Cultural Evolution and Cultural Psychology

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Abstract

Cultural evolution is a branch of the evolutionary sciences which assumes that (i) human cognition and behaviour is shaped not only by genetic inheritance, but also cultural inheritance (also known as social learning), and (ii) this cultural inheritance constitutes a Darwinian evolutionary system that can be analysed and studied using tools borrowed from evolutionary biology. In this chapter I explore the numerous compatibilities between the fields of cultural evolution and cultural psychology, and the potential mutual benefits from their closer alignment. First, understanding the evolutionary context within which human psychology emerged gives added significance to the findings of cultural psychologists, which reinforce the conclusion reached by cultural evolution scholars that humans inhabit a 'cultural niche' within which the major means of adaptation to difference environments is cultural, rather than genetic. Hence, we should not be surprised that human psychology shows substantial cross-cultural variation. Second, a focus on cultural transmission pathways, drawing on cultural evolution models and empirical research, can help to explain to the maintenance of, and potential changes in, cultural variation in psychological processes. Evidence from migrants, in particular, points to a mix of vertical, oblique and horizontal cultural transmission that can explain the differential stability of different cultural dimensions. Third, cultural evolutionary methods offer powerful means of testing historical ("macro-evolutionary") hypotheses put forward by cultural psychologists for the origin of psychological differences. Explanations in terms of means of subsistence, rates of environmental change or pathogen prevalence can be tested using quantitative models and phylogenetic analyses that can be used to reconstruct cultural lineages. Evolutionary considerations also point to potential problems with current cross-country comparisons conducted within cultural psychology, such as the non-independence of

data points due to shared cultural history. Finally, I argue that cultural psychology can play a central role in a synthetic evolutionary science of culture, providing valuable links between individual-oriented disciplines such as experimental psychology and neuroscience on the one hand, and society-oriented disciplines such as anthropology, history and sociology on the other, all within an evolutionary framework that provides links to the biological sciences.

Introduction

In the last few decades, cultural psychologists have demonstrated that it is a mistake to assume that people everywhere think the same way (Heine, 2011; Kitayama & Uskul, 2011). Significant and systematic cultural variation has been shown in people's self-concepts (Markus & Kitayama, 1991), social orientation (Oyserman, Coon, & Kemmelmeier, 2002; Triandis & Gelfand, 1998), cognitive reasoning (Nisbett, Peng, Choi, & Norenzayan, 2001), perception and attention (Kitayama, Duffy, Kawamura, & Larsen, 2003; Nisbett & Masuda, 2003), aggression (Nisbett & Cohen, 1996), cooperation (Henrich et al., 2005), personality (Heine & Buchtel, 2009; McCrae, Yik, Trapnell, Bond, & Paulhus, 1998) and moral reasoning (Haidt, Koller, & Dias, 1993), amongst many other domains. Phenomena once considered to be fundamental, universal aspects of human psychology, such as the so-called 'Fundamental Attribution Error' (Ross, 1977) or linear stages of moral reasoning (Kohlberg, 1969), have been shown to be far from universal (Haidt et al., 1993; Heine & Hamamura, 2007). As one memorable review put it, psychologists' over-reliance on studies of people from W.E.I.R.D. (Western, Educated, Industrialised, Rich, Democratic) societies to draw conclusions about a single 'human' psychology is hugely problematic, as such people are far from representative of our species as a whole (Henrich, Heine, & Norenzayan, 2010).

Interestingly, just as psychologists are beginning to appreciate the role that culture plays in shaping cognition and behaviour, so too are evolutionary scientists. The field of cultural evolution (encompassing gene-culture coevolution, sometimes called dual-inheritance theory) is based on the premises that (i) human cognition and behaviour is shaped not only by genetic inheritance, but also cultural inheritance (aka social learning), and (ii) this cultural inheritance constitutes a Darwinian evolutionary system that can be analysed and studied using tools borrowed from evolutionary biology (Henrich, 2015; Mesoudi, 2011, 2015, 2016; Richerson & Boyd, 2005; Richerson & Christiansen, 2013). 'Culture' here is defined in a broad way to encompass all of the knowledge, beliefs, values, attitudes etc. that we acquire from others via social learning / cultural transmission (e.g. via imitation or spoken/written language).

My aim in this chapter is to illustrate the numerous conceptual and methodological compatibilities between the fields of cultural psychology and cultural evolution, and the mutual benefits that can be gleaned through their further integration (see (Mesoudi, 2009a) for a similar argument for social psychology). Essentially, evolutionary theory and methods provide answers to 'why' questions. In biology, this might concern why particular biological adaptations (e.g. eyes or wings) exist, why species are distributed geographically in the way that they are, and why and how populations change genetically over time. For culture, including culturally-influenced psychological processes, cultural evolutionary theory and methods can answer equivalent questions: why culturally-variable psychological processes or dimensions exist in the first place, why psychological processes are distributed geographically in the way that they are, and why and how they change culturally over time. Cultural evolution theory provides rigorous, quantitative methods for answering such questions that have proven hugely successful in the biological sciences. Although cultural psychology has its roots in more humanities-based cultural anthropology traditions such as semiotics (Shweder & Sullivan, 1993), aligning the field with the evolutionary/biological sciences promises to open new opportunities, introduce powerful new methods, and add new significance to cultural psychologists' important findings.

The following section explains the basic tenets of cultural evolution theory. The subsequent section explores a fundamental but often taken-for-granted question: why should psychological processes be culturally variable at all? I then discuss how the maintenance of cultural variation in psychological processes might be explained in terms of cultural transmission pathways, before discussing how cultural evolutionary methods can shed light on the historical origin of that variation. I conclude by noting that cultural psychology can play a crucial role in a synthetic evolutionary science of culture.

What is cultural evolution?

