Exploring gene–culture interactions: insights from handedness, sexual selection and niche-construction case studies

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Genes and culture represent two streams of inheritance that for millions of years have flowed down the generations and interacted. Genetic propensities, expressed throughout development, influence what cultural organisms learn. Culturally transmitted information, expressed in behaviour and artefacts, spreads through populations, modifying selection acting back on populations. Drawing on three case studies, I will illustrate how this gene–culture coevolution has played a critical role in human evolution. These studies explore (i) the evolution of handedness, (ii) sexual selection with a culturally transmitted mating preference, and (iii) cultural niche construction and human evolution. These analyses shed light on how genes and culture shape each other, and on the significance of feedback mechanisms between biological and cultural processes.

Keywords: gene–culture coevolution; niche construction; handedness; sexual selection; human evolution; evolutionary psychology

1. GENE–CULTURE COEVOLUTION

With the human genome sequenced, attention has been focused on analyses of the genetic data that have been generated. One such set of analyses are attempts, by mathematically minded geneticists, to detect statistical signatures in the genome of recent, rapid selection—genes favoured by natural selection over the last 100 000 years (Sabeti *et al.* 2006, 2007; Voight *et al.* 2006; Wang *et al.* 2006; Nielsen *et al.* 2007; Williamson *et al.* 2007). Such signals include high-frequency alleles in linkage disequilibrium, unusually long haplotypes of low diversity, and a variety of other signatures. While relatively sensitive statistical tests for positive selection have been developed, such methods are in their infancy (Wang *et al.* 2006). Rather than giving absolute numbers of selected genes, in definitive terms, the analyses specify the likelihood that specific genes have been subject to a recent selective sweep, which means that it is difficult to give a clear answer as to precisely how many genes are involved. Nonetheless, a reasonable reading of the data suggests that, thus far, somewhere between a few hundred and a couple of thousand human genes have been identified, which show signals of very strong and recent selection. The best-known cases are alleles that provide resistance to diseases such as malaria, and alleles that allow the metabolism of lactose in cow's milk.

One of the more intriguing categories, well represented (more than 15%) in inferred selective events, is neuronal function (Wang *et al.* 2006), including the serotonin transporter (*SLC6A4*), glutamate and glycine receptors (*GRM3*, *GRM1* and *GLRA2*),

olfactory receptors (*OR4C13* and *OR2B6*), synapse-associated proteins (*RAPSN*) and a number of brain-expressed genes with largely unknown function (*ASPM* and *RNT1*). There is evidence that the evolution of nervous system genes has been accelerated in humans (Dorus *et al.* 2004), with faster evolution of gene expression in the human brain compared with other primates (Wang *et al.* 2007) and with an increased rate of changes in the genomic regions responsible for the regulation of brain development in the human genome (Pollard *et al.* 2006). In other words, a substantive proportion of recently favoured genes are expressed in the human brain, which has undergone significant recent remodelling.

Humans possess approximately 25 000 genes, so researchers should not be surprised that a small proportion shows signs of recent selection. Moreover, a substantial fraction (perhaps even a quarter) of human genes are expressed in the brain so, even allowing for slower evolution in brains than elsewhere as molecular insights from comparison of human and chimpanzee genome imply (Hill & Walsh 2005), we have every reason to expect recent evolution of the human brain. Minimally, a small subset of neural genes, and perhaps many more, have been targets of positive selection (Hill & Walsh 2005). Yet the dominant view within North American evolutionary psychology has been that our species has undergone comparatively little evolutionary change in recent millennia, particularly with respect to mental adaptations, which were regarded as products of resistant-to-change gene complexes (Cosmides & Tooby 1987). I suggest that the large numbers of human genes now known to have been subject to recent positive selection, including those expressed in the brain and behaviour, are an embarrassment to this evolutionary psychology viewpoint.

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Nonetheless, frequent signs of recent selection make a lot of sense when one considers the dramatic changes in selection pressures that our species has experienced. Among other challenges, in the last 100 000 years, humans have spread from East Africa around the globe, experienced an ice age, begun to exploit agriculture, witnessed rapid increases in densities and, by keeping animals, experienced a new proximity to animal pathogens. They have also domesticated hundreds of species of plants and animals (Smith 2007). What is immediately striking about these major challenges is that all except one (the ice age) have been self-imposed: that is, human activities have modified selection pressures, for instance by dispersing into new environments with different climatic regimes, devising agricultural practices or domesticating livestock.

These activities are instances of human 'niche construction' (the modification of environments by organisms), which, I suggest, have precipitated evolutionary responses in the human genome (Laland *et al.* 2001; Odling-Smee *et al.* 2003). However, the capacity for culture is clearly a critical factor underlying the potency of human niche construction: agriculture was not independently invented by each farmer, nor is its presence an unlearned maturational outcome of human gene expression. Moreover, even in the case of climatic regimes, beyond human control, human 'cultural niche construction' would have strongly affected the intensity of selection, for instance, by manufacturing clothes or shelters, or controlling fire.

The argument that human cultural niche construction has been a co-director of recent human evolution is essentially the conclusion reached by the geneticists analysing the human genome:

> Homo sapiens have undoubtedly undergone strong recent selection for many different phenotypes…. Given that most of these selective events likely occurred in the last 10,000–40,000 years…it is tempting to speculate that *gene–culture interactions directly or indirectly shaped our genomic architecture*
> (Wang *et al.* 2006, p. 140, my italics)

This perspective is also supported by some well-researched cases of gene–culture coevolution. For instance, there are several examples of culturally induced genetic responses to human agriculture (Odling-Smee *et al.* 2003). The best known is the coevolution of the gene for lactose absorption and dairy farming (Durham 1991). There is now compelling theoretical and empirical evidence that dairy farming spread prior to the allele for lactose absorption, generating a selection pressure favouring this gene in some human pastoralist societies (Feldman & Cavalli-Sforza 1989; Holden & Mace 1997; Burger *et al.* 2007). Another is provided by a population of Kwa-speaking yam cultivators in West Africa (Durham 1991). These people cut clearings in forests to grow crops, with a cascade of consequences. The clearings increased the amount of standing water, which provided better breeding grounds for mosquitoes and increased the prevalence of malaria. This, in turn, modified natural selection pressures in favour of an increase in the frequency of the sickle-cell *S* allele because, in the heterozygous condition, the
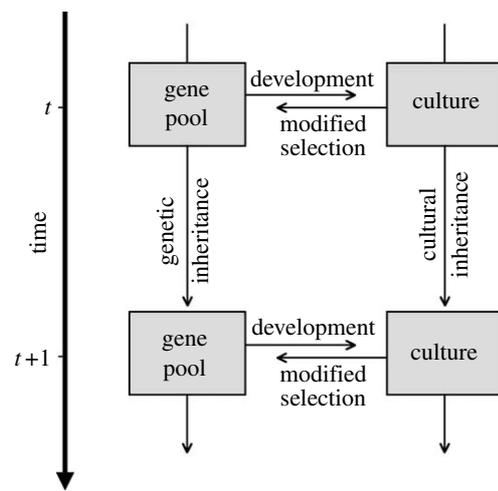

Figure 1. Gene–culture coevolution. Genes and culture are two interacting forms of inheritance. Genetic propensities, expressed throughout development, influence what cultural organisms learn. Culturally transmitted information, expressed in behaviour and artefacts, modifies selection acting back on the genome.

