Blind and incremental or directed and disruptive?

On the nature of novel variation in human cultural evolution

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Abstract

Many scholars have rejected cultural evolutionary theory on the grounds that cultural variation is directed and intentionally created, rather than incremental and blind with respect to function, as is the case for novel genetic variation in genetic evolution. Meanwhile, some cultural evolution researchers insist that cultural variation *is* blind and undirected, and the only directional force is selection of randomly-generated variants. Here I argue that neither of these positions are tenable. Cultural variation is directed in various ways. While this does not invalidate cultural evolution, more attention should be paid to the different sources of non-randomness in culturally evolving systems.

Keywords: cultural evolution, evolutionary psychology, evolutionary theory, generalized Darwinism, memetics

Introduction

Does human culture evolve? Can we draw useful parallels between genetic evolution and cultural change? Can we use similar tools, methods, concepts and theories to understand cultural change as biologists use to understand genetic evolution? The rapid increase in research adopting a cultural evolution framework in the last few decades (Youngblood and Lahti 2018) shows that increasing numbers of scholars are answering “yes” to these questions. Yet in the grand scheme of academic research, cultural evolution remains a fringe pursuit. The majority of the social sciences and humanities reject any kind of evolutionary theorizing for understanding cultural phenomena, including cultural evolution (Slingerland and Collard 2011; Perry and Mace 2010). Even within the evolutionary human behavioral sciences, the theory of cultural evolution is often treated with skepticism (Daly 1982; Atran 2001; Pinker 1997). While there are many reasons for this rejection and skepticism, one common point of contention surrounds the issue of randomness and directionality in the generation of novel cultural variation. This is also a common source of disagreement *amongst* cultural evolution researchers (Lewens 2015; Claidière, Scott-Phillips, and Sperber 2014). In this paper I argue that there are genuine differences between genetic and cultural evolution in this sense. While some novel cultural variation seems to be generated randomly with respect to selection, akin to the generation of novel genetic variation, there are also several forms of directed cultural variation. I argue that while the latter do not invalidate the theory, approach or methods of cultural evolution, more attention should be paid to the different sources of directedness in culturally evolving systems and their consequences.

What is cultural evolution?

Cultural evolution is the idea that cultural change exhibits fundamental similarities to genetic evolution, such that we can profitably view and analyze cultural change as an evolutionary process. ‘Culture’ here is defined broadly as any socially transmitted information that passes from person to person non-genetically, via imitation, language, teaching or any other means of social learning. This includes what we colloquially label knowledge, beliefs, attitudes, norms, customs, skills, words, grammar, and institutions. If evolution is defined in abstract terms – much as Darwin did (Darwin 1859) – as comprising a system of variation, inheritance, and differential fitness (Lewontin 1970), then cultural change appears to meet the criteria of being an evolutionary process. Cultural traits (beliefs, ideas, attitudes etc.) vary within a population; they are (by definition) inherited from person to person, not genetically but socially, via social learning; and not all traits are equally likely to persist over time, with some ideas or beliefs spreading at the expense of others (Mesoudi, Whiten, and Laland 2004).

This parallel was first suggested by Darwin himself who, in *The Descent of Man* (Darwin 1871), pointed out the similarities between the evolution of species and of human languages. Despite initial interest in this parallel within the nascent social sciences of the late 19th century (Hodgson 2005), the idea fell from favor as the social and natural sciences diverged during the early 20th century. A resurgence began in the 1970s with memetics (Dawkins 1976), evolutionary epistemology (Campbell 1974), and the mathematical modeling of culture using the methods of population genetics (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). The latter in particular stimulated an ongoing empirical program that includes lab experiments, archaeological analyses, linguistics, history and non-human comparative work (Mesoudi 2011, 2017).