The earliest attempt to apply evolutionary theory to human behaviour and cognition, *sociobiology* (Wilson, 1975), tended to treat culture as a proximate means by which genes act to maximise inclusive genetic fitness (see Laland and Brown (2011) for a detailed history of the human evolutionary behavioural sciences). The focus of sociobiology was on human universals that were assumed to reflect the genetic unity of the human species, or at most genetically determined responses to environmental regularities. This continued within prominent strands of *evolutionary psychology*, such as Tooby and Cosmides' (1992) emphasis on universal psychological mechanisms (Brown, 1991; Tooby & Cosmides, 1992 p.45) and on 'evoked' rather than transmitted culture (Gangestad, Haselton, & Buss, 2006; Tooby & Cosmides, 1992 p.116), in which universal genetic programs are triggered by particular environmental conditions. This focus on universality and genetic inheritance left little room for exploring or explaining cross-cultural variation (although see (Apicella & Barrett, n.d.)).

In parallel to this, there developed a strand of evolutionary research that aimed to more comprehensively incorporate culture into evolutionary models of human behaviour, known as *cultural evolution* (incorporating gene-culture coevolution, sometimes called dual inheritance theory) (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981) (see Laland & Brown, 2011). While the first formal, quantitative models of cultural evolution appeared in the 1970s and 1980s, it is interesting to note that this movement took much inspiration from the earlier writings of Donald Campbell (Campbell, 1960, 1965, 1975). This is interesting because Campbell also conducted pioneering early work in cross-cultural psychology (e.g. Segall, Campbell, & Herskovits, 1963), perhaps attesting to the compatibility of the two fields even at that early stage. Cultural evolution theory is based on the premise that cultural change constitutes a Darwinian evolutionary process that acts in parallel to, and interacts ('coevolves') with, genetic evolution. Human cognition and behaviour is therefore constituted by these twin tracks of genetic and cultural inheritance: sometimes the latter may reinforce the former (i.e. culture is genetically adaptive), while sometimes cultural evolution can result in biologically maladaptive or neutral behaviour due to its partial independence.

What is meant by saying that culture is a "Darwinian evolutionary process"? Although many textbook definitions of evolution mention genetic inheritance or the natural selection of genetic variation, Darwin's conceptualisation of evolution in *The Origin of Species* (Darwin, 1859) was actually quite mechanism-neutral, given that little was known at that time of genes or genetic inheritance. In general terms, Darwinian evolution comprises three principles (Lewontin, 1970): (i) variation, such that entities vary in their characteristics; (ii) competition, or differential fitness, such that some entities are more likely to persist than others, and this likelihood is determined to some extent by their characteristics; and (iii) inheritance, such that entities pass on their characteristics to subsequent entities. Over time, those characteristics that make their bearers more likely to persist tend to increase in frequency. For example, finches might vary in their beak size; during a drought finches with larger beaks can open more varied seeds and so survive with greater likelihood; and beak size is passed from parents to offspring. Over time, beak size increases in the population (Grant, 1986).

The same principles apply to cultural change (Mesoudi, Whiten, & Laland, 2004). Cultural traits (beliefs, attitudes, skills, values etc.) vary within a population; some traits are more likely to persist than others (e.g. some ideas are more memorable, some attitudes fit with pre-existing attitudes, some skills are more effective); and traits are passed on to other individuals via social learning (imitation, teaching, spoken/written language etc.). Thus, culture evolves. Importantly, it is not argued that cultural evolution is necessarily identical to genetic evolution in any further details (Mesoudi, 2011). In many respects it appears not to be, and exploring the specific dynamics of cultural evolution is a prime activity of cultural evolution researchers. For example, while genetic mutation is largely blind with respect to selection, cultural 'mutation' (or 'innovation') may well be consciously guided or directed by intentional human agents (Mesoudi, 2008). While genetic variation comes in discrete units (genes), there is no requirement for cultural variation to come in discrete units (while such 'memes' may exist in certain domains, they are not necessary for evolution to occur: (Henrich, Boyd, & Richerson, 2008)). While genetic inheritance usually follows strict Mendelian laws, such as requiring that individuals receive half of their genes from each parent (in sexually reproducing organisms, at least), cultural traits may be acquired from any number of genetically-unrelated individuals and follow non-random social learning biases, such as conformity (see below). Also, while genetic inheritance generally does not itself typically generate evolutionary change, social learning may do so, as traits are transformed during transmission (Acerbi & Mesoudi, 2015).

Recognising these differences, cultural evolution researchers have sought to mathematically model, experimentally simulate and document ‘in the wild’ how cultural evolution operates within populations of individuals: where cultural variation comes from, how it changes over time, and how it is transmitted from individual to individual (Cavalli-Sforza & Feldman, 1981; Mesoudi, 2011, 2016; Rendell et al., 2011; Richerson & Boyd, 2005; Richerson & Christiansen, 2013). These are the details of cultural ‘microevolution’ (see Figure 1). Researchers have examined when and why people copy their parents, as opposed to non-parents (Cavalli-Sforza & Feldman, 1981; McElreath & Strimling, 2008). There are many ways to learn from non-parents, and there has been much research into ‘social learning strategies’ or ‘biases’ (Laland, 2004; Rendell et al., 2011) that describe from whom and how people learn, such as *conformity*, defined as disproportionately copying the most common trait in one’s group (Henrich & Boyd, 1998; Morgan & Laland, 2012), *prestige bias*, defined as preferentially copying high status individuals (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich & Gil-White, 2001), and *content biases*, where particular ideas are preferentially transmitted, such as those that invoke disgust (Eriksson & Coultas, 2014; Heath, Bell, & Sternberg, 2001) or concern social interactions (Mesoudi, Whiten, & Dunbar, 2006; Stubbersfield, Tehrani, & Flynn, 2014). Migration, population size and other demographic factors that foment cultural change and structure cultural variation have also received much attention (Derex, Beugin, Godelle, & Raymond, 2013; Henrich, 2004; Kempe & Mesoudi, 2014; Powell, Shennan, & Thomas, 2009). Small populations, for example, reduce the available number of skilled demonstrators, potentially resulting in the loss of cultural complexity, as purportedly occurred when Tasmania became cut off from the Tasmanian mainland aournd 10,000 years ago (Henrich, 2004).