S allele confers protection against malaria. The fact that other Kwa speakers, whose agricultural practices are different, do not show the same increase in the *S* allele frequency supports the conclusion that cultural practices can drive genetic evolution (Durham 1991). It is not just yam cultivation that generates this pattern of selection: modern Asian tyre manufacturing is having the same effect, with mosquitoes infesting pools of rainwater that collect in tyres stored outside, and tyre export contributing to the spread of malaria and dengue (Hawley *et al.* 1987). Malaria became a major health problem only after the invention of farming, a human cultural niche-constructing practice, yet there are several additional genes that appear to have been favoured by selection because they provide resistance to malaria. These include *G6PD*, *TNFSF5* and alleles coding for haemoglobin C and Duffy blood groups (Balter 2005; Wang *et al.* 2006). There is also evidence that genes have been selected because they confer resistance to other modern diseases, including AIDS and smallpox (*CCR5*) and hypertension (*AGT*, *CYP3A*; Balter 2005). In all these cases, human modifications of the environment triggered or modified selection on human genes.

The view that genes and culture coevolve was first suggested by pioneers of the field of 'gene–culture coevolution' nearly 30 years ago (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; see Laland & Brown (2002) for an overview). These researchers view genes and culture as two interacting forms of inheritance, with offspring acquiring both a genetic and a cultural legacy from their parents and, in the latter case, other conspecifics too (figure 1). Genetic propensities, expressed throughout development, influence what cultural organisms learn. Culturally transmitted information, expressed in behaviour and artefacts, spreads through populations, modifying selection acting back on populations. Mathematical gene–culture coevolutionary models have shown how our views of human evolution change when both inheritance systems are taken into account (Feldman & Cavalli-Sforza 1976, 1989;

Boyd & Richerson 1985; Richerson & Boyd 2005). Culture is not just a property of humans, it is a fundamental cause of how humans got to be the way they are, a dynamic process that shapes psychological and material worlds (Boyd & Richerson 1985; Richerson & Boyd 2005). Human minds have evolved specifically to exploit the cultural realm.

Gene–culture coevolutionary analyses typically build on conventional population genetic theory. In addition to tracking how allele or genotype frequencies change in response to evolutionary processes such as selection and drift, the analyses also incorporate cultural transmission (by, for instance, learning from parents, or from the previous generation, or conforming to the majority view) into the models, and explore how learned characters coevolve with genetic variation that either affects its expression or acquisition, or whose fitness is affected by the cultural environment, or both.

The theory has deployed in a variety of different ways. First, and primarily, it has been used to explore the adaptive advantages of reliance on learning and culture, for instance, by asking under what circumstances natural selection favours reliance on social learning (Boyd & Richerson 1985; Rogers 1988; Feldman *et al.* 1996; Enquist *et al.* 2007), and what kinds of learning biases are adaptive (Boyd & Richerson 1985; see McElreath *et al.* 2008). Second, it has been deployed to investigate the inheritance of behavioural and personality traits (Cavalli-Sforza & Feldman 1973; Otto *et al.* 1995), frequently finding lower heritabilities and higher influence of social learning than conventional human behaviour genetics twin studies. Third, it has been applied to investigate specific instances of human evolution, including cultural group selection (Boyd & Richerson 1985), and the emergence of incest taboos (Aoki & Feldman 1997).

I will not attempt here to provide a summary of the entire field of gene–culture coevolution, a challenging task given recent growth in this domain of research (see Feldman & Laland (1996) and Richerson & Boyd (2005) for overviews). Rather, in this article, I will restrict myself to presenting work carried out by me and my collaborators, and provide a personal account of what I believe the principal take-home messages of this small body of theory. In §2 I present what are designed to be accessible verbal summaries of three case studies exploring gene–culture interactions through the use of gene–culture coevolutionary models. These studies explore (i) the evolution of handedness, (ii) sexual selection with a culturally transmitted mating preference, and (iii) cultural niche construction and human evolution. In §3 I attempt to synthesize insights from these case studies into a coherent general statement concerning how genes and culture have interacted throughout recent evolution, and what the implications of this interaction are for understanding human behaviour and society.

2. CASE STUDIES OF GENE–CULTURE COEVOLUTION
(a) *The evolution of handedness*
Why is not everyone right-handed? Extensive experimental studies reveal that approximately 90 per cent of

humans are right-handed (Corballis 1991). This estimate is loosely consistent across the world, but does vary to some degree between cultures (Corballis 1991). But there are no cultures in the world in which left-handers are the majority, and this has led researchers to conclude that right-handedness must have been favoured by selection during the course of recent human evolution. But that begs the question, if it is advantageous to be right-handed, why is not everybody? What processes might be preserving left-handers in human populations? The most commonly given answer to this question is genetic variation, preserved through some selective regime such as heterozygote advantage (Annett 1985; McManus 1985) or frequency-dependent selection Faurie & Raymond (2005).

There are two major problems for exclusively genetic models of handedness, and genetic models are currently the leading models of handedness (Annett 1985; McManus 1985). First, such models would predict that concordance for handedness would increase with relatedness, but as Morgan & Corballis (1978) stated: 'knowledge of a person's handedness tells us virtually nothing of the handedness of that person's twin or sibling' (p. 273). This statement remains entirely valid in 2008. One is given no insight into the likely handedness of an individual if one knows that of its siblings. Moreover, genetic models would predict that identical twins would be more alike than fraternal twins, yet they have essentially the same concordance rates for handedness: 0.772 for MZ and 0.771 for DZ twins (data based on a meta-analysis of 14 twin studies from McManus 1985). While isolated studies (e.g. Warren *et al.* 2006) have reported positive heritabilities for some handedness measures, the overall picture across multiple studies remains that handedness, at least as measured in the vast majority of questionnaire and performance studies, does not exhibit strong heritability (McManus 1985; Neale 1988; Su *et al.* 2005).

