**How the Dual Inheritance of Genes and Culture Shapes Behaviour: A Critical Review with a Focus on Human Culture and Behavioural Diversity**

*Human Behaviour & Cultural Evolution Group, Centre for Ecology & Conservation, University of Exeter, Penryn Campus, Penryn, TR10 9FE, UK*

It is estimated that around 6000 mutually unintelligible languages are spoken in the world today (Lewis 2009), and people around the world exhibit a diverse array of beliefs, social rules, rituals, clothing, and ways of life. Despite having originally evolved in the hot savannah environments of Africa, our species has spread out to colonize and inhabit every continent on earth, adapting to a great diversity of environments on the way. This remarkable behavioural diversity is set against the fact that, despite some prominent diﬀerences in biological features such as hair, skin, eye colour, and stature, humans are extremely homogenous genetically, particularly compared to wild populations of our closest primate relatives (Jorde and Wooding 2004). Our ability to adapt to new envi- ronments and create diverse ways of life is the result of the fact that we learn much of our behaviour from other people or, in other words, we have something we generally refer to as culture.

In this chapter, I will discuss how thinking of culture as a distinct inheritance sys- tem, that itself can undergo descent with modiﬁcation, adds to our understanding of behaviour and adaptation. I will illustrate the utility of this approach by discussing how the dynamics of social learning make maladaptive behaviours more likely, how under- standing cultural history helps us to understand present-day behavioural diversity, and how culture has aided the evolution of co-operation on a scale not seen in other species. I will then discuss the potential for coevolution of genes and culture, including the rela- tionship between patterns of genetic diversity and cultural diversity, and how cultural evolution can shape genetic evolution.

3.1 Culture and Behaviour

‘Culture’ is famously one of those terms that has many colloquial meanings. A paper by anthropologists Kroeber and Kluckholm (1952) listed 164 diﬀerent deﬁnitions that they had identiﬁed in the literature. In this section, I will clarify what I mean by culture and why it is useful to draw a distinction between behaviour and culture.

We can think of behaviour as being the actions and responses of organisms that result from the information they receive from internal and/or external stimuli (Levitis et al. 2009). Some behaviours may be largely innate (see Chapters 1, 4, and 5), by which genes build organisms that engage in some automatic response to some internal or external stimulus (e.g. the involuntary, reﬂexive jerk of your leg when hit just below the kneecap). However, behaviour can also be learned, by which exposure to a stimulus causes responses to change over developmental time, either due simply to repeated exposure to a stimulus (e.g. habituation or sensitization) or by making associations between responses and outcomes (associative learning) (Heyes 1994). It is important to note that some innate behaviours can be modiﬁed or shaped by learning, and that many behaviours will have both innate and learned components (see Chapters 1, 4, and 5). In humans and many other species, social learning is a particularly important form of learning (see Chapter 9). Social learning refers to changes in behaviour that result from some kind of interaction or observation of other individuals that can come about through a variety of mechanisms (Hoppitt and Laland 2013). Learning mechanisms themselves must of course be under some kind of genetic control. Our ability to speak a language at all is due to the evolution and development of biological features that control breathing and vocalization, as well as the construction of brains that are able to acquire and process linguistic information and enable infants to learn the particular language they are exposed to (Pinker 2003). However, the speciﬁc content of the language that individuals end up speaking (the particular words and grammatical features) is due to social learning. Just as genes provide *information* that shapes development and aﬀects the pheno- type of organisms (including behaviour), many researchers have found it useful to think of culture as the information that individuals acquire through various forms of social learning that is capable of aﬀecting their behaviour (Richerson and Boyd 2005; Mesoudi 2011). We can describe *cultural behaviours* as those behaviours that are at least partly the product of social learning, and we can similarly refer to these behaviours and other products of social learning such as tools, clothes, laws, and social roles as cultural traits. Cultural traits and behaviours may cover a variety of functional roles. Some varia- tion in traits may represent non-adaptive variation (e.g. much diﬀerence in content of languages, music, or artistic styles). However, other cultural traits and behaviours may have important ﬁtness consequences for the individuals possessing them. Some such traits and behaviours may reﬂect cultural adaptations to local environmental condi- tions. For example, the Inuit are able to live in permanently frozen northern latitudes due to a suite of cultural behaviours and other traits relating to clothing, housing, and subsistence (Boyd et al. 2011). Some cultural behaviours may reﬂect existing social con- ditions or other cultural behaviours. For example, in Ancient Hawaiian society it was forbidden (*kapu*) for ‘commoners’ to look directly at a chief, and they had to prostrate themselves when in sight of him (Kirch 2010). Learning the correct deference behaviours was vitally important as violation of these norms could result in death. Many cultural traits may have less dramatic consequences but can still aﬀect survival and reproduction, particularly when the ‘correct’ cultural trait depends on what others are doing or what cultural practices already exist (e.g. kinship systems and inheritance practices can aﬀect the reproductive success of oﬀspring) (Mace 1998; Ji et al. 2016). Finally, in humans in particular, cultural traits and behaviours are used to demarcate groups. Common group identity markers include the type of language spoken (Fought 2006) and costly social rituals (Sosis et al. 2007). As we shall see below, this structuring of humans into distinct groups has important consequences for co-operative behaviour and the transmission of culture.

The capacity for culture itself also can be considered an adaptation, to the extent that social learning enables individuals to survive and reproduce more eﬀectively than they would through individual learning alone (Boyd and Richerson 1985a; Richerson and Boyd 2001). Models show that one of the beneﬁts of cultural learning over individual learning is that it allows users to adapt to changing environments faster than could be accomplished by genetic evolution (Boyd and Richerson 1985a). Richerson et al. (2001) have proposed that climatic variability in the Pleistocene favoured an increased reliance on social learning and led to the evolution of our great capacity for culture.

This perspective of culture as socially learned information also helps highlight that culture is not necessarily unique to humans. Social learning has been demonstrated in a wide range of species. Early studies of Japanese macaques indicated that a behaviour of washing potatoes in sea water before eating spread through social processes (de Waal 2001). Chimpanzees (Whiten et al. 1999) and orangutans (van Schaik et al. 2003) show behavioural variations across populations. While some of these great ape behaviours could conceivably reﬂect individually learned solutions to diﬀerent ecological con- ditions (e.g. diﬀerent styles of termite ﬁshing), other behaviours appear somewhat arbitrary (e.g. such as clasping hands before grooming). Both whales (Filatova et al. 2010; Cantor et al. 2015) and birds (Nelson and Marler 1994; Marler and Slabbekoorn 2004) have been shown to have dialects in their vocalizations that are at least partially socially learned. Long-term observations of humpback whales oﬀ the coast of Massachusetts, USA, show evidence for a novel feeding behaviour spreading amongst a large propor- tion of the population (Allen et al. 2013). In 1980, one individual added an extra element to a certain hunting technique by striking the water several times before the regular behaviour (shared by the rest of the population) of blowing bubbles around schools of ﬁsh to disorient them. Analysis of a 27-year database indicated that this water-striking practice (known as lobtail feeding) had eventually been adopted by 37% of the popu- lation. Furthermore, the majority of these lobtail feeders adopted the behaviour after being in close association with other individuals that were already practising this technique.

These observational studies of wild populations have been supplemented by experimental studies both in the lab and in the ﬁeld that help rule out alternative explanations, and enable the proximate mechanisms behind social learning to be investigated (Whiten and Mesoudi 2008). A common experimental technique is to train individuals as ‘demonstrators’ in diﬀerent groups with diﬀerent solutions to some artiﬁcial foraging-related task, such as getting food from a plastic box. For example, one solution is to use a stick to lift up an obstacle, the other solution is to poke the obstacle. If individual learning is dominant in such situations then the expectation is that both behaviours should be equally common within groups. However, studies of chimpanzees on such tasks indicate that naïve individuals tend to perform the behaviour that was taught to the demonstrator, and that group diﬀerences in the persistence of the behaviours can be stable over multiple runs.