Cultural macroevolution involves large-scale cultural change over long time periods, and the emergence of cultural variation over large geographical areas. Biologists often study biological macroevolution using *phylogenetic* methods which use the current distribution of species to infer the likely evolutionary history of those species. These histories are often tree-like, given the assumption of high fidelity genetic inheritance that generates lineages of similar individuals. Cultural evolution researchers have used the same methods to reconstruct the evolutionary history of certain cultural traits that have similarly strong descent through high-fidelity cultural transmission, such as languages (Bouckaert et al., 2012; Pagel, 2009), folk-tales (Tehrani, 2013), prehistoric tools (O'Brien et al., 2014) and socio-political systems (Currie, Greenhill, Gray, Hasegawa, & Mace, 2010). Bouckaert et al. (2012), for example, used phylogenetic analyses to show that the Indo-European language family most likely has its origins around 8000-9500 years ago and spread with agriculture, rather than a more recent origin in the Pontic steppes. While cultural macroevolution can proceed at a purely descriptive level to reconstruct historical patterns of cultural change, it is also possible to explain the emergence of such patterns via links to the aforementioned cultural microevolutionary biases. For example, Pagel et al. (2007) showed that more frequently-used words are more likely to be preserved within language phylogenies, potentially due to a conformity-style process. While these examples concern purely cultural evolution, gene-culture coevolution analyses examine the coevolution of genes and culture, often finding that cultural evolution can significantly alter the course of genetic evolution (Laland, Odling-Smee, & Myles, 2010). Examples include the spread of lactose tolerance genes in response to the cultural practice of dairy farming (Itan, Powell, Beaumont, Burger, & Thomas, 2009).

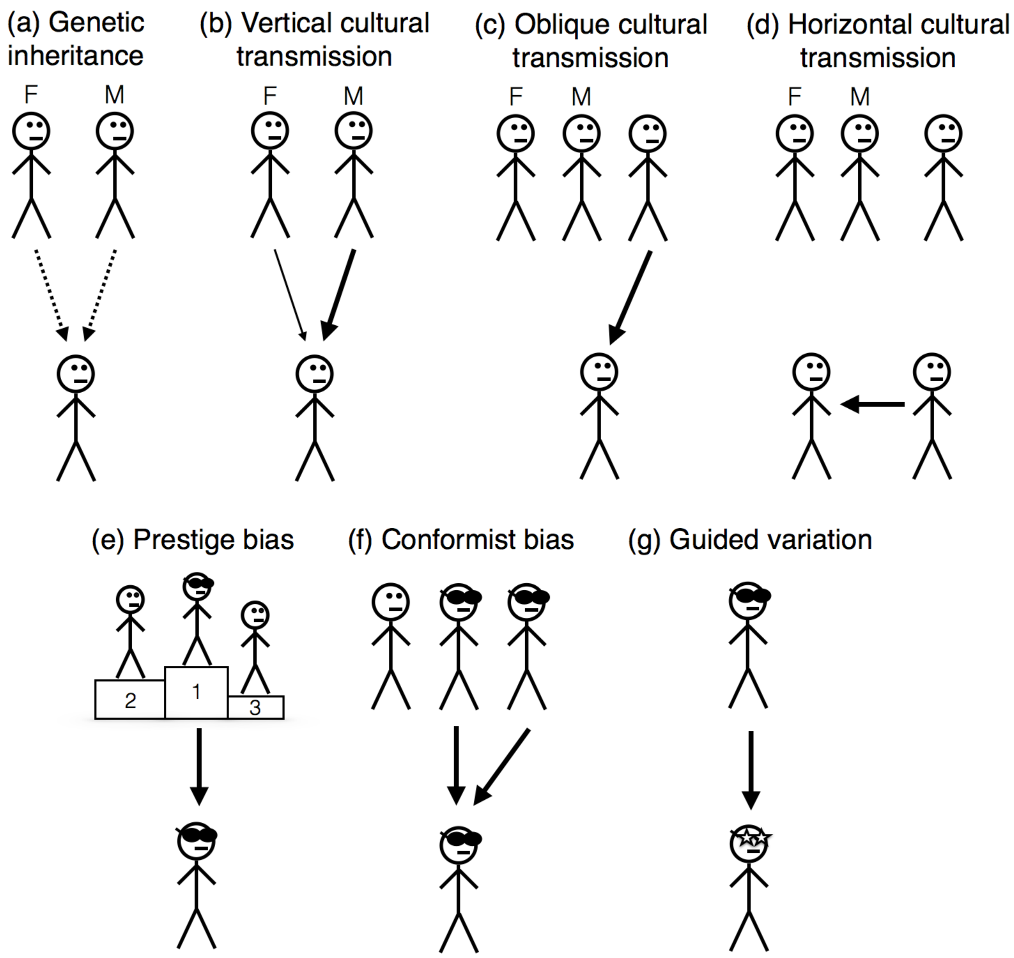

Figure 1 – Commonly studied processes of cultural micro-evolution. Compared to (a) genetic inheritance, in which information is inherited from a father (F) and mother (M), cultural transmission can take many pathways: (b) vertical cultural transmission entails copying biological parents, although one parent might be more influential than the other (here, the mother is more important, as has been shown for traits such as religion: (Cavalli Sforza, Feldman, Chen, & Dornbusch, 1982) – in other cases the father may be more important); (c) oblique cultural transmission entails copying a non-parent from the parental generation (e.g. a teacher or elder); (d) horizontal cultural transmission occurs within generations, between peers. Oblique and horizontal cultural transmission may be

biased in different ways: (e) prestige bias involves copying a successful or high status individual; (f) conformist bias involves disproportionately copying the most popular trait in a group; (g) guided variation, or cultural attraction, occurs when individuals transform traits in a non-selection-like manner.