As in many fields, particularly relatively new ones, there are different approaches to cultural evolution that hold slightly different assumptions. These include memetics (Blackmore 1999; Dennett 2017), cultural attraction or cultural epidemiology (Claidière, Scott-Phillips, and Sperber 2014; Sperber 1996), cultural phylogenetics (Gray and Watts 2017), and work derived from the aforementioned population genetic modeling (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). One dimension on which they vary is the degree to which individuals are seen to be able to direct cultural dynamics by generating or transforming cultural traits non-randomly, in particular directions or towards particular forms. This is also a reason some use to reject the entire cultural evolution approach, as explored in the next section.

Randomness and directionality in the generation of genetic and cultural variation

It is a fundamental axiom of genetic evolutionary theory that novel genetic variants arise randomly with respect to function. Beneficial mutations are no more likely to arise when they are needed (i.e., no more likely to subsequently confer fitness benefits to their bearer) than when they are not needed (Luria and Delbruck 1943). The primary directional component of genetic evolution is selection, which increases the frequency of variants that happen to confer a fitness advantage on their bearers (i.e., makes them more likely to survive and reproduce). The generation of variation, via mutation or recombination, is random, not directional. ‘Random’ here does not mean that all genetic mutations are equally likely to occur, given the existence of developmental constraints that make some variants more likely to occur than others, and variation in mutation rates across loci. Rather, it means that the chance of a particular mutation occurring does not depend on whether or not that mutation is evolutionarily advantageous to its bearer. While there is some evidence for ‘adaptive mutation’, where the mutation rate increases during times of stress when beneficial mutations are most needed (Foster 2004; Rosenberg 2001), this does not change the basic point that genetic mutation is undirected. Adaptive mutation, if it exists, increases the rate of random mutation, such that beneficial and non-beneficial mutations are both increasingly likely to occur, with no bias towards beneficial mutations. Similarly, ‘facilitated variation’ (Gerhart and Kirschner 2007) highlights the major constraints that conserved components of development and physiology place on the kind of phenotypic variation that genes can generate. While this may make phenotypic variation more likely to be adaptive, this is due to past selection of random genetic variation.

The generation of novel cultural variation, however, seems far more directed and intentional. People strive to solve specific problems, invent useful or profitable products, instigate political and social change that they believe will advance their chosen cause, and so on. This difference has frequently been used to argue against the claim that culture evolves. Pinker, for example, writes “Memes such as the theory of relativity are not the cumulative product of millions of random (undirected) mutations of some original idea, but each brain in the chain of production added huge dollops of value to the product in a non-random way.” (Pinker, cited in (Dennett 1995 p.355)). Similarly, Orr criticizes cultural evolution on the grounds that “new ideas - but not genes - are produced by a sort of directed mutation. Newton did not uncover the Fundamental Theorem of Calculus by conceiving millions of random ideas.” (Orr 1996 p.470). Hallpike writes “there is no significant resemblance between the *mutation*, the basic source of variation in the Darwinian scheme of things, and social *invention*, which is purposeful, responsive, and can be diffused. Whereas biological variation can be treated as random, social variation is the product of particular societies and cultural traditions, and therefore far from random” (Hallpike 1986 p.36, italics in original). Fracchia and Lewontin state that “[cultural v]ariations emerge not randomly, but as attempts by specific individuals and/or groups to solve specific social/cultural problems; and their origins are not unrelated to their fate.” (Fracchia and Lewontin 2005 p.21). Or this from Sternberg, in an entire article criticizing the blind-variation assumption of cultural evolution: “The blind-variation model is inadequate in accounting for all of human creativity, if only because the research on expertise ... shows that humans do not blindly vary hundreds or even thousands of candidates for propagation - or mutations - for every one that succeeds.” (Sternberg 1998 p.171).

This collection of quotes from psychologists, biologists, historians and anthropologists reveals the breadth of the criticism that culture cannot be said to evolve because the generation of cultural variation is not random or blind with respect to function.

Is cultural variation randomly generated?