Researchers have debated whether this kind of copying behaviour reﬂects direct imi- tation or is actually the result of emulation (by which an individual is copying the goal of the behaviour rather than speciﬁc actions that lead to the goal) (Whiten et al. 2009). By adding an arbitrary behaviour in these tasks, such as placing a plastic token in one of two diﬀerent holders, researchers can investigate the extent to which individuals also copy elements that are not essential to successful completion of the task or achievement of a goal. Studies on chimpanzees show that these arbitrary behaviours also spread, which strengthens the interpretation that true imitation is involved (Bonnie et al. 2007). In ﬁeld experiments in South Africa (van de Waal et al. 2013), vervet monkeys were trained to eat corn that had been dyed a particular colour (e.g. blue), with the opposite colour (e.g. pink) being artiﬁcially made bitter. Four months after this training period, the dyed corn was again presented to the monkeys, but this time both colours were non-bitter. Young individuals that had been born into these groups, and were now able to eat solid food, preferentially chose the colour of corn that their group had been trained on. Inter- estingly, during the experimental period 10 males moved between the groups (which had been trained with the alternative bitterness/colour association). The majority of these males (7 out of 10) changed their colour preference to that of the group they moved into, which indicates that social learning could override the previous negative experi- ences associated with alternative behaviour, and potentially indicates a tendency to copy the most prevalent behaviour of the group (see below). Whilst noting these continuities between human and non-human animal culture, the complexity of human culture and the diversity of behaviours across human populations seem to be vastly greater in humans compared to other species. This suggests that there are also important diﬀerences between human and animal culture. Cultural behaviours in humans appear to build on other cultural behaviours in a heavily cumulative manner (Boyd and Richerson 1996; Caldwell and Millen 2008; Kempe et al. 2014). Behaviours and material products such as tools can be modiﬁed, combined, and improved upon such that beneﬁcial modiﬁcations and innovations can be retained and expanded upon over several generations. This leads to our ability to solve complex, adaptive problems that would be impossible for a single individual to solve within their own lifetime – we literally do not have to reinvent the wheel. This is most obvious in the evolution of technologies that show increasing abilities to hunt, cultivate food, process and trans- mit information, extract energy from the natural world, and, unfortunately, to wage war (Kurzweil 2000; Mesoudi et al. 2013; Morris 2013). This capacity for cumulative culture requires high-ﬁdelity transmission, otherwise beneﬁcial behaviours will be gradually lost from one generation to the next (Lewis and Laland 2012). Social learning in humans appears to have a number of features that maintain accurate transmission of behaviour from one generation to the next. Language facilitates direct teaching of ideas and intentions and helps correct ‘errors’ in the transmission of skills, practices, etc. Humans also seem to be extreme copiers, often engaging in ‘overimita- tion’ whereby they will copy exactly what others do (Whiten et al. 2009), which may be particularly important in situations that are causally opaque or do not lead to imme- diate rewards. Humans also seem particularly sensitive to following social norms and conventions, including situations where these might be costly (Cialdini and Trost 1998; Sosis et al. 2007; Henrich 2015).

**3.2 Cultural Evolution**

As we have seen, in species that engage in social learning, individual behaviour (and phenotypes more generally) can be inﬂuenced by both information from genes and information acquired through individual and social learning. However, unlike purely individual learning, cultural information can be inherited from one generation to the next. Culture therefore represents a parallel system of inheritance to genetic inheritance (also see Chapter 10). This has implications for the evolutionary processes that shape the behaviour of humans and other cultural species.

The standard neo-Darwinian paradigm views evolution as changes in gene frequen- cies within a population over time (Scott-Phillips et al. 2014). Genetic changes arise through mutations in the genome, and these mutations are passed on to subsequent generations via reproduction. Changes in the distribution of alleles (varieties of the same gene) in a population can occur via a number of process but chief among them are genetic drift (random ﬂuctuations, which can potentially lead to substantial increases or decreases in the representation of alleles) and selection (alleles that lead to increased survival and/or reproduction are better represented in subsequent generations) (Futuyma 2013). Selection is important because it leads to adaptation and the appearance of organismal design without the need to invoke a deliberate, purposeful guiding force or designer (Darwin 1859; Dawkins 1986). However, as we have seen, adaptively relevant information can be passed on through social learning, and survival and reproduction may be linked not to genetic variation but to variation in cultural traits and behaviours. Focusing too narrowly on genes, therefore, may lead to problems in adequately explaining important variations in phenotypes and their systematic changes. If we understand evolution more generally as change in the inherited characters of a population over time (Ridley 2004; Richerson and Boyd 2005; Laland et al. 2015), then we can see that systematic changes in behaviour can come about as a result of either genetic evolution or cultural evolution (or both).

**3.2.1 Processes of Cultural Evolution**

At a broad scale, we can recognize that there are processes of variation, inheritance, and selection that occur in cultural evolution that are analogous to those of genetic evolution. In this section, I describe what variation, inheritance, and selection look like in cultural systems. While drawing parallels between these two systems is an important exercise, it is also important to acknowledge the diﬀerences between genetic and cultural systems, and the consequences this has for how cultural evolution works.

**3.2.1.1 Variation**

Any evolutionary system requires the generation of variation. In genetic evolution, vari- ation is generally thought to be generated through random genetic mutation (by which we mean that these changes occur without reference to their likely phenotypic eﬀects). Indeed, most mutations are either silent (i.e. they don’t produce a change in pheno- type), selectively neutral, or actually have a deleterious eﬀect on ﬁtness (Eyre-Walker and Keightley 2007). Random mutation may also play a role in generating cultural vari- ation. In cultural systems, ‘mutations’ can result when individuals make copying errors such as misuse of or misremembering words. Consistent with this idea, Pagel and col- leagues (Pagel et al. 2007; Calude and Pagel 2011) have shown that across diﬀerent languages, the rate at which words are estimated to change is related to the frequency with which those words are used. Words that are used less frequently change at a faster rate potentially because copying errors are more likely to go unnoticed, meaning new forms of words can spread and become ﬁxated. New traits may also come about through ‘happy accidents’, where a beneﬁcial innovation is discovered by chance rather than from purposeful planning. Many foodstuﬀs or traditional medicines may have been discovered this way. A more recent example is the discovery of the antibiotic penicillin by Alexander Fleming. Reportedly, Fleming noticed that bacterial growth in a petri dish had been inhibited by a *Penicillium* mould, due to accidental contamination as the result of a laboratory window being mistakenly left open (Diggins 1999). Accidental, unintentional, or otherwise non-directed changes in cultural traits can and do occur. However, many changes may also be distinctly non-random, and instead variation can be guided towards a particular goal (Boyd and Richerson 1985b). For example, people undoubtedly make adjustments to technological items with the intention of improving their eﬃciency, power, functionality, etc. Sometimes changes to whole languages are enacted purposefully. Several instances have been recorded in New Guinea where communities have made a conscious decision to change aspects of their language in order to diﬀerentiate themselves from other groups (in one case switching certain masculine and feminine elements to be the opposite of neighbouring dialects) (Thomason 2007). If organisms are able to design solutions to an adaptive problem themselves, this may at ﬁrst appear to invalidate the need to talk about culture in evolutionary terms. Sev- eral points can be made in response to this argument. An evolutionary process only requires that variation be generated and does not require a particular type of process such a blind mutation to generate this variation. Evolutionary theory rests on popula- tion thinking, and even if an individual develops an improved trait, that trait still needs to spread through the population, and many other processes (as we shall see below) may aﬀect whether or how this occurs. Many adaptive problems could have multiple, equally appropriate solutions (e.g. chopsticks versus cutlery). Guided variation might be part of the explanation as to why populations ﬁnd these solutions at all, but population-level processes would be needed to explain why diﬀerent populations might converge on dif- ferent solutions. Even if variation is guided, it does not mean that complex adaptive traits will necessarily emerge fully formed. Many problems that we face are complex and causally opaque such that any improvements we make may only be incremental. The presence of guided variation certainly can aﬀect evolutionary dynamics by enabling a population to reach an adaptive peak more quickly, but it does not automatically inval- idate the utility of an evolutionary approach to understanding cultural change.

3.2.1.2 Inheritance

Inheritance in genetic systems occurs when individuals create oﬀspring that resemble themselves through some form of reproduction. In cultural systems, the analogue of inheritance (which is more commonly referred to as transmission) occurs when indi- viduals learn a behaviour, or otherwise acquire a trait from another individual, and then exhibit that trait (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985b; Mesoudi et al. 2004). A common distinction made between these two systems is that whereas the predominant mode of inheritance in biology is vertical (i.e. parent to oﬀspring, tied to reproduction), in cultural evolution traits can be transmitted from parents to oﬀspring and can also be transmitted from other individuals too. Some modellers have referred to transmission between individuals of the same generation as horizontal transmission, while non-parent-to-oﬀspring transmission across generations is referred to as ‘oblique’ transmission (Cavalli-Sforza and Feldman 1981). While this distinction is somewhat arbitrary, it could be adaptive in some cases to learn primarily from individuals of similar age (e.g. when traits are evolving quickly) or from older generations (e.g. when ability in a certain task is correlated with experience and that task is still relevant). For some pro- cesses, mode of transmission is indeed an important and relevant distinction. However, for many processes this distinction is not important, and in many cases equating bio- logical inheritance with vertical transmission and cultural inheritance with horizontal transmission is overly simpliﬁed.