It is important to note that there is no assumption within modern cultural evolution theory that societies must progress along fixed stages of increasing 'complexity'. This was a common assumption of 19th century socio-cultural 'evolutionary' schemes (e.g. Tylor, 1871) but stemmed from a misunderstanding of evolutionary theory. Neither biological nor cultural evolution entails inevitable progress along fixed, predetermined stages of increasing complexity, because no such stages exist; there is no sense in which one society is 'more evolved' than another society, just as one species cannot be 'more evolved' than another species (Freeman, 1974; Mesoudi, 2011). The aforementioned loss of complex cultural traits on Tasmania due to reduced population sizes provides a good illustration of the possibility of the loss, rather than inevitable increase, in complexity. There is also no requirement within modern cultural evolution theory to focus on any single level of cultural organisation: some studies focus on individual cultural traits, e.g. artifacts such as handaxes or arrowheads (Mesoudi & O'Brien, 2008; O'Brien et al., 2014), others on entire socio-political systems or nations (Currie et al., 2010; Pagel & Mace, 2004), depending on the research question of interest. Multi-level models can incorporate multiple levels of analysis, simultaneously tracking changes in, and interactions between, individual traits (e.g. pro-sociality) and larger societal organisation (e.g. empires) (Turchin, Currie, Turner, & Gavrilets, 2013).

The evolution of culture: Why have cultural psychologies at all?

Before getting to cultural dynamics themselves, it is useful to consider a more basic question: why did a capacity for culture, and particularly cultural evolution, evolve in the first place? This is a deceptively simple question that has received much attention in the cultural evolution literature. Many species get by with just genetic evolution, possibly with some individual learning (e.g. classical or instrumental conditioning) to respond to environmental uncertainties that arise after birth. So why bother biologically evolving large, expensive brains that have a capacity for culture? This is not just a tangential issue: knowing the likely evolutionary function of a trait can help to understand its current operation. And by considering this question, cultural psychology can forge links to other disciplines such as comparative psychology, behavioural biology and biological anthropology.

One way of finding out about the evolutionary origin of culture is by looking for it in other species. This raises the immediate problem of how to define 'culture'. History has shown that it is not particularly fruitful to spend too long arguing over definitions, and whether different species do or do not have it: this typically results in territorial arguments between researchers over whether their favourite species can be placed in the 'culture' club (Laland & Hoppitt, 2003). Comparative researchers have instead found it more scientifically productive to start with a broad definition, and explore the different elements of culture found across different species.

Surprisingly many species exhibit some form of social learning – defined as learning from conspecifics - which can be considered the basic foundation of culture (Laland & Galef, 2009). Bees learn the direction and distance to food via intricate waggle dances (Leadbeater & Chittka, 2007), many fish species learn routes to food or nesting sites by following others in shoals (Laland, Atton, & Webster, 2011), juvenile male songbirds of several species learn songs by listening to their fathers (Catchpole & Slater, 1995), whales learn from one another hunting techniques such as using bubbles to trap prey (Whitehead & Rendell, 2014), and non-human primates learn tool-use behaviours such as nut-cracking from others (Whiten, Horner, & Marshall-Pescini, 2003). In some species, social learning is of sufficiently high fidelity that it may generate between-population differences in behaviour, often called cultural traditions. Examples include song dialects of birds and whales, or tool-use traditions in different groups of chimpanzees (Whiten et al., 1999). Some chimpanzee groups crack nuts, others do not, and this population-level difference seems to be because individuals in nut-cracking groups learn nut-cracking from one another, rather than any genetic differences or factors that might encourage individual learning in one group rather than the other, such as the availability of nuts (Whiten, Horner, & de Waal, 2005).

These findings show that culture – in the sense of learning from others and generating group differences in behaviour – is far from unique to humans, and indeed can be found in species such as fish or insects that have historically been dismissed as behaviourally ‘simple’ or ‘primitive’. The widespread existence of social learning across animal species is consistent with findings from theoretical evolutionary models which show that social learning can readily evolve when (i) environments change fast enough such that genes cannot predict what behaviour will be adaptive during an organism’s lifetime (otherwise genetic adaptation is sufficient), but not so fast that other individuals’ solutions to problems become outdated (otherwise individual/asocial learning is more effective) (Aoki & Feldman, 2014; Aoki, Wakano, & Feldman, 2005); and (ii) when individual learning is costly or difficult (Boyd & Richerson, 1985). Other models suggest that social learning is most effective when it is combined with individual learning (Boyd & Richerson, 1995; Enquist, Eriksson, & Ghirlanda, 2007), and when it is follows certain non-random rules, such as a preferential tendency to learn from certain individuals (e.g. successful, older or prestigious individuals) or to copy the group majority (conformity), as noted above (Laland, 2004; Rendell et al., 2011). Indeed, these social learning strategies are found in many non-human species: fish preferentially copy the food source preference of more successful group members (Kendal, Rendell, Pike, & Laland, 2009) while great tits conform to the majority foraging behaviour in the group (Aplin et al., 2014).