While some approaches to cultural evolution explicitly incorporate non-random, or ‘guided’ variation (see next section), some strongly imply that cultural variation is random with respect to selection. Campbell’s evolutionary epistemology adopted an explicit ‘blind-variation-and-selective-retention’ model of cultural evolution and creativity in general (Campbell 1974, 1965). While this did not necessarily require that novel cultural variation is blind, only that it is generated by mechanisms (e.g., cognition) that themselves were the product of blind variation and selection (e.g., natural selection), followers of this approach have insisted upon the blindness of novel cultural variation (Simonton 1999b, 1999a). Memeticists, in drawing close parallels between cultural change and genetics, also tend to focus on the selection of randomly generated variation at the expense of direction by individual minds (Blackmore 1999). (Dennett (2017), an advocate of memetics, has recently argued that the assumption of random or blind variation applies to *past* cultural evolution to explain the emergence of apparent design in cultural systems without any conscious intention on the part of individuals, but not *recent* cultural evolution, such as that resulting from the scientific method or corporate research and development, which is more directed and ‘intelligently designed’).

What does the evidence say? Memetics and evolutionary epistemology are often frustratingly evidence-free domains of enquiry. However, Simonton (1999b, 1999a) has most forcefully defended Campbell’s blind-variation model of cultural evolution, drawing on historical studies of creativity. Simonton points to the many inventions and discoveries throughout the history of science and technology that, rather than being the intended product of a genius inventor or scientist, were actually the result of accident, serendipity or blind trial and error. These include anaesthesia, electromagnetism, ozone, photography, dynamite, the gramophone, vaccination, saccharin, X-rays, radioactivity, classical conditioning, penicillin, Teflon and Velcro (Simonton 1995). The classic example is Alexander Fleming famously discovering penicillin when it accidentally killed some staphylococci cultures that he left exposed while on holiday. Basalla (1988) makes a similar argument to Simonton for the history of technology. Through a series of case studies, he argues that, contrary to the common 'great leaps by great minds' model of history, key inventions such as the steam engine were usually relatively minor and often unplanned modifications of previous technologies, rather than the disruptive innovative jumps commonly portrayed in popular imagination.

While suggestive, this evidence is far from conclusive. Examples and case studies can be consciously or unconsciously cherry-picked to demonstrate a point. While discoveries such as that of penicillin may be reported as accidental, a great deal of prior work had gone into getting to a point where this was possible (as per the saying, 'fortune favors the prepared mind'). As Sternberg (1998) reasonably notes, if cultural variation is blindly generated, it is hard to explain why some individuals (e.g., Edison, Einstein, Marie Curie) were responsible for multiple discoveries or inventions, and others contribute none. This highlights a major omission of the purely blind variation hypothesis: individual learning during the lifetime. People surely gain knowledge through training, practice or education, and increase their chances of making significant cultural modifications. The role of individual learning is considered further in the next section.

However, we should not discount the possibility or importance of randomly generated variation in cultural evolution. Indeed, perhaps the most rigorous test of this hypothesis found in its favor. Nia et al. (2015) analyzed the cultural evolution of violin 'f-holes', the holes in the violin body that affect acoustic conductance and, consequently, the quality of the sound produced by the violin. By analyzing several centuries of violin design, Nia et al. showed that these holes gradually evolved from circles in the 10th century which had little acoustic effect, to the now-familiar f-holes in the 18th century, which hugely enhance the acoustic properties of the violin. Most pertinently, they showed that this change was so gradual as to be consistent with random, accidental changes introduced by each generation of violin-makers due to imperfections in the manufacturing process. Those violins within the existing range of variation that happened to sound better were preserved and copied, and those that sounded worse were not. No disruptive or directional jumps in violin acoustics were observed, and no assumption that violin makers were intentionally creating better-sounding violins is necessary to explain the historical trend. There is even a wonderful counterexample: two early 19th-century violin makers *did* explicitly create novel violins that they believed would be superior to the standard design: Savart's trapezoidal violin and Chanot's guitar-shaped violin. Both were demonstrably novel and beyond the normal range of random variation found by Nia et al. Contrary to their inventors' intentions, however, these novel violins had poorer acoustics than the standard design, and are now forgotten evolutionary dead-ends.