Second, purely genetic accounts of handedness fail to explain the well-established cultural influences on handedness. Left-handers are found at lower frequencies in societies that associate it with clumsiness, evil, dirtiness or mental illness, such as some middle and far eastern countries (Harris 1980; Corballis 1991). Studies of school children in China and Taiwan report only 3.5 and 0.7 per cent used their left hand for writing, compared with a 6.5 per cent estimate for Oriental school children living in the USA (Hardyck *et al.* 1976; Teng *et al.* 1976; Hung *et al.* 1985).

As the worldwide dominance of right-handers strongly suggests a genetic influence or constraint, yet the cross-cultural variation reveals a cultural influence, handedness appears to be well suited to a gene–culture coevolutionary analysis. Laland *et al.* (1995a) constructed a gene–culture coevolutionary model of handedness that made the following assumptions. First, there are two phenotypic states: that is, individuals are characterized as right- or left-handed (there are no ambidextrous individuals and no degrees of handedness). While this assumption would be contested by some researchers (Annett 1985), simulations reveal that this assumption, made for mathematical convenience, does not greatly affect our conclusions, and

other researchers have argued compellingly that handedness data are strongly bimodal in distribution (McManus 1985). Second, following McManus's notation, we assume that the probability of becoming right- or left-handed is influenced by alleles D and C at a single locus. This is not to suggest that we believed only a single gene influences handedness, but rather we focused on a single hypothetical gene as a means of exploring how any autosomal genetic variation is likely to respond. Below I argue that our model implies a series of selective sweeps of handedness genes throughout human evolution, each ratcheting up the proportion of right-handers. Third, we assumed that culturally transmitted biases also affect handedness, primarily through a parental influence. This assumption is justified by the observation that handedness is usually fully developed by the age of 2–3 (Bishop 1990).

Hence, an individual's handedness depends on its genotype and the handedness of its parents. The probability of a right-handed child being born to parents with various different patterns of handedness, given the three possible offspring genotypes, is given in table 1. Here, the parameter ρ represents the dextralizing effect of genotype DD, α represents the increase in right-handedness caused by having two right-handed parents (or the decrease caused by two left-handed parents) and β represents the change in handedness affected by parents of mixed-handedness. Since non-human primates may exhibit individual hand preferences, but evidence for population-level biases is, at best, contentious (Palmer 2002), we assume as a starting point for our analysis an ancestral population in which individuals were not genetically predisposed towards either hand (a CC population). We consider two forms of selection, favouring either right-handedness directly or allele D, the latter representing cases in which handedness is favoured owing to selection on some other lateralized structure or function. The analysis found that irrespective of the starting frequency of right-handedness, the magnitude of the selective advantage to right-handers or the degree of dominance of the alleles, all genetically variable populations converge on a single evolutionary trajectory, and continue to evolve until allele D is fixed, and the frequency of right-handers is given by

$$P_{DR} = \frac{2\alpha + 2\beta - 1 + \sqrt{4\alpha^2 - 4\alpha + 4\beta^2 + 1 + 8\beta\rho}}{4\beta}.$$
$$(2.1)$$

Given this finding, how can variation in handedness be reconciled? Clearly, the gene–culture interaction has not preserved variation in handedness. The hypothesis that human populations are currently evolving towards the equilibrium specified in (2.1) is inconsistent with data revealing a decreasing trend in right-handedness in the USA and Australia over the last century (Corballis 1991), data generally interpreted as reflecting a relaxation in the social pressure to conform to a right-handed standard. While simulations reveal that selective regimes such as heterozygote advantage and frequency-dependent selection could preserve genetic variation, as mentioned above, such explanations are inconsistent with the observation that handedness has low heritability. However, the analysis suggests an alternative

Table 1. The probability of a right-handed child being born to parents with various different patterns of handedness, given the three possible offspring genotypes. (Here, ρ represents the dextralizing effect of genotype DD, α represents the increase in right-handedness caused by having two right-handed parents (or the decrease caused by two left-handed parents), β represents the change in handedness affected by parents of mixed-handedness and h_1 is a parameter specifying the dominance of D and C alleles.)

parental mating	DD	DC	CC
right×right	$1/2 + \rho + \alpha$	$1/2 + h_1\rho + \alpha$	$1/2 + \alpha$
right×left	$1/2 + \rho + \beta$	$1/2 + h_1\rho + \beta$	$1/2 + \beta$
left×left	$1/2 + \rho - \alpha$	$1/2 + h_1\rho - \alpha$	$1/2 - \alpha$

explanation: human populations may have reached the equilibrium specified by (2.1), such that no genetic variation underlies variation in handedness, but left-handers would nonetheless remain in the population if $\alpha + \rho < 1/2$.

We explored this possibility by collating data on patterns of handedness in families. We found 17 studies that gave the frequencies of right- and left-handed offspring born to two right-handed parents, one right and one left, and two left-handed parents, which give rise to decreasing proportions of right-handed offspring. (The datasets derive from western Europe and North America, for which the incidence of left-handedness is relatively consistent.) We then carried out a maximum-likelihood analysis in which we used the familial dataset to estimate the best-fit values of α, β and ρ, the three remaining free parameters in our model at equilibrium. In the first instance, β came out very close to zero, so we eliminated it from the model and reconducted the analysis, which gave values of $\alpha = 0.14$ and $\rho = 0.28$. With these values, the model gives a good fit to 16 out of the 17 studies, and across all studies combined ($G = 44.33$, d.f. $= 32$, $p > 0.05$). Similar maximum-likelihood analyses to the same kind of data applied to the leading genetic models give a poorer fit—our model gives a good fit to more studies and a poor fit to fewer studies than any other model.

The analysis suggests that all humans are born with a predisposition to be right-handed of $(1/2) + \rho = 0.78$; that is, all other factors being equal, 78 per cent of people would be right-handed. However, all other factors are not equal, since parents exert a bias on patterns of handedness. Two right-handed parents increase the probability that their child will be right-handed by a further 14 per cent ($\alpha = 0.14$), to give an overall probability of 0.92, while two left-handed parents decrease the probability by the same proportion, leaving the probability of a right-hander at 0.64. Parents of mixed-handedness cancel out each others' influence ($\beta = 0$). The exact nature of the parental influence is not clear, but we assume that it represents a combination of imitation, inadvertent shaping and direct instruction (see Laland *et al.* (1995a) for discussion).