Many cultural psychologists would probably argue that we are still missing some fundamental qualities of human culture in these descriptions of non-human culture. Indeed, there have been suggestions that much non-human social learning is underpinned by the same psychological mechanisms as associative (asocial) learning, just with other individuals as stimuli (Heyes, 2012; Leadbeater, 2015). Humans, on the other hand, seem to possess specific cognitive adaptations that allow the high fidelity transmission of information, which uniquely allow us to possess *cumulative* culture, in the sense that we learn from others that which we could never have invented alone (Dean, Vale, Laland, Flynn, & Kendal, 2014; Tomasello, 1999). Think of computers, cars, quantum physics or financial markets: such phenomena are the product of countless previous generations' minor modifications. Even the most sophisticated non-human cultural behaviours, such as chimpanzee nut-cracking, could plausibly have been invented by a single chimpanzee alone (Tennie, Call, & Tomasello, 2009). Recent experimental evidence comparing humans with non-human primates points to a set of cognitive abilities that uniquely support this cumulative culture, including teaching, language, and imitation (Dean, Kendal, Schapiro, Thierry, & Laland, 2012). One key capacity is 'over-imitation', the tendency of children (Lyons, Young, & Keil, 2007) and adults (Flynn & Smith, 2012) to copy behaviours performed by others even when those actions have no immediate payoff or utility, such as tapping on the top of a puzzle box with a wand, before then using the wand to open the box and obtain food. Chimanzees, by contrast, fail to over-imitate, readily ignoring irrelevant actions (Horner & Whiten, 2005). Humans also show powerful norm-following in tasks with no material payoff at all, i.e. we follow behavioural rules demonstrated by others seemingly without any need for reinforcement or reward (Chudek & Henrich, 2011; Rakoczy, Warneken, & Tomasello, 2008). In one study, 2 and 3 year olds shown how to play a novel rule-based game later corrected a puppet that was playing the game 'wrongly', often using normative language when doing so (e.g. "that's not how it's done") (Rakoczy et al., 2008). All of these abilities allow the high-fidelity transmission of information, and indeed accumulation of beneficial ideas, skills and institutions, over successive generations. According to this perspective, we inhabit a 'cultural niche' where the major means of adaptation to novel environments is not genetic or via individual learning, as in other species, but primarily via cumulative cultural evolution (Boyd, Richerson, & Henrich, 2011).

Within this context, it is not so surprising to find cultural variation in human psychological processes. Humans, compared to other species, are cultural sponges, possessing cognitive adaptations for acquiring knowledge and behaviour from others even with no reward or reinforcement, and in an open-ended manner that is not restricted to a single learning domain (e.g. song or food location). This flexibility and spontaneity seems absent in other species, despite their frequent use of social information in foraging, vocal communication and other specific contexts. When considering cultural psychological patterns, then, it is useful to keep these broader evolutionary considerations in mind. Cultural adaptation can, and indeed should, occur at local levels in particular societies in response to particular selection pressures – there is no reason to assume or expect a universal human psychology, which we might expect under genetic adaptation. Most of the time these cultural responses will be biologically adaptive for the individuals that possess them, given that culture itself is a biologically evolved trait that, on average, increases inclusive fitness. But evolutionary models also show that this does not always lead to biologically adaptive behaviour in practice. The very reason for culture's existence is to track environmental change that is too fast for genes to track, and to acquire from others information that cannot be stored in DNA. We should therefore expect some degree of decoupling between cultural and genetic inheritance, such that genetically maladaptive behaviours may arise. This might occur, for example, in phenomena such as copycat suicide (Mesoudi, 2009b), where our tendency to copy others, particularly prestigious others, can lead to the spread of biologically maladaptive traits.

Cultural transmission pathways: proximate explanations for the maintenance of cultural variation

Cultural psychologists have documented much variation across societies in various psychological processes. But how is this variation maintained over time, especially in the face of frequent migration? And in cases where cultural *change* has been documented over time, such as the increasing individualism in the US and Japan (Hamamura, 2012; Twenge, Campbell, & Gentile, 2012), what causes this change in some traits but not others?

At a proximate level, such questions can be addressed in terms of transmission pathways: how are psychological characteristics transmitted from one person to another? And how do these individual-level dynamics link to population-level patterns of stability and change? Cultural evolution researchers have modelled the population-level consequences of *vertical cultural transmission*, i.e. learning from one's biological parents, *oblique cultural transmission*, i.e. learning from unrelated elders, and *horizontal cultural transmission*, i.e. learning from same-generation peers (Cavalli-Sforza & Feldman, 1981; Cavalli Sforza et al., 1982; McElreath & Strimling, 2008) (Figure 1a-d). These models suggest that vertical transmission causes slower cultural change than oblique transmission, which is slower in turn than horizontal transmission, as one might expect given that the former occur over successive biological generations while the latter occurs within generational time frames. Ethnographic studies inspired by these theoretical models have shown that parents are often stated as a source of knowledge using self-report methods (Hewlett & Cavalli-Sforza, 1986). However, studies that sidestep the problems of self-report and instead infer transmission from patterns of shared knowledge show that oblique and horizontal transmission from more knowledgable elders and peers are often more important overall, and particularly during late childhood, adolescence and early adulthood, following brief vertical cultural transmission during early childhood (Aunger, 2000; Demps, Zorondo-Rodríguez, García, & Reyes-García, 2012; Hewlett, Fouts, Boyette, & Hewlett, 2011; Reyes-Garcia et al., 2009).

Another possibility, of course, is that putative 'cultural' variation in psychological processing is actually genetic, or at least genetically influenced. Few, if any, researchers would argue for a direct genetic explanation (e.g. that there are genes 'for' collectivism, and that those genes are higher in frequency in more collectivistic societies). However, there has been increasing interest in gene-culture interactions, with certain genes determining people's susceptibility to cultural inputs (Kim & Sasaki, 2014). This may provide an indirect explanation for between-population differences. For example, Chiao and Blizinsky (2010) argued that collectivism arose in East Asia as a cultural response to a higher frequency in those populations of an allele of a serotonin transporter gene, which is linked to a greater risk of mood and depressive disorders.

One "semi-natural" experiment that can shed light on these transmission pathways is migration (semi-natural in the sense that migrants are not an entirely random sample of the original population, yet they are also not participating in a psychological experiment). If migrants from a society that typically has different psychological processes to the adopted society fail to shift to the local psychological processes even after several generations, this provides support for a direct genetic explanation or for exclusively vertical cultural transmission. At the other extreme, if 1st generation migrants shift immediately or soon after migration, this suggests powerful horizontal cultural transmission, perhaps via cultural interactions or cultural products within the new environment (Morling & Lamoreaux, 2008). If 1st generation migrants retain the psychological processes of their heritage society, and a shift is observed in the 2nd and subsequent generations who were born and raised in the adopted society, this indicates some mix of vertical, oblique and horizontal transmission, with the speed of acculturation indicating the precise mix.