In discussing these issues, it is important to distinguish between transmission at the micro-level (i.e. within populations or species) and at the macro-level (i.e. between pop- ulations or species). For example, a trait may be spread horizontally or obliquely within a population, but if there are barriers to transmission between populations then trans- mission would be characterized by vertical transmission at the macro-scale, that is, individuals will exhibit traits that resemble those of previous generations from the same population, and when cultures split, the descendant, ‘daughter’ cultures will maintain many of the traits of the original, ‘parental’ culture (see section 3.4). Similarly, horizon- tal transmission at the macro-scale involves the transfer of traits or information between populations, and could occur even if transmission within populations tended to be pre- dominantly from parents to oﬀspring.

Diﬀerent modes of transmission can aﬀect the rate at which a novel trait can spread through a population. When genetic information is only transmitted vertically then the rate at which an allele will increase in frequency within a population is constrained by the rate at which individuals reproduce (and by the strength of selection). However, for cul- tural traits, the rate-limiting step is how often the trait can be observed and successfully copied (Cavalli-Sforza and Feldman 1981). This means that potentially a cultural trait can be adopted by a large proportion of the population extremely quickly. For example, the use of hybrid corn by farmers spread rapidly across the United States in approxi- mately 25 years beginning in the 1930s (Griliches 1960) (see Kandler and Steele (2009) for an example of how the dynamics of such spreads have been analysed using cultural evolutionary theory). In some ways, this ability to spread horizontally makes cultural evolution somewhat epidemiological, and indeed some authors have argued that culture (or at least some aspects of it) can be thought of as like ‘viruses of the mind’ (Dawkins

1993; Brodie 2009). Therefore, as we shall see later, this horizontal mode of transmission potentially has consequences for genetic ﬁtness (see section 3.3.1).

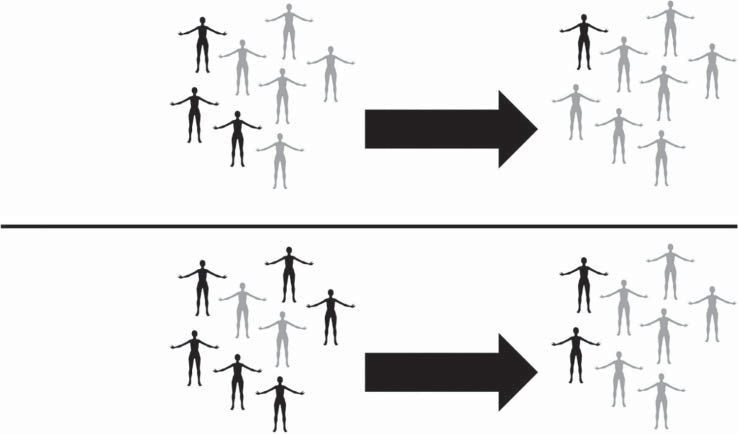
Horizontal transmission is not unique to cultural systems, however, and the messy truth is that horizontal transfers of genetic information are widespread in biology. At a microevolutionary level, horizontal transfer of genetic material between bacterial cells is extremely common and thought to be an important means of resistance to antibiotics (Barlow 2009). At the macro-level, genes (commonly transposable elements) from one species can become incorporated into the genome of another species via some kind of vector (virus, bacteria, etc.) (Schaack et al. 2010; Peccoud et al. 2017), and hybridiza- tion and introgression (Futuyma 2013; Harrison and Larson 2014) have been increas- ingly recognized as major processes in evolution (Maynard Smith and Szathmáry 1995; Rivera and Lake 2004; Ge et al. 2005). Indeed, recent studies have shown how early human ancestors interbred with Neanderthals and Denisovans and that modern human genomes contain genes from these species (Wills 2011; Huerta-Sanchez et al. 2014). Furthermore, cultural transmission is not necessarily dominated by non-vertical trans- mission, particularly at the macroevolutionary scale. As we shall see below, cultural evolutionary processes may inhibit transmission of cultural traits between populations, meaning that the historical relationships between cultures may be usefully represented using the kind of phylogenetic techniques that are used to represent macro-scale pat- terns of descent in biological species.

So far, we have talked in general terms about the transmission of information, but what is the mechanism by which this form of inheritance occurs? In seeking to show the gen- eral applicability of Darwinian thinking and replication, Richard Dawkins (1976) coined the term ‘meme’ to describe a theoretical unit of cultural inheritance that is analogous to genes. While some authors have tried to develop the meme concept (Dennett 1996; Aunger 2000; Blackmore 2000; Dennett 2006; Brodie 2009), the existence of discrete cultural units is not a necessary precondition for an evolutionary approach to culture (Laland and Brown 2002). The key point is that information is transmitted between indi- viduals with suﬃcient ﬁdelity that the same phenotypic character can be observed over a relevant time span. Models have been developed in which cultural traits are modelled as continuous rather than discrete (Richerson and Boyd 2005). In contrast to genetic systems, where we know a huge amount about the mechanisms of inheritance, the psy- chology and neuroscience of cultural transmission are less well understood and is an important area for future research. However, we can take comfort from the fact that, famously, Darwin knew little about the mechanisms of biological inheritance in devel- oping his ideas. Similarly, our current ignorance about the details of cultural transmis- sion should not prevent us from developing and testing cultural evolutionary models, including understanding how diﬀerent possible inheritance mechanisms might aﬀect the processes of cultural evolution.

**3.2.1.3 Selection and Fitness**

A consequence of the fact that genetic and cultural information have diﬀerent channels and modes of transmission is that genetic ﬁtness and cultural ﬁtness can be quite dis- tinct (El Mouden et al. 2014). Genetic ﬁtness relates to the representation of a particular gene in subsequent generations and to production and subsequent reproduction of one’s own oﬀspring (direct ﬁtness), or indirectly through the oﬀspring of related individuals (weighted by the degree of relatedness). By cultural ﬁtness, I mean the ‘transmission success’ of a particular cultural trait in terms of it being transmitted between individ- uals (i.e. the representation of a trait in the population at a later point in time due to social learning). In some cases, genetic ﬁtness and cultural ﬁtness will be driven by the same processes. If oﬀspring inherit the cultural traits of their parents, and if individuals possessing certain cultural traits leave more oﬀspring than individuals possessing other cultural traits, then the representation of cultural traits in subsequent generations can be aﬀected by natural selection just like any other phenotypic trait. I will return to the relationship between genetic and cultural ﬁtness later in this chapter but in this section, I discuss other selective processes acting on culture.

If individuals choose who to copy at random, then the frequency of a trait in a pop- ulation will not change substantially over time (this is with the caveat that population size is important in this respect – in small populations, drift-like processes may be an important component of change over time). Models of cultural evolution have attempted to explore the eﬀects of diﬀerent psychological learning biases that may create a ‘selection-like’ process, in that they lead to certain cultural traits being more readily transmitted than others (i.e. they aﬀect cultural ﬁtness) (Boyd and Richerson

t0 t1

t0 t1

Figure 3.1 Transmission biases can aﬀect the prevalence of cultural traits over time. Context biases involve information about the situation in which individuals ﬁnd themselves. In the top example, the individuals are following a learning rule that indicates that they should preferentially copy (with some probability and some possibility for error) the most common behaviour in the population. In this case, at time t0, the most common behaviour is for individuals to wear grey. At time t1, two of the individuals that were wearing black have followed this rule and switched to wearing grey. Content biases (*lower panel*) relate to information about the trait itself. In this example, grey is considered a more attractive colour (which could be an innate or learnt preference) and individuals wearing grey are more likely to be copied as a result. By time t1, four individuals have switched from wearing black to wearing grey. 1985b; Henrich 2001; Richerson and Boyd 2005; Mesoudi et al. 2006a; Henrich et al. 2008; Mesoudi 2008). These transmission biases are often categorized as relating to either content or context (Figure 3.1). Content (or direct) biases refer to properties of the cultural trait themselves that make them more or less likely to be copied. Context biases, on the other hand, refer to biases in transmission that are the result of the situation in which a trait is being transmitted. These biases may reﬂect properties of the individuals who are copied (model-based biases) or may relate to population-level properties. Examples of model-based biases would be preferences to copy prestigious or successful individuals (Henrich and Gil-White 2001; Mesoudi 2008). The main examples of population-level biases relate to the existing representation of a cultural trait in the population. Copying can be frequency dependent such that individuals actively assess the frequency of a trait in the population and choose to copy the most common trait (Mesoudi and Lycett 2009). This leads to conformity in the sense that rarer traits will have an even lower probability of being adopted and a popula- tion will tend towards homogeneity over time (even in the absence of ideas that a particular behaviour *must* be followed, or mechanisms for punishing those who do not exhibit such behaviours) (Morgan and Laland 2012; Aplin et al. 2015). Anticon- formity biases, in which individuals would preferentially adopt rare traits, are also possible.