Nia et al.'s analysis of violin design goes beyond anecdotes to show that directional cultural evolutionary change can, and most likely was, generated by blind variation and selective retention. Of course, this may not apply to other cases, only to those situations where the problem (here, how to maximize acoustic conductance in a musical instrument) is beyond the understanding of unaided human intuition. Nevertheless, there are many other similar cases where we are only just beginning to understand the underlying physical and chemical principles that underpin performance, such as the manufacture of glass (Macfarlane and Martin 2002) or swords (Inoue 2010). For other more intuitive problems, or for more recent scientifically-driven cultural evolution (Dennett 2017), variation may well be directed.

Adding individual learning, or 'guided' variation

As noted above, while there are some demonstrable cases of blind variation and selective retention fitting the historical data, a major potential omission is individual learning. People surely improve their ability to generate useful solutions to problems as they acquire more practice, knowledge and skill. More skilled and more knowledgable individuals would be more likely to generate beneficial variation.

This possibility was not only acknowledged, but also mathematically modeled, in some of the earliest formal work on cultural evolution. Boyd and Richerson (1985) dedicated a whole chapter to 'guided variation'. As they write:

> "When individuals learn, phenotypic variation is not random. Instead, the frequency of certain (usually favorable) variants is increased. If such learned variants are culturally transmitted, the result is a force that increases the frequency from one

> generation to the next of the same variants whose frequency is increased within a generation by learning. We call this force ‘guided variation’” (Boyd and Richerson 1985 p.82)

Note the words “usually favorable”. Guided variation is always non-random, and usually results in the generation of cultural variation that is beneficial. As noted above, it is the latter that violates the parallel with genetic mutation, which may be non-random but is not more likely to be beneficial.

Boyd and Richerson’s models show that guided variation can generate directional, adaptive evolutionary change in the complete absence of selection or selection-like copying biases. Even if traits are copied entirely at random, the directionality introduced by individual learning will generate directional, typically beneficial change at the population level. As Boyd and Richerson note, this kind of change is sometimes labelled ‘Lamarckian’ and contrasted with ‘Darwinian’ change, although in reality the term ‘Lamarckian’ is used in many different, and usually misleading, ways (Darwin, for example, was a Lamarckian in his views of biological inheritance).

Boyd and Richerson (1985) consider two kinds of individual learning that may generate beneficial variation: trial-and-error or reinforcement learning as commonly studied within behavioral psychology, and Bayesian models of rational choice from economics and cognitive science. Subsequent models and empirical work has extended the latter, showing that one can model cultural evolution as a Bayesian process of inductive bias (Griffiths, Kalish, and Lewandowsky 2008) or iterated learning (S. Kirby, Dowman, and Griffiths 2007). Assuming learners are rational, both processes (reinforcement learning and Bayesian inference) result in the outcome described by Boyd and Richerson (1985): convergence on whatever behavior, belief or hypothesis is most consistent with the available data given the learners’ preferences and biases (e.g., behaviors that yield higher monetary payoffs, languages that allow effective communication, categories that accurately describe the world, scientific hypotheses that best fit the empirical data). This provides a potential alternative to the typical cultural evolution approach. If all cultural change can be explained as a product of directional individual learning, all one would need to understand all cultural change is how individual learning works. We would be able to infer cultural dynamics by studying a single person. There is no need to consider population-level dynamics of who is copying whom, of migration or demography, or the other between-individual processes within cultural evolution models. The critics quoted above who argue that directionality invalidates cultural evolution would be vindicated.

However, there are at least two problems with guided variation as a complete explanation of cultural change. First, as noted above, many of the real problems faced by people are too complex to be solved by individual learning alone (Boyd and Richerson 1985). Violin acoustics, glasswork or metallurgy are governed by physical or chemical processes that scientists are only beginning to understand now. Such processes would have been way beyond the understanding of most people throughout history, yet violins, glass vessels and swords have nevertheless steadily increased in complexity and effectiveness. As shown by Nia et al.'s (2015) violin analysis, random, undirected variation plus selection of variants that happen to be beneficial is a way of surmounting this limitation, as people do not need to know how or why the beneficial variants are beneficial.