Several cross-cultural studies have included Asian Americans alongside North American and East Asian non-migrants, finding that Asian Americans are typically intermediate between their Asian parents and local American psychological characteristics on measures such as self-enhancement (Heine & Hamamura, 2007) and reasoning style (Norenzayan, Smith, Kim, & Nisbett, 2002). This partial shift rules out a genetic or exclusively vertical cultural transmission explanation for broader between-population differences, as well as an explanation in terms of exclusively horizontal cultural transmission. It points instead to a mix of horizontal/oblique and vertical cultural transmission ('oblique' in this case indicating transmission from older members of the adopted society, such as school teachers, rather than older members of the heritage society who may have migrated too, although both are possible: I will call these 'local-oblique' and 'heritage-oblique').

A recent study from my lab (Mesoudi, Magid, & Hussain, submitted) sought to add to this evidence base, and in addition specifically address the issue of cultural transmission pathways derived from the cultural evolution literature by also measuring potential markers of horizontal cultural transmission (e.g. mass media exposure) and vertical cultural transmission (e.g. time spent with one's family). We applied a battery of psychological measures previously shown to vary cross-culturally to 1st and 2nd generation British Bangladeshi migrants living in East London, along with non-migrants from the same area. Several measures showed the expected differences, with 1st generation migrants exhibiting higher collectivism and more situational / less dispositional attribution than the non-migrants, and with the 2nd generation UK-raised British Bangladeshis intermediate between these two groups. We also used model-comparison techniques developed within ecology (Burnham & Anderson, 2010), which weights the evidence for different theoretically-derived models to avoid the weaknesses of null hypothesis testing and an over-reliance on p-values (Cumming, 2013), to compare the predictive power of different transmission pathways for different measures. Individualism and dispositional attribution were predicted almost entirely by markers of horizontal cultural transmission, including country of respondent's birth, mass media exposure and years of formal education. Collectivism, social closeness and situational attribution, on the other hand, were predicted mostly by markers of vertical or heritage-oblique cultural transmission, including country of parents' (but not participant's) birth, religiosity and frequency of family contact, and secondarily by horizontal cultural transmission. If generalisable to other populations, then these dynamics might explain the aforementioned patterns of cultural macro-evolution: individualism has increased while collectivism has changed little in both the US and Japan (Hamamura, 2012) because the former is transmitted horizontally, and thus changes rapidly, while the latter is transmitted vertically, and thus changes more slowly.

Further studies are needed to more precisely identify the transmission pathways responsible for maintaining cultural variation in psychological processes, and for causing cultural change in those cases where change has been documented. As noted, migrants are a particularly good semi-natural experiment for doing this, as parental and peer influences are disassociated, but longitudinal studies (e.g. Greenfield, Maynard, & Childs, 2003) will also be useful. Model comparison statistics can be borrowed from ecology (Burnham & Anderson, 2010) to not just test single predictors against vague null hypotheses at an arbitrary level of significance, but to assess the relative strength of evidence for different transmission pathways. Further analyses might go beyond our initial attempts (Mesoudi et al., submitted) and test specific models of horizontal cultural transmission, such as prestige bias or conformity (Figure 1e-g). Existing quantitative models of cultural evolution will provide a useful starting point.

Testing ultimate explanations for the origin of cultural variation

While transmission pathways and social learning biases concern the proximate means by which cultural variation is transmitted and changed from one generation to the next, a complementary question concerns the ultimate origins of that cultural variation. Historical evidence suggests that psychological differences have roots in the distant past, with contemporary dimensions such as individualism-collectivism and analytic-holistic cognition found in the ancient philosophical modes of thought of Ancient Greece and Ancient China (Nisbett et al., 2001). Assuming that these traits are not genetic (and as seen in the previous section, migration data suggests that they are not), these psychological traditions can be seen as examples of long-term cultural macro-evolution, much like long-term language lineages and tool-use traditions. As such, we can ask, what were the cultural evolutionary selective pressures that gave rise to these different systems of thought?

Several hypotheses have been proposed to explain the origin of psychological differences. Only one of these, to my knowledge, has been directly inspired by cultural evolution theory. Chang et al. (2011) argued that East-West differences in psychological dimensions (e.g. collectivism-individualism, interdependence-independence) arose as a result of different weightings given at a society level to social and individual learning. As noted earlier, theoretical models suggest that neither social nor individual learning alone are an effective means of adaptation; instead we should expect a mix of both (Boyd & Richerson, 1995; Enquist et al., 2007). Yet the precise mix should depend on various factors. One factor that has received much attention is the rate of environmental change. Stable environments favour relatively more social learning, as other people's knowledge will remain relevant, while unstable environments favour more individual learning, as others' knowledge may become outdated (Aoki & Feldman, 2014; Aoki et al., 2005). Chang et al. (2011) applied these insights to East-West psychological differences. The primary societal means of cultural adaptation in the East (primarily China), they argued, was weighted towards social learning. This was and is reflected in stronger social ties and social interdependence, greater respect for elders and conformity to social norms, more rote learning and less innovation in educational systems, etc. The primary means of adaptation in the West (primarily Western Europe), meanwhile, was and is individual learning. This was and is reflected in weaker social ties, less rigid following of elders and existing social norms, more innovation in science and technology, encouragement of creativity and independent thinking in educational systems, etc. In a recent direct test of this, Mesoudi et al. (2015) found higher rates of social learning in a computer-based artifact-design task in people from mainland China, compared to participants from the UK, as well as Western-exposed Chinese students in the UK and a sample from Hong Kong (see also Bond & Smith, 1996).