Processing

Figure 3.2 Cultural evolution may be aﬀected by cultural attractors that shape information as it is transmitted between individuals. In this example, a piece of music (*top left*) is represented by a horizontal line with vertical lines representing the beats. A preference for (or bias towards) a regular beat in music acts to make an initially arhythmic piece of music into something that has a more regular beat as it goes through repeated stages of individuals hearing the music (perception), processing it, and then attempting to reproduce the piece of music (production). The actual psychological and/or behavioural mechanism by which such an attractor works could in theory take place at any stage in

the transmission process (e.g. perceptual constraints could mean certain sounds aren’t even registered, or more attention could be paid to certain features during cognitive processing, or mechanical constraints could make certain behaviours easier or more likely than others).

Some researchers have argued that these selection-like processes are not the most important factor aﬀecting change in socially transmitted traits, but rather information received by individuals is transformed and altered by pre-existing knowledge or psy- chological biases. Under this view, certain ideas or concepts may represent ‘cultural attractors’ and channel behavioural variation towards certain outcomes (Figure 3.2). These biases may result from aspects of our innate, evolved psychology, and poten- tially have themselves been shaped by natural selection. For example, socially learned dietary choices may be inﬂuenced by innate preferences for sweet, salty, and fatty foods that would have produced adaptive dietary behaviours throughout much of our evolu- tionary history. Lab-based experimental studies are an important way of studying these issues given their ability to construct scenarios that isolate diﬀerent mechanisms and alternative explanations, and reduce some of the noise present in real-world datasets (Mesoudi 2007; Whiten and Mesoudi 2008; Mesoudi 2016). For example, experimental studies have shown that colour terminology tends to converge on a relatively limited number of terms, potentially as a result of features of our perception systems that are universal across human societies (Xu et al. 2013). Studies of the transmission of music have indicated that humans impose and pass on elements of rhythm when such elements were not present in the original recording (Ravignani et al. 2016). This mirrors observed cross-cultural regularities in features of human music (Savage et al. 2015).

Cultural attractors and ideas of cultural transmission as a transformative process were originally framed as an alternative to the selective mechanisms described above, which assumes that ﬁdelity of transmission is generally high. However, recent approaches have recognized that both processes are probably at play, and that transformative ideas are compatible with existing models of cultural evolution. Cultural attractor theory focuses attention on what actually happens psychologically when information is socially trans- mitted and may be particularly important in understanding widespread or universal features of human culture. However, cultural attractors have not received the same level of formal modelling as selective mechanisms and it is unclear to what extent such trans- formative processes aﬀect the dynamics of cultural evolution at the population level in ways that are not captured by existing models of guided variation and content biases. While transmission biases and cultural attractors have received large amounts of the- oretical attention, the existence or importance of these biases is still an area of emerging research. Cross-cultural studies of these biases will be important as it is likely that the importance attached to diﬀerent sources of information and weighting of diﬀerent psy- chological biases will vary between cultures. For example, food taboos present in some cultures may go against innate preferences, yet may be adaptive especially if information comes from experienced or knowledgeable individuals (Henrich and Henrich 2010), or if they are used as costly markers of group membership (Sosis and Alcorta 2003). An overall picture of how various transmission biases are integrated and combined to shape human behaviour in diﬀerent cultures and contexts remains an important area for future study.

3.3 Insights from Cultural Evolutionary Approaches

The sections above have shown how analogies can be drawn between cultural and genetic evolution, and how evolutionary thinking can be applied to cultural inheritance systems. However, drawing analogies between the processes of biological and cultural change is not by itself very useful. It is therefore important to articulate how this perspective provides a more complete framework for studying behaviour in humans and other cultural species. In the following sections, I provide examples from four areas of study where cultural evolutionary theory helps provide a better understanding of behavioural diversity: adaptation and maladaptive behaviour, cultural history, the evolution of co-operation, and gene–culture coevolution.

3.3.1 Adaptive and Maladaptive Behaviour

The psychological mechanisms by which we acquire cultural information from others is likely to have been shaped by natural selection to enable individuals to behave adap- tively – individuals with brains that learn the wrong things and behave inappropriately end up leaving fewer oﬀspring. However, the dual-inheritance perspective outlined above also recognizes that the dynamics of cultural transmission can lead to individuals behaving in a suboptimal or maladaptive manner. Laland and Williams (1998) used transmission chain experiments in which small groups of guppies, *Poecilia reticulata*, were initially trained to follow a more circuitous and energetically costly feeding route or a less costly shorter route. These founding individuals were gradually replaced by untrained individuals. Even several days after all the founders had been removed, the groups of untrained ﬁsh tended to follow the feeding behaviour of their founders. This indicates that these feeding routes were being socially learned, and that more costly behaviours were being passed on, even when less costly alternatives were available (see also Bates and Chappell 2002). In humans, Durham (1991) argues that the ritual practice of cannibalism amongst the Fore of New Guinea was ultimately maladaptive in that it led to the spread of a deadly, neurodegenerative disorder known as *kuru*. It is estimated that in the 1940s and 1950s, hundreds of Fore people were dying each year due to *kuru*, out of a total population of only approximately 12 000 (Liberski 2013). Such maladaptive behaviours may be sustained due to a number of factors and features of social learning. Model-based copying biases based on status/prestige or similarity can result in the spread of maladaptive behaviours if the models being copied exhibit such behaviours (Mesoudi 2009). Even when social learning is unbiased in this way, other factors that relate to observing the trait and making links between behaviours and outcomes will aﬀect what behaviours get adopted. Tanaka et al. (2009) wanted to understand why a large market still exists for ‘complementary’ medicines and ‘tradi- tional remedies’, which sometimes have poor safety records and for which there is little evidence that they work as intended. They developed a mathematical model of the condi- tions under which eﬃcacious, non-eﬃcacious or even maladaptive medical treatments are able to spread by social learning. The key features of this model were that people adopt a practice based on having witnessed it, but can abandon it if it does not work. Under some circumstances, maladaptive practices could spread because they resulted in longer periods of treatment (i.e. the fact that they don’t work means that people take longer to recover), meaning that more people saw the practice and adopted it. As long as the rate of conversion due to this process is greater than the rate at which individuals will abandon the practice due to its lack of eﬀectiveness, then the maladaptive behaviour can spread. In the *kuru* example above, the decades-long gestation period of the dis- ease meant that the link between cannibalism practices and the disease was diﬃcult to establish, and *kuru* was instead attributed to malevolent sorcery by hostile individuals (Lindenbaum 2008).

Under a dual-inheritance perspective, we might expect to see cultural species exhibit- ing some maladaptive behaviour; social learning mechanisms should on average pro- duce adaptive outcomes but occasionally will lead to stable behaviours that are at odds with genetic ﬁtness. However, how common maladaptive behaviours actually are and the extent to which cultural inheritance leads to maladaptive outcomes are still open ques- tions. Simple social learning mechanisms may create traditions, including arbitrary or maladaptive ones (Franz and Matthews 2010). Thornton and Malapert (2009) used ﬁeld experiments in wild meerkats to show that arbitrary behavioural traditions could arise through copying the behaviour of individuals trained to visit certain landmarks in order to gain a reward. However, these traditions quickly disappeared as individual learning led some individuals to explore other landmarks. So although conformity or other biased social learning mechanisms are not required for traditions to emerge, it may be that they are necessary for enabling maladaptive outcomes to persist over substantial peri- ods of time. Furthermore, if cultural ﬁtness is at odds with genetic ﬁtness then we would expect natural selection to lead to improved social learning capabilities that increasingly bias the acquisition of cultural behaviours towards more adaptive outcomes (Lumsden and Wilson 1980; El Mouden et al. 2014). It is also important to distinguish genuinely maladaptive outcomes (where there are reductions in direct or inclusive ﬁtness from pursuing a behaviour) from behaviours that appear costly but ultimately are associated with other beneﬁts, such that on balance they produce net increases in direct or inclusive ﬁtness. For example, some authors (Dawkins 1993; Blackmore 2000) have argued that religious beliefs are maladaptive and that they constitute a ‘virus of the mind’. However, a number of adaptive explanations for religion have also been put forward, for example that certain religious practices may be costly signals of group membership (Sosis et al.