Second, individual learning is short-sighted. When the design- or solution-space within which cultural evolution occurs is multimodal (i.e., there are multiple solutions to a problem of varying quality, and one solution does not give clues to another, better solution), then even highly effective individual learners can get stuck on local optima and miss global optima. Any attempt to explore alternative solutions in the design space reduces immediate payoffs, despite the presence of better solutions elsewhere. This limitation can be overcome by copying the solutions of others who happen to have found better solutions, via a selection-like bias to copy successful others. Michael O'Brien and I have explored this scenario both experimentally (Mesoudi and O'Brien 2008b) and using models (Mesoudi and O'Brien 2008a), showing that (i) people are effective reinforcement learners, and non-randomly converge on locally optimal solutions to an artifact design task, (ii) people nevertheless get stuck on locally optimal but globally suboptimal solutions, and (iii) when allowed to copy others' artifacts, people escape these local optima and significantly increase their payoffs. This exploitation-exploration tradeoff has been explored extensively in cognitive and computer science (Hills et al. 2015), the findings of which underscore the difficulty of individual learning alone to correctly balance this tradeoff. What is needed is both: individual learning acts as a directional 'mutational' force that helps cultural evolution along, but selection-like social learning biases do much of the work especially when technological and social systems exceed the understanding of a single individual.

Genetically evolved learning biases and culturally attractive cognitive biases

The individual learning processes described in the previous section are relatively domain-general. Reinforcement learning reinforces whichever behavior is rewarded. Evolutionary psychologists, however, have argued that learning is typically domain-specific, and this domain specificity is the result of a history of natural selection (Tooby and Cosmides 1992). According to this argument, genetic evolution has shaped our cognition to more readily learn about stimuli that are adaptively relevant, that is, stimuli that would have affected our ancestors' chances of surviving and reproducing. Genetically evolved domain-specificity in learning was demonstrated in the animal learning literature in the 1950s, with the finding that rats more readily learn to associate nausea with tastes than with sounds, because tastes, unlike sounds, are characteristic of foods that may actually cause sickness (Seligman 1970).

This again would be a challenge to standard cultural evolution approaches, but with genetic evolution providing the 'direction' in the generation of directional cultural variation. If individual learning dominates cultural change, and individual learning reflects genetically evolved domain-specific biases, then cultural representations should converge on forms that reflect these genetically evolved biases. This is essentially the argument made by prominent evolutionary psychologists (Tooby and Cosmides 1992). Several plausible and empirically supported examples of this can be given. Fessler and Navarette (2003) show that food taboos proscribing meat are more common cross-culturally than plant-based food taboos, reflecting greater disgust sensitivity for meat than plants. This bias is adaptive given that meat is more likely to contain parasites and endanger health than plants. In general, disgust-inducing stimuli are more memorable, and more likely to be culturally transmitted, than non-disgusting stimuli (Eriksson and Coultas 2014), and this disgust bias is likely to be adaptive, if not now, then certainly in our ancestral past (although see Eriksson, Coultas, and Barra 2016 for evidence of non-universality of disgust bias). Other examples include learning biases that predispose towards information about the dangerousness of animals, which is even found in Los Angeles children with little exposure to, let alone risk from, dangerous animals (Barrett and Broesch 2012).

A similar argument takes into account genetically evolved cognitive architecture, but may not necessarily result in adaptive cultural representations. Evolutionary scholars of religion, for example, argue that cross-cultural regularities in religious beliefs may result from over-active agency detection (Boyer 2002). An understanding of other peoples' agency and minds, or 'folk psychology', is ordinarily adaptive because it allows us to predict others' behavior better. This may misfire, however, when people interpret agency in the occurrence of earthquakes, famines and other natural phenomena, resulting in a belief in a higher agency or deity. This is therefore a by-product of genetically evolved cognitive processes. Other examples of cognitive by-products include preferences for direct over indirect eye gaze in portraits (Morin 2013), or blood-letting as a medical practice (Miton, Claidière, and Mercier 2015). Blood-letting is not adaptive – and indeed is maladaptive when it leads to blood infections – but it fits our intuitions about how illness works (it releases 'bad blood' from the body).