Chang et al. (2011) argued that these different learning styles are in turn related to environmental differences: they point to greater instability and fluctuation in Western

Europe than in China in domains such as climate, governance, migration, warfare, agriculture and pathogens over the last several thousand years. For example, 19 of the worst recorded famines and droughts occurred in Europe, while China has only experienced 9; China has experienced political unity over most of its 2000 year history, while Western Europe has long been much more politically and linguistically diverse, with frequent conflict and exchange of territories. While Chang et al.'s (2011) hypothesis needs further testing, particularly to quantify and formally test the historically different rates of environmental change, this proposal has the benefit of stemming from theoretical modelling work that has received independent empirical support.

Other suggested ultimate explanations for the origin of psychological differences relate to means of subsistence. Nisbett et al. (2001) suggested that Western analytic thinking arose in ancient Greece as a result of the solitary herding common in the mountainous terrain of this region, while East Asian holistic thinking arose in ancient China as a result of rice farming, which necessitates more communal coordination and closer social ties. Uskul et al. (2008) provided support for this hypothesis by showing that Turkish farmers and fishermen who all work closely together show more holistic and less analytic thinking than herders from the same region, who typically work alone. Talhelm et al. (2014) argued for more fine-grained differences within the 'farmers' category, showing that regions of China that have a history of rice farming are more collectivistic than regions that have a history of wheat farming, because the latter requires less social cohesion than labour-intensive rice farming. Kitayama et al. (2006), meanwhile, suggested that frontier regions foster independence, analytic thinking and individualism due to their lawlessness and environmental uncertainty, by showing that residents of the recently-settled Japanese island of Hokkaido are higher on these measures than people from other parts of Japan with no recent history of being on a frontier. Finally, several studies have linked psychological differences to historical levels of pathogen exposure, arguing that the close social ties and distrust of outsiders found in highly collectivistic (e.g. East Asian) societies emerged as a means of protecting the in-group from dangerous pathogens brought by members of out-groups (Chiao & Blizinsky, 2010; Fincher & Thornhill, 2012). Support comes from positive cross-country correlations between collectivism and historical levels of pathogen prevalence (Chiao & Blizinsky, 2010; Fincher, Thornhill, Murray, & Schaller, 2008).

All of these hypotheses appear plausible, and all have some degree of support. They may also not be mutually exclusive: Kitayama et al.'s (2006) frontier theory possibly overlaps with Chang et al.'s (2011) environmental change theory, given that frontiers by definition are associated with environmental novelty and uncertainty, which is predicted to favour stronger individual learning and thus individualism. However, there is great opportunity to use cultural evolution methods to more rigorously test all of these hypotheses. One major methodological problem is the lack of correction for shared cultural descent when conducting multi-country correlations (Figure 2). Fincher et al. (2008) and Chiao and Blizinsky (2010) both, for example, find significant correlations across several countries between individualism-collectivism and pathogen stress. Yet cultural evolution researchers have long pointed to the problems of conducting correlations that treat countries as independent data points, which is seldom the case due to shared cultural history (Mace & Pagel, 1994). Treating, say, the UK, USA and Australia as independent data points is dubious given their intertwined cultural histories (Currie & Mace, 2012).

Phylogenetic analyses were developed by biologists to solve the equivalent problem in biology, where species are not statistically independent due to shared genetic descent (Felsenstein, 1985; Harvey & Pagel, 1991). The same methods can be used to control for shared cultural descent in cross-country comparisons to provide a more robust test of the aforementioned hypotheses, typically using language as a proxy for cultural relatedness (Mace & Holden, 2005; Mace & Pagel, 1994).

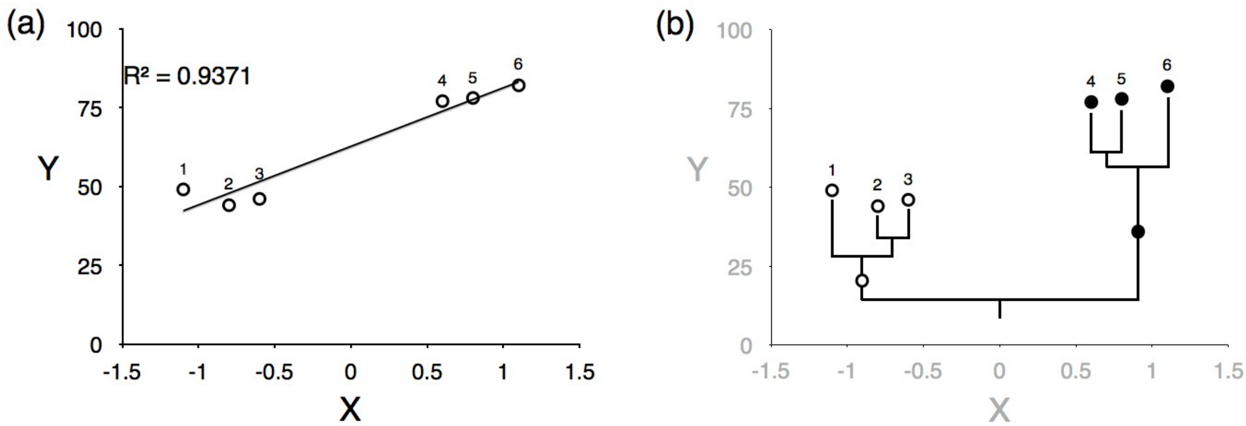

Figure 2 – Apparently strong cross-country correlations can be artefacts of shared cultural descent. The graph in (a) shows a strong correlation across six countries (1-6) between Y (which might be, for example, collectivism) and X (which might be, for example, pathogen exposure). Yet as shown in (b), it is inappropriate to treat these as six independent data points if countries 1-3 share a common cultural ancestor that happened to have low Y (unfilled circles), and countries 4-6 share a common cultural ancestor that happened to have high Y (solid circles). We now have only two independent data points, making the link between X and Y much more tenuous.