2007) or that certain religious beliefs may help organize large-scale human societies

(Norenzayan et al. 2014).

The manner in which cultural evolutionary studies analyse the possibility of mal- adaptive behaviour stands in contrast to other evolutionary approaches to investigat- ing human behaviour. Behavioural ecology focuses mainly on adaptive explanations of behaviour (Smith and Winterhalder 1992; Nettle et al. 2013), while evolutionary psy- chology often proposes hypotheses based on maladaptive mismatches between modern and ancestral environments (Barkow et al. 1992; Buss 2015). Rather than having to com- mit ourselves to either end of this continuum, a cultural evolutionary approach can help integrate and bridge these other theoretical perspectives (Mesoudi et al. 2006b). Furthermore, the mismatch view of evolutionary psychology rarely explicitly consid- ers how and why modern environments arise. Cultural evolution helps to explain how humans have shaped these environments and the ﬁtness consequences of such niche construction, as well as the behavioural and psychological responses to such environ- ments. Taking this approach, we can investigate under what conditions maladaptive behaviours are most likely to occur, which can serve as a motivation for testing between competing hypotheses and assessing how common maladaptive behaviours actually are.

3.4 Cultural History

Biologists recognize that evolutionary history plays an important role in explaining the diversity of life. Species may exhibit many similar traits because they share common ancestral species from which these traits have been inherited (Sober 2009). The emer- gence of biological novelty takes place against this background, and in some cases evolu- tionary history may constrain what changes are possible (Arnold 1992; McKitrick 1993; Blomberg and Garland 2002). These shared patterns of ancestry are often represented in the form of phylogenetic trees. As a description of evolutionary history, phyloge- nies are important both as means of structuring biological diversity (i.e. providing us with a taxonomy) and as a scaﬀold for testing hypotheses about the processes of evo- lution that have shaped this diversity over space and time (Gregory 2008; Nunn 2011). By understanding culture as a system of inheritance, we can similarly appreciate the importance of cultural evolutionary history in helping us explain both the patterns of human cultural diversity and the processes that have generated this diversity (Mace and Holden 2005; Currie 2013). An important area of cultural evolutionary research, that has enabled progress to be made in addressing long-standing questions in the social sciences, has been the application of ‘tree thinking’ and phylogenetic methods to study cultural macroevolution. It has long been appreciated that languages can often be well represented by a branching tree with a nested hierarchy of historical relationships (Hock and Joseph 2009). Traditionally, linguists have relied on rather subjective means to create these family trees and to locate the origins of these languages in time and space. In the last two decades, researchers have begun to apply formal phylogenetic and phylogeographic methods from evolutionary biology to construct evolutionary trees of language and use these to more rigorously test hypotheses about the homelands and routes taken during large-scale demographic expansions (Greenhill and Gray 2005; Gray et al. 2011; Currie 2013). Various techniques have been used but such studies generally take linguistic features that are comparable across languages (e.g. similarities in lists of words with the same meaning from diﬀerent languages) and analyse them using the same kind of phy- logenetic inference techniques that can be applied to morphological data in biology. For example, phylogenetic studies provide support for a hypothesis that links the spread of Indo-European (IE) languages to the emergence of farming. Analyses of lexical data pro- duce phylogenetic trees that place the origin of IE in Anatolia (in modern-day Turkey) (inferred in relation to the structure of the tree, and more recently through explicit phylogeographic modelling), and indicate that IE languages began diverging around 9000 years ago (Gray and Atkinson 2003; Bouckaert et al. 2012; Currie 2013). These kinds of dispersal hypotheses have been tested across a number of diﬀerent language families in diﬀerent parts of the world, including Island Southeast Asia and the Paciﬁc (Gray et al. 2009), sub-Saharan Africa (Currie et al. 2013) (Figure 3.3), South America (Heggarty 2008), and the Middle East (Kitchen et al. 2009). Phylogenetic inference techniques have also been applied to test other cultural evolutionary hypotheses using archaeological data (Coward et al. 2008), material culture (Tehrani et al. 2010), and other aspects of culture (Eagleton and Spencer 2006; Matthews 2012; Brown et al. 2014). Once we have trees representing how diﬀerent cultures are connected, we can also apply phylogenetic comparative techniques to test other hypotheses about cultural evo- lution (Harvey and Pagel 1991; Mace and Pagel 1994; Currie 2013; Currie and Meade 2014). By mapping cultural traits or features of social organization onto phylogenetic trees, we can investigate the processes that lead to variation across societies in these traits. For example, Currie et al. (2010a) examined the evolution of political organization across societies in Island Southeast Asia and the Paciﬁc, and showed that hierarchical complexity of societies evolved through sequential, incremental increases in the num- ber of decision-making levels present in a society, with decreases in complexity also occurring. This is consistent with the idea that societies get bigger by joining together smaller groups, and that they need to develop new institutions and other social mecha- nisms in order to do this in a stable manner (see below). These techniques can also test adaptive hypotheses about the relationships between diﬀerent traits or aspects of their ecology. Holden and Mace (2005) showed that across societies in sub-Saharan Africa, the adoption of cattle keeping led matrilineal societies (in which wealth is passed down the female line, and were typically associated with small-scale farming) to change inher- itance systems and pass wealth down through the male line (patriliny) (see Figure 3.3). This is consistent with adaptive hypotheses that argue that parents should invest prefer- entially in one sex or the other depending on the prevailing socio-ecological conditions (Holden et al. 2003). A number of issues remain about the application of phylogenetic methods to cul- tural systems. A common reservation is that horizontal transmission or other forms of

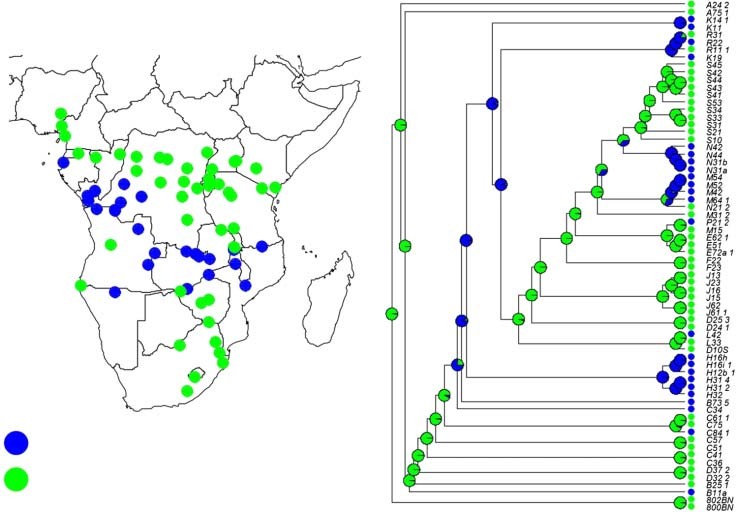
6

1

2 5

4 3

3 5 4

1

6

2

Matrilineal inheritance

Patrilineal and other forms of inheritance

Figure 3.3 Phylogenetic techniques can be applied to study cultural evolution. In this example, the historical relationships between societies from across a large area of sub-Saharan Africa (*left*) can be represented by a phylogenetic tree (*right*). This tree was constructed using comparative linguistic data and is based on analyses in Currie et al. (2013) (codes at the tips refer to diﬀerent languages). The inferred locations of numbered nodes are shown on the map and indicate the main route taken in the large-scale ‘Bantu’ population expansion that began from a homeland in modern-day Nigeria/Cameroon (node 1) around 3–5000 years ago. Other inferences can be made by mapping other traits onto such trees. Here, we can see variation across societies in inheritance systems in terms of whether group membership and property inheritance are traced through the female line (matrilineal inheritance), whether it traced through males (patrilineal inheritance), or whether some other system is employed (data taken from Holden et al. 2003). Based on the distribution of this trait

across the tips of our tree, we can infer whether ancestral societies were more likely to be matrilineal or practise some other form of inheritance (the pie charts at the nodes represent proportional probabilities of these two possibilities) (see Currie et al. 2010a). From this analysis it can be seen that the society that was ancestral to all modern-day Bantu societies (node 1) did probably not practise matriliny, and that matrilineal inheritance probably emerged at several diﬀerent points in the evolutionary history of the societies (e.g. node 2).

