows that larger, more interconnected, populations can evolve both more rapidly and to a better-adapted equilibrium than smaller, or less well interconnected, populations. This may provide an evolutionary explanation why Diamond's observation that rates of technological evolution proceeded at different rates on different continents.

With the adaptive nature of cultural evolution in mind, it is important not to underestimate the degree to which culture, and cumulative cultural evolution, can influence basic facets of human cognition. Consider two aspects of our psychology: (i) spatial cognition and (ii) numerical conceptions of quantity.

Spatial cognition. At most, human languages possess three different systems for describing spatial position: (a) absolute: the ball is north of the tree; (b) object-centered: the ball is on Richard's left [as an object, Richard inherently has a (culturally defined) left, right, front, etc.]; and (c) relative: the ball is to the left of the tree (here an imaginary line is drawn from the speaker or other reference point to the tree, thus creating a 'left' for the tree). However, not all languages have evolved all three systems, with some cultures and languages lacking the relative system, and relying heavily on the absolute system. Cognitively, speakers of these languages (i) possess incredible dead-reckoning abilities and seem to have a constantly running mental compass, and (ii) perform very differently in non-linguistic tests of spatial memory (Levinson, 2003). It seems that the cultural evolution of linguistic system, and associated cultural routines, for discussing and dealing with space and orientation influences our non-linguistic spatial cognition.

Numerical conceptions of quantity. Number systems are an aspect of culture and language that varies substantially among societies. Many societies, for example, only have ordinal numbers up to 3. Recent work using experiments from cognitive science among two Amazonian groups demonstrates that growing up with such number systems greatly influences people's abilities in non-linguistic tasks that involve memory and matching, in dealing with quantity and number (Pierre *et al.*, 2004; Gordon, 2005). Thus, the cultural evolution of a number system influences the brains of those who grow up using it.

38.3.3. The coevolution of ethnically marked groups and ethnic psychology

A curious feature of human societies is their subdivision into self-ascribed arbitrarily marked groups, sometimes called 'ethnic groups' (Barth, 1969). These groups are sometimes the loci of cooperation and collective action (Henrich and Henrich, in press, Chapter 9), as well as out-group hatred (LeVine and Campbell, 1972). Many social scientists hold the opinion that these groups and their markings form out of collective interest alone, or that they are the result of strategic switching and signalling on the part of political actors. While we think this is partly true, the existence of strategic ethnic manipulation makes the maintenance of these arbitrarily marked groups problematic. If individuals can merely choose their ethnicity at any time, then why should anyone pay attention to the cheap labels at all? Models of ethnic markers as signals of cooperative intentions in fact show that the process is unlikely to work (Nettle and Dunbar, 1997; Roberts and Sherratt, 2002; see McElreath *et al.*, 2003 for more discussion of analogous biological models).

To explore the relation between social norms, symbolic markers, and cultural learning, McElreath *et al.* (2003) constructed a mathematical model to study the claim that arbitrary and easily acquired 'ethnic markers' (e.g. dialect, dress, hairstyle) may function to signal hidden, important norms of behaviour that differ among population subdivisions.

The model assumes that the population is subdivided spatially into 'groups' linked by migration. Groups are large and each individual is characterized by one of two norms. Norm differences arise in the model because the authors assumed that the norms solve coordination problems, such that individuals with locally common behaviours are at an advantage in terms of individual success (locally if everyone pays bride price, not dowry, one should also pay bride price, to coordinate with others). The model assumes that these behaviours are not observable, because many norms are unconscious and not easy to anticipate (Nave, 2000; Gil-White, 2001). Each individual also adopts one of two visible markers. These markers are costless, but may be observed prior to interacting based upon the hidden norms. Individuals may preferentially interact with those with the same markers as themselves, but this tendency is allowed to evolve within the model.

Naïve individuals acquire both norms and markers by imitating successful individuals (as discussed above). With some chance, they acquire both from the same individual, which may generate covariance between markers and behaviours. This bundled imitation is also allowed to evolve in the model.

The central question addressed by the model is not whether stable norm differences can evolve, but rather whether, given stable norm differences, stable regions of ethnic marking will arise that covary with norm boundaries. That is, do adaptive cultural learning mechanisms sometimes give rise to ethnic groups, as an emergent by-product? And, if they do, how does this emergent social environment influence the genetic evolutionary processes that shaped human psychology? It is important to realize that in a purely genetic model ethnic groups would be unlikely to emerge, as migration between subdivisions would normally swamp selection. Yet, empirically we know that ethnic groups manage to maintain apparent norm differences despite migration rates of one sex approaching 1: along the Vaupes river linguistic exogamy means that people must marry someone from a group who does not speak their language (Jackson, 1983). Only extreme selection could maintain genetically based behaviour differences under such migration. However, as mentioned in the preceding sections, both social interactions and mechanisms like conformist transmission can maintain differences between social groups, even when interaction and the physical movement of bodies is common. Likewise, selective cultural-learning processes can be strong even when the direct pay-off differences among behaviours are small (see McElreath and Henrich, this volume, Chapter 39).

A feedback loop generates and maintains ethnic marking, as long as migration exists but is not too strong relative to the selective processes created by success-biased cultural learning (that arise from the need to coordinate social interactions). The model works as follows.

1. Migration creates small amounts of covariance between specific markers and behaviours within each local group. This occurs even if there is initially no covariance within each group. The reason is subtle. If local groups differ at all in their frequencies of markers and behaviours, then there is covariance at the population level. Population structure is represented by the covariance across groups. Migration among local groups transfers this population covariance into within-group covariance.
2. Direct selective processes favouring common behaviours create indirect selection on markers, proportional to the covariance between behaviours and markers. This increases markers associated with common behaviours, within each local group.
3. Natural selection favours a psychological bias for interacting with those with the same marker as oneself, because there is always some covariance between markers and behaviours, due to migration. As this interaction bias increases, selection increases the covariance further, because then makers and behaviours form co-adapted pairs.
4. While migration may be needed to get the process going, if it is too strong, it swamps the selective forces above, leading to unmarked groups, sometimes even if behavioural (norm) differences remain. This is where the plausibility of weak migration relative to the strong forces of our cultural learning psychology is crucial to the model. If individuals are not strongly disposed to learn from group members with higher pay-offs, then mixing will erode differences between neighbouring groups.

Once regions of norms and ethnic markers exist, selection on genes favours an increased predisposition to interact with those who look like oneself (share one's markers). It also favours acquiring bundles of traits, norms and markers together, from the same individual during social learning (this may further enhance the tendency of individuals to learn things from successful models that do not directly relate to their domain of success or expertise). Importantly, the cultural evolution of behaviourally distinct groups and their markers leads to natural selection on aspects of psychology. This is the kind of culture–gene coevolution that we think is common in human evolution.

In conclusion, if we are right, then constraining ourselves to purely genetic models of human evolution will handicap our attempts to understand important domains of human behaviour, because the crucial selective forces that may account for some of our psychological adaptations arose first through the evolution of culture.

This is not to say that humans may have in any sense 'transcended' natural selection, any more than domesticated animals have. Rather, the sources of our selection pressures may often be different in important respects from those of closely related species, because of our evolved capacities for cultural transmission. Our bet, bolstered now by more than two decades of formal models of culture–gene coevolution and substantial evidence from laboratory and field sciences, is that it will prove very hard in the long run to understand the structure of human psychology without reference to the dynamic population processes that help to construct our selection pressures.

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