Three independent tests of our model were performed. First, we plugged the values of α, β and ρ into equation (2.1), to derive an overall expected frequency of right-handers of 0.88, very close to the

observed value. Second, we collated studies giving the frequency of right–right, right–left and left–left pairs of monozygotic and dizygotic twins, and, compared with the observed data, our predictions of expected proportions in each category given the overall number of twins in the study. Using the same parameter values derived from the familial dataset, our model generated expectations that were a good fit to 27 out of the 28 twin datasets we could find, and across all studies combined ($G = 35.76$, d.f. $= 28$, $p = 0.38$). Once again, our model outperforms all other models subjected to this analysis. Third, we used the values of α, β and ρ to compute expectations for the degree of concordance for handedness in unrelated individuals and monozygotic twins, which gave values of 0.79 and 0.8, respectively. This explains Morgan & Corballis's (1978) observation that knowledge of a person's handedness tells us virtually nothing of the handedness of that person's twin or sibling. These three independent tests of the model lend confidence in our conclusions.

In summary, patterns of inheritance and variation in handedness are the outcome of a gene–culture inter-action. A history of selection on handedness has created a universal genetic predisposition towards right-handedness; our genes load the die to favour the right, but in a facultative rather than obligate manner. However, patterns of variation in handedness within families and across societies are the product of a cultural influence—specifically, a parental bias leading individuals to shape their child's handedness to resemble their own. In this respect, I anticipate variation between societies will correspond to different values of α (and possibly β), a hypothesis that is open to testing. Since our model assumes no genetic variation underlying current variation in handedness, it is consistent with humans possessing many handedness-distorting genes of small effect, reflecting multiple selective sweeps over the course of human evolution, and, in this respect, is consistent with human genetic data. (By contrast, those models reliant on genetic variation underlying variation in handedness typically assume that a single gene of major effect influences handedness, and such strong single-gene effects on behaviour are extremely rare). It is plausible that selection for right-handers may have occurred over millions of years, and may perhaps even have begun in a common ancestor of humans and chimpanzees. Studies of handedness in chimpanzees provide increasingly compelling evidence for a population-level handedness bias to the right, although Palmer (2002) notes effect sizes shrink as the number of recordings per individual and sample size increase. However, if this pattern is confirmed, it is clear that the bias is small—56 per cent of hand use by common chimpanzees is right-handed (Palmer 2002). Archaeological data, based on patterns of flint knapping or skeletal data, provide evidence for increasingly strong biases in Lower Pleistocene hominids (0.57), Middle Pleisto-cene hominids (0.61) and Neanderthals (0.8–0.9) (Toth 1985; Uomini in press). Thus, the comparative data, weak though it is, support the suggestion that handedness distorters have been repeatedly favoured by selection over hundreds of thousands, and perhaps even millions of years. With each selective sweep

favouring a dextralizing allele, the proportion of right-handers would be ratcheted up, not just owing to the immediate effect of the gene, but also because, by increasing the frequency of right-handed parents, the proportion of children exposed to a cultural bias favouring right-handedness increases. Although the extent to which culture shaped selection pressures is unknown, I suspect that both directly, by constructing an environment suited to the right-handed majority, and indirectly, by introducing new behaviour patterns that benefited from hand specialization, hominin cultural processes increasingly reinforced selection favouring right-handedness.

(b) *Sexual selection with a culturally transmitted mating preference*

The field of evolutionary psychology is dominated by experimental and questionnaire studies of human mating preferences and behaviour, for which sexual selection interpretations are rife (Buss 1994; Barrett *et al.* 2001). By contrast, theoretical analysis of human sexual selection is relatively understudied. Certainly, there is a well-established general body of theory investigating the interaction between genetically trans-mitted traits and preferences (e.g. Kirkpatrick 1982), but it is not clear to what extent human mating preferences are influenced by genetic variation. In their classic book, Gould & Gould (1989, p. 254) wrote:

> Much of our thinking about the role of sexual selection in shaping modern human behaviour is paralyzed by the difficulty of separating the effects of nature and nurture.

The clear implication of this statement is that learning and culture may shape human mating behaviour, obscuring understanding of how sexual selection has acted. Similarly, social science critics of human sociobiology and evolutionary psychology frequently argue that sexual selection explanations for human mating behaviour are implausible given the cultural influence on human preferences (Ford & Beach 1951; Tan 1979; Aronson 1995).

Contrary to these positions, here I show that the interaction of cultural and selective processes can itself result in sexual selection. That is, even if human mating preferences are learned, socially transmitted, and culture-specific, sexual selection will still result; indeed, culturally generated sexual selection may be even more potent than its conventional gene-based counterpart.

Laland (1994) combined sexual selection and gene–culture coevolutionary theory to explore the impact of a culturally transmitted mating preference favouring genetically inherited traits in the opposite sex. Gene–culture interactions are likely to be important here for several reasons. First, evidence for the cultural transmission of human preferences is pervasive in human societies (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Hewlett & Cavalli-Sforza 1986). Second, as an increasing number of species (currently many hundreds, including some inver-tebrates) are found to exhibit a capacity for social transmission (see Galef & Laland (2005) for a review), the possibility emerges that gene–culture interactions may have shaped selection in other species. For

instance, mate-choice copying has been observed in birds and fishes (Dugatkin 1992; White & Galef 2000), and theoretical models of mate-choice copying reveal that learned preferences could plausibly coevolve with gene-based traits (Kirkpatrick & Dugatkin 1994). Third, gene–culture interactions may significantly affect evolutionary rates, speeding them up and slowing them down under different circumstances (Laland 1992; Laland *et al.* 1995*b*, 2001).

Laland's (1994) analysis was based on Kirkpatrick's (1982) sexual selection model, but incorporated vertical cultural transmission, although an oblique transmission model gave qualitatively similar results. Cultural biases, variously termed 'cultural selection' (Cavalli-Sforza & Feldman 1981) or 'biased transmission' (Boyd & Richerson 1985), in the form of differential social learning of behavioural alternatives, affect the frequency of cultural variants in a population over time. Laland explored the consequences of biased and unbiased cultural transmission of mating preferences (expressed in either sex) on the sexual selection of gene-based traits in the opposite sex. Both haploid and diploid models were constructed, reliant on either uniparental or biparental inheritance of preferences. In the simplest case, members of one sex (here males) exhibit one of two traits, T_1 and T_2, the latter exhibiting a viability deficit of $1 - s$ relative to the former, and the other sex (here females) exhibit one of two culturally learned preferences, P_1 and P_2, for traits in their mating partners, with P_1 (females) unbiased and P_2 (females) preferring to mate with T_2 (males) *a* times more frequently than T_1 (males). The principal finding is general to all models: sexual selection is the outcome of this interaction.