non-vertical inheritance (e.g. ‘hybridization’ or large-scale ‘blending’ of cultures, dialect chains, etc.) may be more common in cultural systems and thus these techniques are not appropriate (Borgerhoﬀ Mulder et al. 2006; Nunn et al. 2006). However, transmis- sion isolating mechanisms (TRIMs) can decrease the probability that cultural traits from another group will be copied, even in cases where individuals might physically move between and join other groups (Durham 1992). TRIMs can be active in that they identify the source of cultural traits and either favour traits that originate in the local population (e.g. active promotion of conformity, norms encouraging parochialism, or promotion of an individual’s ethnic group) or discourage the adoption of traits from other pop- ulations (e.g. xenophobic norms). For example, the Academie Francaise is an oﬃcial body in France that tries to prevent anglicization of the French language, and even recommends and promotes the use of new words derived from French rather than the adoption of loanwords to describe new terms (Pagel and Mace 2004). TRIMs can also be more passive and can occur if copying is frequency dependent such that individuals will tend to copy the behaviour of the majority of individuals. In such a scenario, this would mean that if a limited number of migrants enter a population, they are unlikely to transmit their behaviour to individuals such that it spreads widely in the new popula- tion. Furthermore, as previously stated above, this view often underestimates the extent to which, at the macro-scale, non-vertical forms of transmission occur in biological evolution. Ultimately, whether horizontal transmission aﬀects phylogenetic analyses is an empir- ical question. Measures of support are often used to assess the degree to which the data being used can be explained by a branching model of evolution (Douady et al. 2003; Collard et al. 2006). The use of Bayesian methods of inference, which allow us to assess and incorporate various sources of uncertainty into our analyses, is particularly impor- tant in this respect (Greenhill and Gray 2005; Holden et al. 2005). We can also assess how sensitive our inferences are to diﬀerent assumptions. Previous simulation work has demonstrated that both phylogenetic inference (Greenhill et al. 2009) and comparative methods (Currie et al. 2010b) are robust to degrees of non-vertical transmission that are typically seen in the kinds of cultural datasets to which such methods have been applied. A challenge for future work in this area will be to reﬁne these techniques so as to consider the mode of horizontal transmission and the eﬀect it may have on analyses (Currie et al. 2010b). Just as in studies of biological evolution, the use of phylogenetic networks, cophylogenetic techniques (such as those used in analyses of host–pathogen coevolution) (Tehrani et al. 2010; Baudet et al. 2015), and comparative techniques that model diﬀerent transmission processes (such as modelling the eﬀects of both phylogeny *and* geography) (Freckleton and Jetz 2009; Towner et al. 2012) are likely to be important in this regard. There are clearly challenges involved in applying phylogenetic methods to cultural systems but these techniques have proven extremely valuable in helping us move beyond purely verbal arguments and plausible narratives. By employing these kinds of explicit quantitative approaches, we can better frame questions and provide more explicit tests of competing hypotheses about cultural macroevolution.

**3.5 Culture and the Evolution of Co-operation**

Humans are a highly social and co-operative species. Co-operation presents an evolu- tionary puzzle because individuals engage in some kind of costly behaviour that provides beneﬁts to other individuals (West et al. 2007; Gardner and Foster 2008; Cronk 2015). Even when individuals gain some kind of net advantage from co-operating, such col- lective behaviours run into many potential challenges (Olson 1965). The production of public goods is vulnerable to free-riding as people can gain the beneﬁts of the public good without paying the costs. The collective use of common-pool resources is vul- nerable to the ‘tragedy of the commons’ as those who do not restrain themselves from using the resources will do better, thus leading to the overexploitation of the resource (Ostrom 1990). Common solutions to these problems seen in biological systems, such as reciprocity (Trivers 1971; Nowak and Sigmund 2005) and inclusive ﬁtness (Hamilton 1964), run into diﬃculties when trying to explain the existence of the huge societies composed of millions of genetically unrelated individuals that we live in today.

Culture may play an important role in enabling large-scale co-operation in humans. However, social learning by itself does not necessarily promote co-operation. In fact, it may even be harmful especially if social learning is pay-oﬀ biased, as free-riders are more likely to be copied due to the fact that their pay-oﬀs are highest (Lehmann et al.

2008). While these models provide important insights, they do not take into account the speciﬁc ways in which humans are structured into groups, which is an important feature of human social organization (Boyd and Richerson 2010). In particular, culture enables groups to construct social norms and rules (or institutions) that help stabilize co-operative behaviour (Richerson and Henrich 2012; Powers et al. 2016). Furthermore, the group-level nature of cultural variation can enable co-operative behaviours to spread through a process of cultural group selection (CGS) (Richerson et al. 2014).

Human societies are structured by what we refer to as ‘institutions’, which are col- lections of interrelated social norms and rules that proscribe roles and set expecta- tions about social interactions, including the consequences of not following these rules (Currie et al. 2016). These rules can alter the pay-oﬀs to diﬀerent strategies and in eﬀect change a ‘game’ in which the evolutionarily stable solution is to free-ride to one in which the best strategy is to co-operate (Powers et al. 2016). This can happen, for example, when the rule states that if an individual defects (i.e. doesn’t uphold their end of an agree- ment) then they will receive some kind of punishment. For example, in irrigation systems in Nepal, communities have rules about maintenance of the irrigation system, and how much water can be taken (Anderies and Janssen 2016). If an individual is deemed to have not followed the rules then they receive a punishment. The transgressor has one of their cows placed in a pen in the middle of the village. Since the community is small, everyone in the village knows whose cow this is, and also other villagers are able to take milk from this cow. The cow is only released once a ﬁne is paid. Therefore, someone who breaks the irrigation rules suﬀers directly by having to pay the ﬁne and from losing the ability to milk the cow whilst it is in the pen. They also suﬀer reputational damage which, in turn, may entail opportunity costs by inhibiting future interactions with other community members.

In humans, norms and institutions are made possible through a combination of language, other forms of social learning, and aspects of our social cognition involving shared intentionality and theory of mind. Language is important in discussing, agreeing, and communicating what the rules are. Social learning is important in transmitting what the rules are to everyone in the group, and individuals can also learn what happens when rules are broken and the likely pay-oﬀs for either co-operating or defecting by observing others. For institutions like this to work, transgressions must be punished, and be seen to be punished, in order for compliance with the rules to be maintained and co-operation to be sustained (Ostrom 1990; Boyd and Richerson 1992; Anderies and Janssen 2016).

To what extent institutions are possible in non-linguistic species or in species without our psychological capabilities is an open question (Akçay et al. 2013). These features certainly make it easier to develop and transmit rules, but conceivably mechanisms surrounding reputation (and indirect reciprocity), punishment, and expectations about behaviour and the consequences of defecting could be transmitted via social learning in other species to create behavioural patterns that were similar in some respects to institutions. Because they appear to be peculiar to humans, institutions have received relatively little attention in evolutionary models of co-operation, even when applied to humans. While institutions have been a focus of study in several social science ﬁelds, understanding how institutions interact with other culturally inherited traits and how both evolve together over time has received less formal attention and is an important topic for future research in cultural evolution (Currie et al. 2016).