These explanations play a central role in cultural attraction or cultural epidemiology approaches to cultural evolution (Sperber 1996; Claidière, Scott-Phillips, and Sperber 2014; Morin 2015; Buskell 2017). Here the focus is often on universal cognitive mechanisms that explain cross-cultural regularities in cultural representations, such as food taboos, supernatural agency, direct eye-gaze in portraits or blood-letting. Such favored representations are called cultural attractors. These may directly reflect genetically evolved individual biases, or constitute by-products of genetically evolved cognition. In all cases there is a distinctly non-random domain-specificity: certain traits are universally and predictably favored over others. In theory, as for domain general individual learning, this could explain cultural variation and change entirely in terms of individual learning biases.

There is persuasive evidence for the existence of cross-cultural regularities in cultural representations that are consistent with genetically evolved individual learning biases (e.g., for disgust-inducing stimuli) or by-products of normally adaptive cognitive processes (e.g., overactive or misfiring agency detection). Here, novel cultural variation is non-random and directional. This has led some to criticize cultural evolution approaches that focus on selection, and instead advocate for an understanding of culture in terms of genetic evolution (Tooby and Cosmides 1992) or individual cognition (Claidière, Scott-Phillips, and Sperber 2014), rather than population-level processes of cultural selection or selection-like transmission biases.

There are some problems with these claims, however. First, such accounts are good at explaining cultural regularities and stasis, but not cultural variation and change. Universal cognitive biases predict cultural universals. But how are we to explain the extensive human cultural diversity seen in the ethnographic record (K. R. Kirby et al. 2016), not to mention post-industrial technologies? It is also hard to explain cases of cumulative cultural evolution that seem to exceed or replace genetically evolved or attractive biases. Blood-letting, for example, has been replaced by unintuitive, 'unattractive' medical practices such as vaccination or surgery. Intuitive supernatural and religious beliefs have often been replaced by naturalistic explanations of the world, such as evolutionary theory, which is demonstrably unintuitive (Shtulman 2006). As noted above, complex traits such as violins or glassware have appeared and accumulated in complexity despite their unintuitiveness.

Second, cross-cultural regularities could in principle also arise from random variation and selective retention. While it is possible that evolved cognitive biases act to bias the generation of novel cultural variation, it is also possible that such biases act at the selection stage of cultural evolution, to preserve randomly-generated variants that happen to fit cognitive biases. More fine-grained historical data, such as that used by Nia et al. (2015), are needed to test this.

As argued above for domain-general individual learning, domain-specific genetically evolved or cognitively attractive biases are likely to play an important role in cultural evolution in certain cases, but not in others (Acerbi and Mesoudi 2015). For domains that are evolutionarily relevant (i.e., subject to past genetic evolution), like emotional disgust reactions to food, or for domains that are cognitively intuitive, like blood-letting, such explanations will be useful. For cases that are unintuitive or too novel to have been subject to genetic evolution, like much technology or complex social institutions, random variation and selection will play a bigger role.

Causal understanding and mental models

A final source of non-random variation invokes cognition more explicitly than the simple cognitive biases discussed previously. The cognitive niche hypothesis (Barrett, Cosmides, and Tooby 2007; Pinker 2010) posits that human adaptation occurs partly by domain-specific, genetically evolved cognitive biases, but also via ‘improvisational intelligence’. Here, learners generate solutions to adaptive challenges on-the-fly, through the construction and manipulation of mental models of the world and applying causal reasoning to such models. Pinker (2010) gives the example of armadillo hunting by members of the Yanomamo, drawing on Changon’s classic ethnographic account (Chagnon 2012). Yanomamo hunters will light fires at tunnel entrances to smoke out armadillos, block out entrances to prevent them escaping, and push vines through tunnels to locate asphyxiated armadillos. This is possible by constructing causal mental models of armadillo behavior (e.g., they dislike smoke) and of the physical environment (e.g., how smoke diffuses through tunnnels, or how to use vines to locate armadillos underground).