Indeed, when cultural transmission is unbiased the haploid system is formally equivalent to Kirkpatrick's (1982) classic model of sexual selection, and exhibits the same familiar curve of neutrally stable equilibria (shown as the thick line in figure 2*a*). As in Kirkpatrick's model, for the trait allele to have any non-zero equilibrium frequencies, it is required that $s < 1 - 1/a$. If a population is on the curve, cultural drift (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985) or individual learning could change the frequency of the preference, and hence indirectly alter the frequency of the trait. As with genetic models, a statistical association equivalent to linkage disequilibrium builds up between genetic trait and cultural preference, as the offspring of $P_2 \times T_2$ matings inherit both characteristics. If the covariance between trait and preference and the frequency of P_2 is sufficiently high, P_2 generates selection favouring T_2 in spite of the trait's viability deficit and hitch-hikes to fixation on the back of it; that is, P_2 and T_2 exhibit runaway sexual selection.

As with the genetic models, the observed curves of neutrally stable equilibria are structurally unstable, and disappear with selection on the preference. Here, with any degree of bias in favour of P_2 during cultural transmission, there is only one stable equilibrium point, with P_2 and T_2 fixed if $s < 1 - 1/a$ (figure 2*b*) and with P_1 and T_1 fixed if $s > 1 - 1/a$. Strong biases quickly result in the fixation of P_2, and a subsequent rapid increase in the frequency of T_2. At the extreme (strong transmission bias, large *a*, small or negative *s*), traits may be
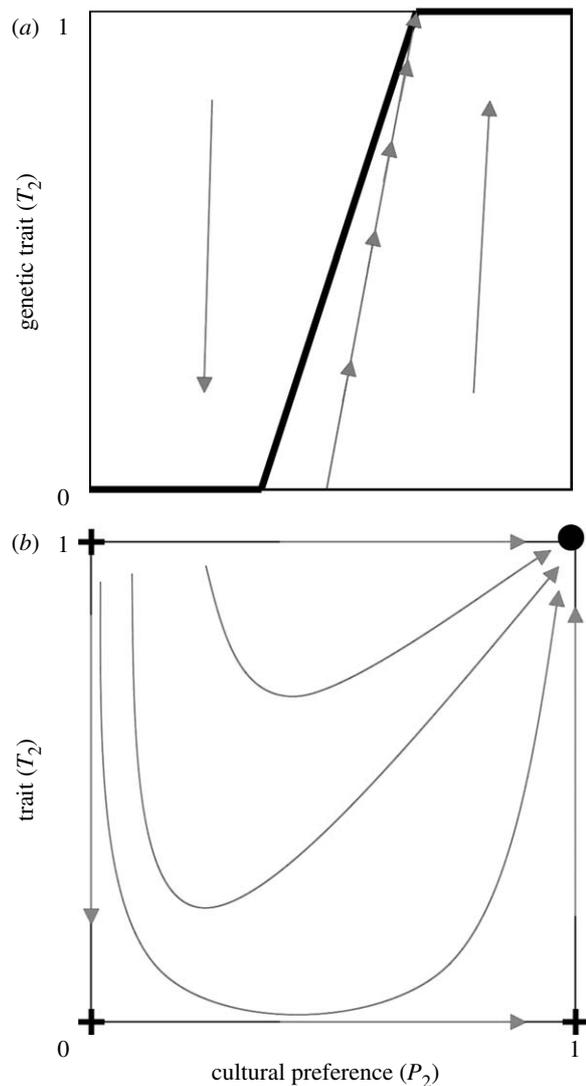

Figure 2. Sexual selection resulting from a culturally transmitted mating preference (P_1 or P_2) in one sex for a genetically transmitted trait (T_1 or T_2) expressed in the other, where P_1 individuals are unbiased and P_2 individuals prefer T_2 mates. (*a*) Unbiased vertical cultural transmission and (*b*) biased transmission favouring P_2.

taken from low to high frequency in just a handful of generations. Even weak biases typically bring about more rapid patterns of genetic change than conventional gene-based models, since cultural preference frequencies typically increase faster than genetic preferences. The findings hold for both biparental and uniparental inheritance of preferences, for haploid and diploid genetics, and for both 'Fisherian' and 'good genes' scenarios (positive and negative *s*). Oblique transmission (learning from non-relatives) weakens the covariance between trait and preference, but compensates by inducing more rapid spread of the preference, such that strong sexual selection is again the outcome.

In summary, the analysis reveals that a culturally transmitted mating preference that reaches a significant frequency through drift, asocial or social learning can under most circumstances generate selection that takes a preferred trait in the opposite sex to fixation, or to non-zero frequencies, even if that trait is costly, and frequently with the preference hitch-hiking along.

Given the pervasiveness of cultural influences on human mating preferences (Darwin 1871; Tan 1979; Gould & Gould 1989; Aronson 1995), social transmission may exert a powerful influence on the selection of secondary sexual characteristics, and other physical and personality traits that affect human mate choice. The hypothesis could plausibly apply to many human traits, including skin colour, facial features, facial and body hair, body shape, height, degree of character symmetry, degree of neoteny, level of aggressiveness, emotionality and a variety of personality traits.

The analysis leads to several predictions. First, it suggests that we should expect to see mate-choice copying and, second, the social transmission of mating preferences, in humans. Third, it predicts society-wide correlations between culturally transmitted preferences and gene-based traits (in both sexes). Evidence is now starting to accumulate that supports these predictions. Jones *et al.* (2007) conducted experiments in which images of male faces were presented to females adjacent to images of females that were either smiling or looking impassively at the males. Females rated the smiled-at faces as more attractive than the alternatives, indicative of mate-choice copying. A similar study by Little *et al.* (2008) revealed that this process can generate preferences for particular characteristics of the smiled-at male that are expressed in other males, indicative of the social transmission of mating preferences. Several recent studies of human mating preferences report differences in the perception of female attractiveness in different cultural groups, and preferences that change rapidly over time (e.g. Furnham & Baguma 1994; Craig *et al.* 1996; Yu & Shepard 1998; Wetsman & Marlowe 1999; Marlowe & Wetsman 2001; Tovee *et al.* 2006), again strongly suggestive of culture-specific and culturally transmitted mating preferences. Indeed, Darwin (1871) devotes an entire chapter (XIX) of *The Descent of Man* to documenting cross-cultural differences in human mating preferences and points out that these coincide with physical characteristics in the opposite sex. He writes (p. 353): 'It is certainly not true that there is in the mind of man any universal standard of beauty with respect to the human body'. Assuming he is correct, this mechanism could be a major source of cross-cultural variation in anatomical and behavioural traits.