Features such as institutions and social norms are group-level emergent properties of the interactions between individuals that are made possible by social learning (Smaldino 2014). This has implications for how selection can act on groups and lead to the spread of co-operative behaviour. If there is competition between groups then traits that lead to increased group survival, reproduction or recruitment can spread via a process of CGS (Richerson et al. 2014). In genetic models of group selection, the genetic vari- ation between groups that is required for selection at this level to act upon can be destroyed by even low levels of migration of individuals between groups (Williams 1966; Okasha 2008). However, cultural evolutionary processes may create conditions under which selection between groups can become an important force. As we saw in a previ- ous section, frequency-dependent processes and active conformism can act to maintain cultural variation between groups even in the face of physical migration of individuals (Boyd and Richerson 1985b; Bell et al. 2009). Importantly, as we are dealing with a cul- tural process, the extinction of groups does not have to involve the death of all group members (Soltis et al. 1995). Individuals can be incorporated within the victorious group or disperse into other groups. The key point is that the previous group and its associated norms and institutions no longer exist. For example, Lindenbaum (2008) describes how the Fore of New Guinea defeated a neighbouring group in warfare and absorbed those who were not killed; the survivors had their origins ‘made invisible’ and they ‘became Fore’ (p. 3716). Groups may also go extinct if individuals migrate based on the traits that diﬀerent groups exhibit, or due to the perceived success of diﬀerent groups (Boyd and Richerson 2010). Biased copying of traits, based either on the traits themselves or indi- rectly on the success of groups that possess them, can also lead to the spread of certain traits and has been argued to bea form of CGS. The idea of CGS has not met with universal acceptance (see Richerson et al. (2014) and associated commentaries). This appears to be partly due to the long and contro- versial history of group selection in biology and a conﬂation of CGS models with early naïve group selection models in biology. More generally, there also appears to be a con- fusion around how terms are deﬁned and used in diﬀerent research traditions: What are the most salient units of analysis, and what are appropriate measures in attempting to assess these models? An important issue that is common to all group selection mod- els is how group ﬁtness should be measured (Okasha 2008). Is it an additive measure of individual ﬁtness? The number of descendent groups? The stability or longevity of a group? Or simply the frequency of the group-level trait in the population? Indeed, it appears that the diﬀerent ‘modes’ of CGS mentioned above (group extinction, migra- tion, biased adoption) are associated with diﬀerent measures of ﬁtness. Furthermore, the relationship between cultural group ﬁtness and individual genetic ﬁtness in verbal descriptions of CGS is not entirely clear and is often not dealt with explicitly. This has consequences for understanding the extent to which culture may have shaped genetic evolution (see below) in relation to the evolution of genetic traits that would help canal- ize prosocial behaviours.

A lot of the research on CGS to date has focused on establishing whether the assumptions underpinning CGS are supported. For example, researchers have used cross-national survey data to assess the extent to which suﬃcient variation in traits exists between groups (Bell et al. 2009; Richerson et al. 2014). Measures of the ﬁxation index (FST, which quantiﬁes the degree of variation between populations) were calcu- lated to be roughly an order of magnitude larger for cultural traits than genetic FST, indicating that the range of scenarios under which CGS might be an important force is greater than for genetic group selection. The results also indicated that for many cultural traits, the FSTs were suﬃciently high that only relatively small group-level beneﬁts would be needed to outweigh individual-level costs. In an analysis of cultural group extinction in New Guinea, Soltis et al. (1995) found that rates of extinction varied from about 2% to 32% of groups per generation, and estimated that under such conditions traits would take 500–1000 years to spread through the metapopulation. While this rate of change makes CGS an unlikely mechanism for changes in many cultural traits, it could explain changes in slowly evolving traits such as political institutions (Carneiro

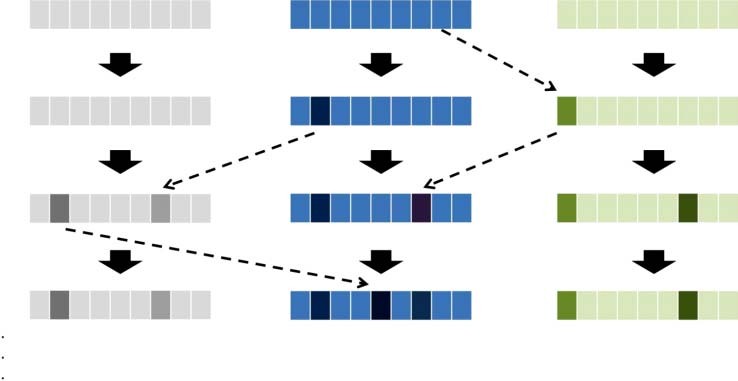
1978; Spencer and Redmond 2001; Turchin et al. 2013). However, some authors have conducted empirical studies of co-operation in diﬀerent populations that challenge the assumptions about the degree of variation within and between groups, and the extent to which competition between groups is associated with in-group co-operation (Lamba and Mace 2011; Mace and Silva 2016).

Future work also needs to test the predictions of CGS hypotheses, in order to assess how well they can explain real-world data (Turchin and Currie 2016). As an example of the kind of approach that is possible, Turchin et al. (2013) developed an agent-based sim- ulation within a CGS framework and matched the outputs of these models against data on the historical distributions of large-scale societies. The results of this study suggest that between-group competition can select for increasing group size which is facilitated by the adoption of costly institutions involved in complex social organization. CGS is potentially an important process in cultural evolution, and the challenge for future work in this area is to clarify certain concepts and provide further empirical tests of both the assumptions and predictions of CGS hypotheses.

3.6 Gene–Culture Coevolution

The above discussions have largely considered cultural evolution as a separate process from genetic evolution. However, the messy truth is that the two are intertwined (Figure 3.4). We have already discussed how genes keep cultural evolution on some- thing of a long leash, and that genes will build organisms that will on average learn from others in ways that are adaptive. In this section, I give further consideration to the possibility that the two can coevolve such that biological evolution can have important consequences for cultural evolution and vice versa, a process we can call gene–culture coevolution (Lumsden and Wilson 1980; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985b; Durham 1991; Feldman and Laland 1996; Laland et al. 2010).

The adoption of a new cultural practice can expose genes to new selection pres- sures in two ways (Richerson et al. 2010). First, cultural traits can make survival and reproduction possible in novel environments and facilitate migration into environments to which genes had not previously been exposed. As noted above, anatomically modern

Genes Culture t0

t1

a t2

b

t3

Environment c

d

*Figure 3.4 Genes and culture represent diﬀerent systems of inheritance which can coevolve. Here genes, culture, and the environment are represented in an artiﬁcially abstract manner as collections of speciﬁc units at diﬀerent points in time (t0, t1, …tn). Changes in diﬀerent aspects of these systems are represented by changes in colour. Filled black arrows represent the biological inheritance of genes, transmission of cultural information, and continuity over time in the environment (sometimes referred to as ‘environmental inheritance’). Aspects of one system can permanently alter or cause evolutionary change in another system. Examples are given of (a) a cultural innovation creating a novel selection pressure on a gene, (b) a genetic mutation that facilitates a new cultural trait, (c) a cultural modiﬁcation of the environment, that (d) feeds back and causes a response in a diﬀerent aspect of culture.*

human populations that left tropical Africa were able to move to cooler environments around the world due to the cultural evolution of suitable clothing, shelter, and the use of ﬁre. Exposure to these new environments selected for genetic changes associated with more robust physiques and lighter skin pigmentation, that were better adapted to colder temperatures and lower light levels. Under this mechanism, the relationship between cultural evolution and biological evolution is somewhat indirect, and might be more accurately termed *culture-mediated genetic evolution*.

Second, the adoption of cultural practices can also lead to more direct selection pressures whereby the eﬀectiveness of a cultural adaptation is supported or enhanced by subsequent genetic changes. Perhaps the most studied example of *direct gene–culture coevolution* is the adoption of dairy farming and the evolution of lactose tolerance (Holden and Mace 1997; Tishkoﬀ et al. 2007; Itan et al. 2009; Laland et al. 2010; Richerson et al. 2010). Globally, drinking milk makes most adults ill. This is because the production of the enzyme for digesting milk (lactase) is switched oﬀ in most individuals after infancy. The ability to drink and digest milk provides certain adaptive advantages – it provides a regular source of calories and important nutrients such as vitamin D and calcium. Genetically, lactose tolerance is linked to the possession of the appropriate allele of a single gene (MCM6). The frequency of individuals possessing the lactose tolerance allele is higher in cultures that have a history of keeping sheep, goats, or cattle and commonly drink milk from these animals.

Direct gene–culture coevolution can also occur when a cultural practice or form of social organization creates a change in the social or external environment leading to a change in genetic selection pressures. A potential example is yam farming in Africa and sickle cell anaemia. Yam farming involves chopping down forests, which leads rain to collect and create standing bodies of water, which is an environment conducive to malaria-bearing mosquitoes. It is argued that this drove subsequent selection on genes that cause sickle cell anaemia, which can lead to premature death but also provides pro- tection against malaria (Durham 1991) (but see below). The genetic changes that occur in both culturally mediated genetic evolution and direct gene–culture coevolution can of course result in further feedback processes such that the cultural change is stabilized by the genetic changes.