This extends the argument of the previous section, addressing the problem that genetically evolved biases cannot generate solutions to novel problems. Causal models can guide novel problem solving on-the-fly to exceed fixed genetically-evolved biases. This can generate cultural variation, if individuals generate different solutions to problems, or solutions to differing problems. Here again, novel cultural variation is generated non-randomly, in directions that are likely to be adaptive. No selection-like process is needed to select effective solutions.

It is, however, an empirical question whether causal models can actually explain patterns of cultural variation and change. In response to Pinker (2011), Boyd et al. (2011) argue that in reality humans predominantly rely on received cultural traditions with little explicit understanding of why those traditions work. They cite historical ‘lost explorer’ cases to support their argument, where European explorers set out to explore an unfamiliar region with all the latest equipment and scientific knowledge, yet fail to survive. For example, John Franklin’s 1845 expedition to the Arctic to discover a north-west passage from Europe to North America ended in disaster when his ship got stuck in the ice and him and his crew died of malnutrition. This is despite the fact that hunter-gatherers had successfully lived in the same region for generations. If cultural adaptation occurred via mental models, causal reasoning and improvisational intelligence, Boyd et al. argued, we would expect smart individuals like Franklin to have figured out how to survive. Yet they typically did not. Hunter gatherers succeed where Europeans did not by relying on cultural traditions that have gradually accumulated over many generations, typically via cultural selection of blindly generated solutions rather than explicitly understood causal theories. Arguably, examples such as Pinker's armadillo hunting could also be attributed to socially learned customs, rather than improvisation on-the-fly.

However, these case studies and anecdotes are again vulnerable to cherry-picking. A recent study provides a rare experimental test of the cognitive niche hypothesis (Derex et al. 2019). Derex et al. had participants complete a seemingly straightforward but deceptively difficult task. Each participant was presented with wheels positioned at the top of a downward-sloped track. Each wheel had four weights that could be moved along its spokes, from the centre of the wheel to the edge. The participant's task was to position the four weights to minimize the time it took for the wheel to descend the slope. Each participant had five attempts to change the weights, giving some opportunity for individual learning. The solution to this problem, however, is complex and unintuitive, requiring an understanding of inertia and potential energy. The twist was that participants were placed in transmission chains. Each participant (except the first in each chain) could view the weight positions of the last two trials of the previous participant in their chain. In one condition, this is all the information they received. In a second condition, participants could additionally transmit an explicit written theory about how and why the weights should be placed. Performance (i.e., descent speed) increased along the chains, but contrary to the cognitive niche hypothesis, no significant difference in performance was found between the two conditions. The transmission of causal theories did nothing to enhance performance beyond simply observing others' attempts. In fact, causal theories seemed to decrease performance amongst some participants, by inhibiting exploration of the design-space (weight combinations) and fixating on sub-optimal configurations. This study provides experimental evidence that the incremental accumulation of small, largely undirected changes is sufficient for directional cultural change, and causal understanding is not necessary.

Discussion

In this paper I have explored the issue of whether novel cultural variation is directed and disruptive, or blind and incremental, and the implications of this issue for theories of cultural evolution. Many scholars have rejected cultural evolution altogether on the grounds that cultural variation is directed and intentionally created, rather than incremental and blind with respect to function as is the case for novel genetic variation in genetic evolution. In contrast, some strands of cultural evolution research, most notably memetics and evolutionary epistemology, often argue that cultural variation *is* blind and undirected, and the only directional force is selection of randomly-generated variants.