(c) Cultural niche construction and human evolution

Niche construction is the very general process whereby organisms modify their own and/or each others' niches, through their metabolism, their activities and their choices (Odling-Smee *et al.* 2003). It is far from restricted to humans: numerous animals manufacture nests, burrows, holes, webs and pupal cases; plants change levels of atmospheric gases and modify nutrient cycles; fungi and bacteria decompose organic matter; bacteria fix nutrients (Lewontin 1982, 1983; Odling-Smee 1988; Odling-Smee *et al.* 2003). The defining characteristic of niche construction is the modification of the *relationship* between an organism and its environment (Odling-Smee 1988), and hence niche construction subsumes habitat selection, dispersal and

migration. Advocates of the niche-construction perspective within evolutionary biology stress the active role that organisms play in driving evolutionary and coevolutionary events.

The niche-construction perspective differs from the conventional one in recognizing two major adaptive processes in evolution, natural selection and niche construction, and two general forms of inheritance, genetic and ecological inheritance (Odling-Smee 1988). Ecological inheritance refers to the modified environments (e.g. nests, burrows), incorporating modified selection pressures, which descendant organisms inherit from their ancestors. Organisms transmit to their offspring, and subsequent descendents physically altered selective environments, both through actions on their biological and non-biological environments and by their habitat choices.

Many researchers have explored the evolutionary ramifications of niche construction by developing and analysing mathematical models (Laland *et al.* 1996, 1999, 2001; Odling-Smee *et al.* 2003; Ihara & Feldman 2004; Borenstein *et al.* 2006; Silver & Di Paolo 2006). All such analyses conclude that niche construction is evolutionarily consequential. Typically, population genetic models investigate the dynamics of the joint evolution of environment-altering, niche-constructing traits in organisms and 'recipient traits', whose fitness depends on feedback from natural selection in environments that can be altered by niche construction (Laland *et al.* 1996, 1999, 2001; Odling-Smee *et al.* 2003).

These theoretical analyses suggest that this 'self-imposed' selection resulting from niche construction will often override external sources of selection (i.e. selection acting on the population independent of their niche-constructing activities) to create new evolutionary trajectories, which will lead to the fixation of otherwise deleterious alleles, the support of stable equilibria where none are expected and the elimination of what would otherwise be stable polymorphisms. Among the most significant analyses is Silver & Di Paolo's (2006) study, which found that niche-construction traits can drive themselves to fixation by simultaneously generating selection that favours 'recipient' trait alleles and linkage disequilibrium between niche-construction and recipient trait alleles.

Frequently, the evolution of the recipient trait depends on the frequency of the niche-constructing trait over several generations—that is, on ecological inheritance. Processes that carry over from past generations can change the evolutionary dynamic in a number of ways, generating time lags in response to selection of the recipient trait, momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), opposite responses to selection and sudden catastrophic responses to selection (Feldman & Cavalli-Sforza 1976; Kirkpatrick & Lande 1989; Laland *et al.* 1996, 1999, 2001).

Niche construction also provides a non-Lamarckian route by which acquired characteristics can influence the selective environment. While the information acquired by individuals through ontogenetic processes cannot be inherited because it is lost when they die,

processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction in ways that do modify natural selection. This route is considerably enhanced by social learning, which allows animals to learn from each other. Hundreds of species of mammals, birds and fishes are now known to learn socially (Zentall & Galef 1988; Heyes & Galef 1996), allowing novel learned traits to sweep through populations and exposing individuals to novel selection pressures. This process is further amplified with stable trans-generational culture, and it is now widely believed that such characters were probably important to hominid evolution (Cavalli-Sforza & Feldman 1981; Richerson & Boyd 2005). In humans, culture has greatly amplified our capacity for niche construction and our ability to modify selection pressures. This highlights the requirement for theoretical analyses exploring the evolutionary ramifications of human cultural niche construction.

Laland *et al.* (2001) combined niche-construction and gene–culture coevolutionary models to explore the evolutionary consequences of cultural niche construction. Our models were based on three key assumptions. First, a population's capacity for niche construction is influenced by the frequency of a cultural trait (E or e), where the two traits represent the presence and absence, more and less, or different forms, of niche construction, respectively. Second, the amount of some resource R in the environment is dependent on the niche-constructing activities of past and present generations. This resource could be an artefact (e.g. shelter, tools) that the population constructs, some manufactured or accrued commodity (e.g. food, water), or a modified environmental condition (e.g. temperature). Third, the amount of the resource in the environment influences the pattern and strength of selection acting on alleles (A and a) at a genetic locus. For illustration, in the aforementioned Kwa example, the cultural trait E represents yam cultivation, the resource R is the amount of standing water and the recipient allele is the sickle-cell S allele.

The fitnesses of individuals with cultural traits E or e, and genotypes AA, Aa and aa, are shown in table 2. Two components of selection are represented by these fitness functions: a fixed-fitness component (α, η terms) representing selection acting on the population independent of their niche construction, and a frequency-dependent component (ε, R terms) representing the selection brought about or modified through niche construction, where ε is a constant that weights the relative importance of the two components. Two classes of model were constructed, in which the amount of the resource depended exclusively on prior niche construction, and where additional processes of resource accrual and depletion were acting. The model assumed vertical cultural transmission of the cultural trait (learning from parents) of unbiased, biased or incomplete forms, although, once again, simulations introducing oblique transmission gave qualitatively similar results.

The analysis provided ample evidence that cultural niche construction could plausibly affect human genetic evolution, in a multitude of ways. As with the

Table 2. The fitnesses of individuals with cultural traits E or e and genotypes AA, Aa and aa (phenogenotypes). (Each phenogenotype fitness is composed of two terms: the first (with α and η terms) representing the fixed-fitness component of selection acting on the population that stems from independent sources in the environment, and the second (with ε and R terms) representing the frequency-dependent component of selection resulting from the population's niche construction. Here, ε ($-1 \leq \varepsilon \leq 1$) is a parameter that weights the relative importance of the two sources of selection and R ($0 \leq R \leq 1$) is the frequency of the resource altered through niche construction.)

