

Beyond nature versus culture: cultural variation as an evolved characteristic*

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There is a perceived dichotomy between evolutionary explanations for behaviour and social or cultural ones. In this essay, I attempt to dissolve this dichotomy by pointing out that organisms are susceptible to social or cultural influence because they have evolved mechanisms that make them so. I review two classes of evolutionary explanation for cultural variation, 'evoked' and 'transmitted' culture, and argue that these two classes of mechanism enrich and strengthen existing social science accounts, as well as making new predictions. I suggest a high degree of mutual compatibility and potential gains from trade between the social and biological sciences.

Introduction: the 'nature versus culture' impasse

A central feature of human beings is that they are not the same everywhere. Their ideas, expressed motivations, behaviours, and social groupings are strikingly different from society to society, and changeable over historical time. This observation has often led to a kind of agreed division of labour between biology and the social sciences, whereby biologists agree to not to pursue their – generally Darwinian – explanations for behaviour into the human realm, because of the phenomenon of culture, and social scientists simply start from the fact of 'culturality' and feel no obligation to reconcile their work with the theories of evolutionary biology. Thus, for example, Dawkins (1976), towards the end of a memorable hymn to the power of neo-Darwinism for understanding behaviour, suggests that humans, uniquely, have a second system of inheritance, memes, or culturally transmitted ideas, and as such cannot be understood in the same way as other animals can. Social scientists, in similar vein, are happy to concede that having culture might itself be a kind of adaptation, whose benefit is to allow humans to survive in a wider range of environments (Geertz 1973), but restrict the role of Darwinian evolution to setting up this adaptation in the first place. Once it is working, it attains its own momentum, and the dynamics of culture can only be understood in their own terms. As G.P. Murdoch put it, 'the laws of culture are independent of the laws of biology' (Murdoch 1932: 200).

These issues have come to the fore recently with the rise of an influential intellectual movement known as evolutionary psychology (see Barkow, Cosmides & Tooby 1992;

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Buss 2005). Evolutionary psychology violates the tacit division of labour by pursuing Darwinian adaptationist explanations into the realm of human behaviour. Its proponents have been critical of existing social science (see, e.g., Pinker 2002; Tooby & Cosmides 1992), whilst social scientists have attacked it for implying 'genetic destiny' and 'de-emphasiz[ing] the influence of social circumstances' (Nelkin 2000: 22). This has led to considerable debate about what the proper relations are between social and biological explanations (Barkow 2006; Eagly & Wood 1999; Gangestad, Haselton & Buss 2006; Wilson 1998).

The purpose of this article is to approach the 'social-versus-biological' issue from a slightly different direction. First, I argue that to endorse the central ideas of evolutionary psychology (and Darwinism more generally) need in no way imply genetic determinism or de-emphasize the importance of culture. Instead, evolutionary considerations lead us strongly to predict that 'culture' in a broad sense will be a more important force than genes in the proximate determination of human behaviour. I review two broad classes of evolved mechanism that can account for cultural differences, namely 'evoked' and 'transmitted' culture. I argue that these mechanisms can be reconciled with, indeed usefully underpin, traditional social science accounts of how cultural differences arise. The lesson for social scientists is that neo-Darwinism is not opposed to social and cultural determination of behaviour, but is a framework for understanding why such determination exists; thus adopting a Darwinian perspective can add depth and value to work in the social sciences. On the other hand, if transmitted culture turns out to be very important – and this is an open question – then evolutionists may have to concede a central point to social constructionists, namely that human behaviour in some domains does not serve the reproductive interests of the individuals who do it, but instead is a side-effect of the human capacity for social and symbolic learning.

Social determination, evolutionary explanation

Human beings are living things, and as such, their behaviour must be a consequence of their biology in the broadest sense. On the other hand, that human social life cannot be accounted for by 'mere biology' is almost a unifying dogma of the varied traditions of social science. I have argued at greater length elsewhere (Nettle 2008*a*) that the denial of the explanatory value of biology by social scientists in fact amounts to a denial of the explanatory value of some small sub-set of biological explanations. If we consider the full scope of modern biology, it is far less clear that biology falls short of being able to account for human social life.

One influential critique of the explanatory value of biology is that of Boas (1940). Boas's central claim is that differences in social organization and behaviour between human groups are a consequence of social transmission, not heredity. Here he is reacting to earlier racial and hereditarian thought. However, there is nothing non-biological about the idea that local differences in phenotype are not a consequence of differences in genotype. For example, many species of grasshopper have green and dark forms. Which form a particular individual develops depends on local environmental input. A grasshopper placed on a dark or burnt background grows a dark body, whereas one placed on a light or green background develops a green one (Burt 1951). Thus, the differences between the green and dark populations are environmentally determined, and not in any sense hereditary. An offspring of dark parents translocated to a grassy field becomes a green adult.

However, being dark in a burnt environment is still an evolved adaptation. It is good for reproductive success, because it makes individuals who happen to have been born in the aftermath of a fire less conspicuous to predators. Although the colour of the adult grasshopper is environmentally determined, the capacity to change colour according to local circumstances is a genetic characteristic of grasshoppers, a characteristic that has been fixed by natural selection. Thus, genes are involved not in the determination of body colour, but in the meta-determination of body colour. That is, genes make it the case that body colour is a consequence of the environment, and Darwinians can and do legitimately ask the question of why the genes for the particular pattern of plasticity observed had a selective advantage over their competitors.