A second problem is that many of these hypotheses for the origin of cultural variation in psychological processes are expressed as verbal, informal historical narratives, rather than formal mathematical or simulation-based models that are amenable to precise testing. Turchin (2003, 2008) has argued that despite the traditional reluctance of historians to quantify their hypotheses for historical phenomena, or to posit general mechanisms that operate across multiple societies and time periods, actually such an endeavour is entirely possible – and hugely beneficial – by using modelling techniques borrowed from evolutionary biology and ecology. For example, Turchin (2003) used population dynamic models from ecology to explain the historical rise and fall of empires in Europe according to a small number of explicit assumptions, primarily the individual-level trait of social cohesion (named 'asabiya' by the sociologist Ibn Khaldun) and its effects on population-level societal dynamics. Turchin argued that small social groups in frontier regions at the edges of larger empires have high asabiya and intense ingroup cooperation due to their small size and common enemy (the empire). This makes them more effective in inter-group competition, as their members are more likely to work together, fight together, contribute to common goods etc. These small groups grow larger via conquest of smaller neighbours, and eventually conquer larger empires which have lower asabiya due to their large size and problems of free-riding elite classes. The conquerers therefore themselves become an empire, yet as they grow larger, asabiya drops again due to free-riding elites. This allows smaller frontier regions with high asabiya to successfully invade the larger empires, and the cycle continues over time. Turchin (2003) expressed all of this in mathematical terms using models originally applied to predator-prey cycles in ecology, derived specific quantitative predictions for the turnover of empires, and demonstrated that these predictions are supported by the best available historical data (see Turchin et al. 2013 for a more geographically explicit simulation model of similar historical dynamics).

There is great opportunity to do the same for the aforementioned historical explanations for psychological variation. Indeed, Turchin's / Khaldun's concept of asabiya resembles the collectivism or interdependence seemingly captured by many psychological constructs. Yet Turchin suggests the opposite to Kitayama et al. (2006): Turchin argues that frontier regions should be high in asabiya, Kitayama et al. that they should be low. Contradictions and disagreements such as this can often be best resolved using precise mathematical models, which force theorists to be explicit and generate specific quantitative predictions: words and verbal theories can often be interpreted in many different ways, and result in vague predictions.

Finally, previous studies have simulated historical or prehistoric patterns of technological change in the lab, in order to gain insight into the individual-level processes that generate population-level (e.g. archaeological) change (Kempe, Lycett, & Mesoudi, 2012; Mesoudi & O'Brien, 2008; Morgan et al., 2015; Schillinger, Mesoudi, & Lycett, 2014). For example, Mesoudi and O'Brien (2008) showed that patterns of arrowhead variation documented in the archaeological record are consistent with different learning dynamics: prestige bias reduces artefact variation in experiments (and by extension in the archaeological record) as a single prestigious demonstrator's design is copied, whereas individual learning increases variation as different people converge on different designs. There is opportunity to conduct experimental simulations of the aforementioned historical hypotheses for psychological differences. Participants might, for example, conduct tasks designed to simulate different means of subsistence (e.g. rice vs wheat farming) or the social connectedness entailed in each, to see whether psychological processing is shifted in the predicted direction. This assumes that such characteristics are flexible enough to be primed in this way, although previous studies suggest that they are (Oyserman & Lee, 2008).

Conclusion: Placing cultural psychology within an evolutionary science of culture

I have argued here that there are numerous links that can be drawn between cultural psychology and the burgeoning, interdisciplinary field of cultural evolution. The two fields are highly compatible: cultural evolution researchers assume that the major means of human adaptation is cultural, rather than genetic, due to our capacity for high-fidelity social learning that supports cumulative culture and long-lasting lineages of cultural descent. According to this perspective, it is not surprising that cultural variation has emerged in human psychological processes. Yet this does not necessitate a culture vs. biology dichotomy that has pervaded the social sciences and humanities for much of their history, where evolution is assumed to be irrelevant to human behaviour. Instead, culture can be placed within an evolutionary context, with models and cross-species comparative evidence speaking to the reasons why culture evolved in the first place, its evolutionary function, and which of its aspects are uniquely human, and which are shared by other species. By analysing cultural change itself as an evolutionary process that shares fundamental characteristics to biological/genetic evolution, powerful methods, tools and concepts can be borrowed from biology, suitably modified where appropriate, to analyse and explain cultural change, such as mathematical modelling techniques for linking individual-level behaviour to population-level patterns, or phylogenetic methods for reconstructing history. And one of the major benefits of the field of cultural evolution is its interdisciplinarity, linking those branches of the social sciences concerned with individual-level behaviour (e.g. psychology, micro-economics, neuroscience, ethnography) with those concerned with population-level patterns of behaviour (e.g. archaeology, history, macro-economics, comparative sociology) (Mesoudi, 2011; Mesoudi, Whiten, & Laland, 2006). Cultural psychology can provide an important link between these two levels, by exploring the influence of large-scale cultural variation on individual-level psychological processes, and vice versa.

In turn, cultural psychologists can offer valuable guidance on some of the hypotheses, models and empirical tests constructed by cultural evolution researchers. It is typically assumed in cultural evolution models, for example, that people everywhere exhibit the same social learning, conformist, or prestige-biased tendencies, and often that such tendencies are genetically inherited and subject to natural selection. While this may be a convenient modelling simplification in many cases, it is clearly not realistic given evidence for cultural variation in learning biases (Bond & Smith, 1996; Chang et al., 2011; Mesoudi et al., 2015), and models are needed that allow for the learning of learning biases from others (e.g. Acerbi, Enquist, & Ghirlanda, 2009; Ghirlanda, Enquist, & Nakamaru, 2006). Cultural psychologists also have rich data on how social ties and relationships vary in different groups, which may be useful for models of cultural group selection (Richerson et al., 2015), which concerns the selection of group-level variation and the spread of group-beneficial traits. In sum, there is much potential for mutual transfer of ideas between cultural evolution and cultural psychology.

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