	$E(\alpha_1)$	$e(\alpha_2)$
$AA(\eta_1)$	$W_{11} = \alpha_1\eta_1 + \varepsilon R$	$W_{12} = \alpha_2\eta_1 + \varepsilon R$
$Aa(1)$	$W_{21} = \alpha_1 + \varepsilon\sqrt{(R(1-R))}$	$W_{22} = \alpha_2 + \varepsilon\sqrt{(R(1-R))}$
$aa(\eta_2)$	$W_{31} = \alpha_1\eta_2 + \varepsilon(1-R)$	$W_{32} = \alpha_2\eta_2 + \varepsilon(1-R)$

above sexual selection model, gene–culture niche-construction models with unbiased cultural transmission simplify to the equivalent purely genetic niche-construction models. However, the case of unbiased cultural transmission with overdominance at the A locus, has some interesting features: for example, curves of stable fully polymorphic equilibria are found that exhibit monotonic relationships between the frequencies of the cultural trait and the alleles at the A locus, similar to those found with the purely genetic models when selection operates at the A locus (Laland *et al.* 1999). Such curves might represent situations similar to that of the effect of yam cultivation (the cultural niche-constructing trait or E) on the frequency of the sickle-cell allele (the allele maintained through overdominance or A) and illustrate the sensitivity of allele frequencies to cultural niche construction.

Biased cultural transmission frequently increased the range of parameter space over which niche construction has an impact. For instance, in the face of external selection favouring allele A, cultural transmission may generate counter selection that increases the likelihood of fixation on a. Similarly, cultural niche construction will increase the chance of convergence to equilibria polymorphic for A and a, if cultural transmission favours E when an increase in the amount of the resource results in a decrement in the fitness of genotypes containing A (e is negative). In both cases, cultural niche construction is driving genetic evolution. Because cultural processes typically operate on a faster timetable than natural selection, biased cultural transmission is likely to have a much greater influence on the consequences of niche construction than would natural selection on E. These findings illustrate processes by which cultural niche construction may have played an instrumental and active role in hominid evolution, initiating novel evolutionary events through the creation of novel selection pressures, and changing the direction of evolution by modifying established selection pressures. Moreover, they confirm the hypothesis that the hominid capacity for niche construction is likely to have been greatly enhanced by, and coevolved with, a capacity for cultural transmission.

Weak transmission biases favouring a cultural niche-constructing behaviour can also generate interesting evolutionary scenarios. For instance, if transmission bias results in a change in frequency of cultural niche-constructing traits, then selection at the A locus may be modified or even reversed, as R may have increased or decreased beyond the $R=0.5$ switch point. In the case of weak biases, there may be many more generations of selection favouring one of the alleles at the A locus than would be the case for strong biases before selection switches to favour the other allele, and as a consequence one or other allele may reach a very low frequency before increasing in frequency again. In reality, small populations that follow this trajectory may lose genetic variation at the A locus before selection could favour the allele that had previously been selected against. This type of process could easily create and maintain genetic differences between semi-isolated populations, and in hominids may have played a role in biological speciation events.

If cultural transmission and natural selection on E conflict, there are circumstances under which cultural transmission can overwhelm selection. If the two processes act in concert, cultural transmission accelerates the rate at which the cultural trait spreads.

When the amount of the resource is a function of more than one generation of niche construction, the analysis reveals time lags at the A locus in response to a change in selection pressures caused by the spread of the E trait, as were observed in the population genetic models. Typically, the time lags are shorter than in the case of the purely genetic systems, principally because the cultural trait reaches equilibrium faster than an analogous genetic trait. It is only if there is no selection and weak transmission bias that time lags of the order seen in the genetic models are observed. With incomplete transmission, neither E nor e goes to fixation, but provided a cultural transmission bias favours trait E, A will eventually fix. Here, a cultural niche-constructing trait only has to spread through the population enough to increase the frequency of the resource R above 0.5 before it can generate selection that will fix A.

As with gene-based niche construction (Laland *et al.* 1996, 1999), these models demonstrate that cultural niche construction will commonly generate counter selection that compensates for, or counteracts, a natural selection pressure in the environment. A reasonable inference from such findings would be that competent niche constructors should be more resistant to genetic evolution in response to autonomously changing environments than less able niche constructors. As culture enhances the capacity of humans to alter their niches, it would seem plausible to infer that hominid niche construction, in general, has been more flexible than that of other mammals.

This finding can be used to develop a number of predictions about human evolution. For instance, one might expect hominids to show less of an evolutionary response in morphology to fluctuating climates than other mammals, assuming that the latter must have been less well equipped than the former to invest in counteractive niche construction. Similarly, more technologically advanced hominids should exhibit less of a response to climates than less technologically advanced hominids.

Moreover, it should also be possible to reverse this inference and use the fossil record to draw conclusions about the niche-constructing capabilities of animals, including hominids. Here, the greater the phenotypic (as opposed to extended phenotypic) response to environmental change by hominids, the more restricted must have been their capacity for niche construction. If hominids have evolved more in response to self-constructed selection pressures than other mammals and less in response to selection pressures that stem from independent factors in their environment, then hominid populations may have become increasingly divorced from local ecological pressures. Support for this line of reasoning comes from Guglielmino *et al.*'s (1995) study of variation in cultural traits among 277 contemporary African societies in which most traits examined correlated with cultural (e.g. linguistic) history rather than ecology.

In the light of these findings, the view that modern human populations are adapted to an ancestral Pleistocene habitat, or environment of evolutionary adaptedness, is likely to be misleading because it treats humans as passive victims of selection rather than as potent niche constructors (Laland & Brown 2006). Our recent evolutionary history may well reflect our capacity continuously to create solutions to self-imposed problems caused by prior niche construction. This adaptability may mean that, rather than being adapted to a particular environment, humans adapted to a broad range of potential environments that they and their ancestors were involved in modifying.

In summary, the analysis suggests that where cultural traits are transmitted in an unbiased fashion from parent to offspring, cultural niche construction will have a similar effect to gene-based niche construction, but cultural transmission biases favouring particular cultural traits may increase the range of parameter space over which niche construction has an impact. The analysis also reveals circumstances under which cultural transmission can overwhelm natural selection, accelerate the rate at which a favoured gene spreads, initiate novel evolutionary events and trigger hominid speciation. Because cultural processes typically operate faster than natural selection, cultural niche construction probably has more profound consequences than gene-based niche construction, and is likely to have played an important role in human evolution.