The theoretical possibility of gene–culture coevolution is long established, and can be more generally linked to the ideas of niche construction (Odling-Smee et al. 2003) (see Figure 3.4) and the Baldwin eﬀect (i.e. that learned behaviour can in certain cir- cumstances aﬀect genetic evolution) (Sznajder et al. 2012). Whilst there has been a lot of theoretical development of the idea of gene–culture coevolution (including a large num- ber of mathematical models), empirical studies and concrete examples of gene–culture coevolution have been fewer. The evolution of lactose tolerance remains very much the go-to example of gene–culture coevolution due to the twin facts that the genetics under- lying lactose tolerance are relatively simple and it relates to a cultural innovation that occurred relatively recently in certain parts of the world.

Recent years have seen an explosion in our knowledge of human genetics and this may help to provide evidence for gene–culture coevolution. Genetic and genomic techniques enable us to identify regions of the genome that show statistical signatures of having undergone selection (Hawks et al. 2007; Cochran and Harpending 2010; Laland et al. 2010; Richerson et al. 2010). The function of many putatively selected genes can be inferred based on previous knowledge or inferences about genotype–phenotype relationships (e.g. genetic screens, knock-out studies, gene expression analysis). A pattern emerges from these analyses (Tishkoﬀ 2015) in that they commonly relate to diet (detoxiﬁcation of plant secondary compounds, alcohol metabolism, digestion of milk and dairy products, processing of high levels of dietary fat in Inuit populations), immunity or responses to pathogens (e.g. sickle cell anaemia in response to malaria, cholera resistance), or responses to physical environmental conditions (e.g. cold climate, altitude, light skin pigmentation in response to low levels of vitamin D, and short stature in rainforest-dwelling populations). While in all these cases it is clear to see how conditions could aﬀect survival and reproduction and that biological responses would increase genetic ﬁtness, many of these examples may reﬂect culture-mediated genetic evolution rather than direct gene–culture coevolution.

Another possibility is that absence of evidence really is evidence of absence. There are a number of reasons why culture may not exert enough of a selective force on genes for coevolution to be important. First, cultural innovations could reduce selective pres- sures on genes. If a novel environment presents some kind of adaptive problem that can be solved genetically or culturally, and a cultural solution is found, it will reduce the strength of selection acting on genes, making genetic evolution less likely. Here again is a potential reason why lactose tolerance is a convincing example; the physiological ability to digest lactose in later life is a biological process for which a cultural response is more diﬃcult (although certain milk-processing techniques such as cheese making and ageing reduce lactose content). Another potential factor aﬀecting the strength of selection on genes is the rate at which culture evolves. Given that cultural transmission is not linked to reproduction then cultural evolution can occur at a faster rate than genetic evolution (Perreault 2012), meaning that the eﬀective environment is not consistent enough to incur a genetic response. This is not to say that all cultural change is extremely rapid, and many cultural traditions can persist over many generations. We have a lot of evidence that human genes have been under selection in recent human history and we can make plausible arguments for the role of culture in either mediating or driving such adaptations. Future work will need to go beyond such plausi- ble narratives and more rigorously test gene–culture coevolutionary hypotheses against competing explanations. For example, Itan et al. (2009) use demographic simulation models ﬁtted to modern genetic data in combination with information from ancient DNA and archaeology in order to test more rigorously the timing, location, and strength of selection on alleles related to lactose tolerance. Ideas relating to earlier stages of human evolution may prove tricky to assess in this respect. A gene–culture coevolu- tion account of the emergence of the human language faculty is plausible, but is hard to test as we know so little about the early stages of language evolution. However, our abil- ity to assess such hypotheses can increase if we know more about more recent examples and the conditions under which gene–culture coevolution is most likely to occur.

So while gene–culture coevolution represents an important process in some aspects of human adaptation, the presence of culture does not automatically mean that gene–culture coevolution will be a major factor in explaining behavioural diversity. This has implications for understanding the potential importance of the eﬀects of culture or social learning on genetic evolution in other species. There are currently few convincing examples of gene–culture coevolution in non-human animals. The socially learned behaviour of using marine sponges whilst foraging has been shown to be linked with geographical patterns of mtDNA genetic structure due to the fact that this sponging behaviour is transmitted from mothers to oﬀspring (Kopps et al. 2014). This, however, represents correlated evolution between genes and culture rather than evidence that any particular alleles have been selected due to this sponging behaviour. Situations where socially learned behaviours have enabled species to move into novel environments or be exposed to new foodstuﬀs, or where social learning has led to environmental modiﬁcations may represent potential candidates for assessing the existence of culturally inﬂuenced genetic selection in other species. The human reliance on culture as a means of adaptation and our capacity for cumulative culture, with high-ﬁdelity transmission and long-lasting behavioural traditions, may mean that gene–culture coevolution is more likely in humans than other species.

**3.7 Conclusion.**

From the above discussion, it can be seen that there are important analogies to be drawn between the processes of genetic and cultural evolution. There are also important diﬀerences in the mechanisms of these two inheritance systems and we should not seek to constrain our understanding of evolutionary processes by insisting that genes are the only important system of inheritance. As Mesoudi (2011) has argued, cultural evolution can be characterized as Darwinian although it is not necessarily neo-Darwinian.

Variation in cultural traits exists and can be generated by a number of processes, some of which may be essentially random, some of which are more guided. These traits can be inherited or transmitted between individuals and populations, but are not restricted to the parent-to-oﬀspring route. The frequency of traits within a population can be shaped by diﬀerent transmission biases leading to selection of diﬀerent traits. Furthermore, if there is competition between groups, then cultural variation between groups may explain which groups win out. Also, while the possibility that selection can occur in cultural systems is important to recognize (and underlines the relevance of taking an evolutionary approach), cultural change may also be shaped by non-selective drift-like mechanisms or transformative psychological biases. Overly rigid attempts to apply genetic mechanisms to cultural evolution have not proven to be productive frameworks for investigating human behaviour. For example, ‘selectionist’ approaches in archaeology (Dunnell 1980) attempted to argue that all cultural mutations were random and that changes in the frequency of artefacts found in the archaeological record could be explained by natural selection aﬀecting the biological ﬁtness of populations (Boone and Smith 1998). Similarly, advocates of ‘memetic’ approaches to cultural evolution focused too heavily on trying to draw parallels between genes as units of biological evolution and memes as units of cultural evolution, when such a step is not necessary (Laland and Brown 2002).

The modern cultural evolutionary perspective helps illustrate the importance of not restricting evolutionary explanations to genetic changes. If we focus too narrowly on genetic evolution, we risk ‘missing the phenotype’. Emphasizing phenotypes is partic- ularly pertinent for at least two reasons. First, natural selection generally acts on phe- notypes rather than directly on genes. Second, for behavioural biologists the phenotype represents the features of organisms we directly observe and is the thing we want to explain. For example, in discussing the potential for maladaptive behaviour caused by cultural inheritance, El Mouden et al. (2014) recast this in genetic adaptationist terms as being simply the genetic system not yet at equilibrium, or constraints on the geneti- cally determined mechanisms that shape behaviour. However, by taking this view, there is a risk of missing what it is about the cultural trait or the context of the situation that leads traits that are genetically deleterious to spread. While it is possible, and per- fectly valid, to frame things around the causes and consequences of genetic evolution, such an approach leaves unexplained important aspects of the processes that ultimately shape phenotypes, including behaviour. Taking a dual-inheritance perspective provides a broader framework in which to assess competing hypotheses about the function of behaviours.

In this chapter, I have attempted to demonstrate the ways in which this approach is able to integrate existing ﬁndings and provide novel insights, but also stressed some of the important goals and challenges of future research in this area. I have argued that explic- itly incorporating culture as a system of inheritance, which can change via evolutionary processes of descent with modiﬁcation, is essential for understanding behavioural diver- sity in species that rely to a great extent on social learning. Rather than culture being something that sets us apart from the rest of the animal kingdom, this scientiﬁc approach to culture helps illustrate the continuities between ourselves and other species. This per- spective helps demonstrate that both genetic and cultural information are important for shaping the behaviour of animals, but equally that genetic and cultural processes are not independent: culture and cultural evolution relies on genetically shaped biological