I have argued here that neither of these positions are tenable. There are some cases where cultural variation does seem to be randomly generated, such as via manufacturing error in the case of violin designs, and directional change occurs via the cultural selection of those variants that happen to perform best (Nia et al. 2015). However, while this may apply to some such cases, it is unlikely to apply to others. Crucially, this blind-variation-and-selective-retention model omits individual learning, either domain-general reinforcement learning, domain-specific genetically evolved or cognitively derived individual learning biases, or causal mental models that allow individuals to generate solutions to problems on-the-fly. Each of these individual learning processes is directional, whether towards reinforced behavior, towards behaviors favored by genetic evolution or by-products of genetically evolved cognition, or the outcome of richer causal models of the world.

Yet we should be wary of over-estimating the influence of individual learning in generating cultural change and variation. Individual learning alone leads to cultural forms that are consistent with this individual learning: what is favored by a population is the same as what is favored by a single individual (Boyd and Richerson 1985; Griffiths, Kalish, and Lewandowsky 2008). This may apply to some adaptively relevant or cognitively intuitive domains, such as blood-letting, portrait eye-gaze, or emotionally salient disgusting stimuli. Other domains, such as violins, glass manufacture, scientific theories like quantum physics, and complex social institutions like financial markets, are unintuitive and seem beyond the reach of individual learning. As Boyd et al. (2011) argue, such phenomena are best accounted for by the incremental, possibly directional, generation of novel variants that are selected by success-biased social learning without the requirement that people understand why those selected variants are successful. Derex et al.'s (2019) experiment shows that technological improvement is possible without causal understanding, consistent with this claim. As long ago as the 1980s, Boyd and Richerson (1985) showed that guided variation is consistent with cultural evolution, given that its importance and potency is mediated by the difficulty of individual learning.

A fuller appreciation of the various ways in which cultural variation can be directed generates novel insights beyond a simplistic 'directed vs blind' dichotomy. For example, the institution of science can be seen as a mix of individually acquired and intelligently modified causal models (scientific theories) that vary across scientists and are selected on the basis of their fit to the available empirical data, at least partly (Hull 1988). As Dennett (2017) notes, different processes may have been more or less important at different times in history: early human culture may have been largely driven by blind variation and selective retention with no explicit causal understanding, while more recent science and technology may be driven by explicit causal models. Perhaps the exponential increase in scientific and technological knowledge (Enquist et al. 2008) can be explained by this shift, with causal understanding increasing the speed of cumulative culture.

There is a general need for more rigorous empirical tests of assertions in this area, beyond simple assertions (see quotes in the Introduction), or potentially cherry-picked historical examples. Nia et al.'s (2015) study is exemplary in quantifying the performance ('cultural fitness') of an artifact (a violin) and testing changes in this artifact over time against an explicit model of random variation and selective retention. Similar approaches have been used in archaeology, testing artifact change against formal 'accumulated copy error' models assuming randomly generated variation (Kempe, Lycett, and Mesoudi 2012; Eerkens and Lipo 2005). Future studies might compare historical and archaeological data against cognitively richer alternative models, to provide a proper alternative to random variation and selective retention. Derex et al. (2019), meanwhile, show how different mechanisms can be simulated in the lab, allowing more powerful inferences than with historical or observational data alone. Derex et al. (2019) used a specific technological task; further studies might use a range of tasks, perhaps tapping different performance criteria and varying the difficulty of the task and hence potency of individual learning.

In summary, the nature of novel cultural variation is of crucial importance for theories and tests of cultural evolution. A simplistic 'blind vs directed' dichotomy is unhelpful, and researchers should consider the many ways in which novel cultural variation may be directed, and the consequences of these. I have argued against the extreme position that any degree of non-randomness immediately invalidates a theory of cultural evolution, as well as the untenable position that all cultural variation is undirected and blind. The reality is somewhere in between, and varies with the difficulty of individual learning. The most profitable approach is to seek to understand how sometimes- and differently-directed variation interacts with selective social learning biases, as well as demographic factors like population structure and migration, to generate cultural change and variation.

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