It can be seen that niche construction changes the evolutionary process in fundamental ways, by creating an ecological inheritance, by modifying phenotypes, norms of reaction and heritabilities, and by allowing acquired characters to play a significant role in evolution. While the niche-construction perspective is controversial (Laland *et al.* 2004), and could not yet be regarded as mainstream opinion, there are reasons to anticipate that it will be less contentious and more readily acceptable to human and social scientists than the conventional perspective. After all, it is quite apparent that human niche construction is highly potent. Moreover, social scientists are rarely content to describe human behaviour as fully determined by naturally selected genes, and typically view humans as

active, constructive agents rather than passive recipients of selection. To be aligned with this viewpoint, evolutionary biology must explicitly recognize the changes that humans bring about in their world to be drivers of evolutionary events.

3. CONCLUSIONS

The three case studies, together with other gene–culture coevolutionary analyses from my laboratory (Kumm *et al.* 1994; Laland *et al.* 1995b; Mesoudi & Laland 2007), and the aforementioned genetic data, provide a number of general insights into human behaviour and evolution. Collectively, these present a very different view of human evolution from the prevailing perspective within the dominant school of evolutionary psychology (Barkow *et al.* 1992; Pinker 1997).

(a) *Genes and culture coevolve*

Genes and culture can, and do, coevolve. Theoretical models, such as the handedness, sexual selection and niche-construction case studies, illustrate the mechanisms, while genetic, anthropological and archaeological data demonstrate that the coevolutionary dynamic is not just a hypothetical possibility, but a reality. Genetic and cultural change can occur on similar time scales. Analysis of the human genome implies that gene–culture coevolutionary interactions are likely to be pervasive.

(b) *The gene–culture leash tugs both ways*

Edward Wilson famously claimed 'the genes hold culture on a leash' (1978, p. 172), by which he meant that genetic propensities shape the acquisition of cultural knowledge. In fact, Wilson failed to emphasize that, for our species at least, the leash tugs both ways. Culture may be shaped by genes, but the architecture of the human genome has been profoundly shaped by culture, as the aforementioned genetic data attest. Human culture and technology are amply manifest in our species' extraordinarily potent capacity for niche construction, and have shaped the selective landscape of human evolution.

(c) *Gene–culture coevolution may be the dominant form of evolution for our species*

Theoretical gene–culture models consistently find that the gene–culture dynamics are typically faster, stronger, operate over a broader range of conditions and are more potent than conventional evolutionary dynamics. Gene–culture coevolution is likely to be the dominant form of evolutionary adaptation for our species. By modifying selection pressures and increasing the intensity of selection, cultural processes can speed up evolution; by providing an alternative means of responding to ecological and social challenges, cultural processes can damp out selection and slow down the evolutionary response. Extensive evolutionary responses to cultural niche construction in our species are likely to mean that human minds are specifically adapted for culture.

(d) *Culture is a potent co-director of evolutionary events*

Cultural processes are every bit as influential as genetic processes in gene–culture coevolution. Theoretical analyses reveal many instances where cultural transmission overwhelms, or reverses, natural selection. Moreover, the observed patterns of selection often depend intimately on the cultural details. For instance, whether female-biased infanticide selects for male- or female-biased sex ratio distorters depends on the culturally transmitted rules that individuals adopt (Kumm *et al.* 1994; Laland *et al.* 1995b).

(e) *Humans are active constructors of their selective environments*

Humans are not passive victims of natural selection, but active constructors of major components of their selective environments. While niche construction is universal (Odling-Smee *et al.* 2003), our species' capacity to control, regulate and transform the environment is uniquely powerful, largely due to our capacity for culture. Theoretical analyses regularly reveal coevolutionary dynamics in which human cultural processes can hitch-hike to fixation on the selection they generate (Laland 1994; Silver & Di Paolo 2006). It may be no coincidence that humans, the species most reliant on culture, have the most potent capability for niche construction (Laland *et al.* 2000); autocatalytic and runaway effects may have fuelled ever more powerful niche construction in our lineage. As reliance on social learning covaries with relative brain size in primates (Reader & Laland 2002), such autocatalytic dynamics may have played a critical role in brain evolution.

(f) *Humans do not have stone-age minds*

Humans are not primarily adapted to ancestral rather than current environments, as some evolutionary psychologists suggest. When humans engage in niche construction they do not do so randomly; in the same way as other animals, they build structures and have other impacts on their world that are often 'extended phenotypes' (Dawkins 1982), adaptations that enhance fitness. Animals also deplete resources and pollute environments, but this too increases fitness in the short term and is often tied to life-history strategies that take account of this activity, for instance through dispersal or migration when resource levels are low or the environment becomes uninhabitable. While niche construction can have negative effects on fitness, Odling-Smee *et al.* (2003) are explicit about their expectation that most niche construction will increase the short-term fitness of the constructor, although it may have negative consequences for other species. This is hardly contentious: the fitness benefits of animal artefacts are well documented. Niche construction is typically functional and adaptive because it is informed, but not determined, by genes, and sometimes also by learning and culture. Humans largely construct their world to suit themselves, leaving human behaviour largely adaptive in spite of the transformations they have brought about in the environment (Laland & Brown 2006).

This adaptiveness is reinforced by two further processes (Laland & Brown 2006). First, humans frequently buffer any adaptive lag through further

cultural niche construction; for instance clothing, fires and air-conditioning buffer extremes of temperature, while new agricultural practices and innovations alleviate food shortages. Such cultural responses eradicate any mismatch between human selective environments and human genotypes. Second, where this does not occur, natural selection ensues, and recent estimates of typical rates of selection suggest that significant human evolution could occur in hundreds of years (Kingsolver *et al.* 2001). Among the malaria-rife regions of the Kwa homeland, being a heterozygote for the sickle-cell *S* allele is adaptive. Similarly, in dairying societies, genes expressed in high lactase activity pay fitness dividends.

Humans do not walk the streets of the urban metropolis left hopelessly unable to cope by the ancestral primate or stone-age brains in their heads, as evolutionary psychologists (and others) have claimed (Morris 1967; Buss 1999). Human minds and human environments have been engaged in a long-standing, intimate exchange of information, mediated by reciprocal bouts of niche construction and natural selection, leaving each beautifully fashioned in the other's image.

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