This helps clarify how we can think about variation between human groups. A particular pattern of behaviour can be an adaptation to the local environment – and thus understood by Darwinian reverse-engineering – without implying that it is a consequence of genetic differences between groups. Indeed, Tooby and Cosmides (1992), in their foundational essay on evolutionary psychology, explicitly side with Boas on the question of inter-group differences, strengthening the Boasian position on the evolutionary argument that selection coupled with sexual recombination tends to eliminate intra-specific variation. Instead, they suggest that mechanisms akin to those involved in the grasshopper example must be important in the diversity of behaviours observed in human societies, meaning that Nelkin's (2000) attack on their position as a form of genetic determinism that de-emphasizes the effect of social circumstances is a complete misreading (see Kurzban & Haselton 2006 for a discussion).

Social scientists have been hostile to biological explanations for a different reason, which involves a different construal of what 'biological' explanations entail. At least since Durkheim, anthropologists and especially sociologists have tended to characterize biological explanations (and psychological ones, the experimental tradition of psychology being seen as a kind of biology in this respect) as concerned only with physiological and cognitive processes within the individual. Thus, such explanations fail to capture the socially determined dimension of human behaviour. Durkheim himself argued that the different suicide rates of Protestants and Catholics demonstrated that the internal processes of anguish (low levels of serotonin activity, as we would now see it) are insufficient to account for suicidal behaviours; the social structures of the two communities are also important (Durkheim 1992 [1897]). Thus, for Durkheim, there is a realm of social facts which supervenes on processes internal to the individual. He writes that 'every time that a social phenomenon is directly explained by a psychological phenomenon, we may be sure that the explanation is false'; this is because '[t]he group thinks, feels, and acts quite differently from the way in which its members would were they isolated' (Durkheim 1962 [1895]: 103, 104).

A problem with this account, of course, is that social facts must be turned into patterns of cognition, ultimately of neurotransmission, in order to influence behaviour. Here, however, I focus on a slightly different issue. Is it really a fair description of biological explanation to say that it is restricted to processes occurring within one individual?

It would be tempting at this point to cite recent studies of primates, which have shown both the stunning complexity of their social worlds and the ways in which their reproductive success depends on the social structure and their place within it (Cheney & Seyfarth 2007; Dunbar 1988; Silk 2007). However, since we are primates, this might tend to imply that there is something biologically special about us and our close

relatives. Instead, I will endeavour to show that even the biology of bacteria, which are about as unlike us as anything in the natural world, cannot be understood without considering the role that the social plays in the life of the individual.

For many decades, bacteria were considered the epitomes of non-social existence, a world 'peopled only by individual cells reproducing *ad infinitum*' (François Jacob, cited by Williams, Winzer, Chan & Camarra 2007: 1119). However, in the last twenty years, we have come to understand that bacteria can enter into many arrangements that can be properly characterized as social. For example, individuals may abandon free living for a time and form higher entities called biofilms on surfaces. Biofilms are composed of many millions of individuals, and have skeleton-like internal bindings, and even specialized cells within them. The switch to biofilm formation is, rather like the grasshopper switch to dark colouration, environmental rather than genetic. Crucially, though, it is also social. A free-living individual gains nothing from investing in biofilm structures if no other individual joins it. Thus, only where there is a quorum of individuals disposed to form a film do any of them make the switch. Microbiologists have discovered a complex array of 'quorum-sensing' chemical signalling systems, which allow bacteria to receive social information about the presence and state of others in its social context, information which is used to undertake collective actions (Basser & Losick 2006; Williams *et al.* 2007). These actions are highly varied and not restricted to biofilm formation. Bacteria perform a variety of behaviours such as antibiotic secretion (to kill competing strains), where the outcome of the behaviour is dependent on what other individuals are doing, and where, because of this, quorum-sensing mechanisms are involved in the individual's decision to change behaviour. Bacteria can also secrete iron-scavenging molecules that provide a local public good, though they risk being exploited by free-riders in so doing (West, Griffin, Gardner & Diggle 2006). They can also swap genes, but only if they detect that they are surrounded by others also ready to do so. Their optimal level of virulence, that is, their demand from their host, depends on what virulence behaviours are occurring around them, and again, social quorum-sensing mechanisms are found to regulate changes in virulence behaviour.

In an important sense, a bacterial quorum is a social construction. Individuals receive quorum signal molecules from their milieu, and respond by producing quorum signal molecules in their turn. This eventually leads to a high local concentration of the molecules, which equates to a quorum, and the population changes its behaviour. However, there is only a quorum because the bacteria all 'agree' that there is a quorum. They have all conspired in its creation, but none would have done so if the others were not also around. All this means that the dynamics of behaviour of a bacterium on an isolated Petri dish, however rich in resources, will not be anything like the behaviour of a bacterium living in a group of conspecifics in the same environment. To paraphrase Durkheim (see above), 'The group secretes, metabolizes, and acts quite differently from the way in which its members would were they isolated.'

It should be obvious from the foregoing discussion that no biological explanation of the behaviour *even of bacteria* could possibly be adequate if it restricted itself to physiological processes internal to one individual. Whether a bacterium is in biofilm or living free, secreting iron-scavengers or not, virulent or not, even which genes it has, will depend upon the social context in which it finds itself. However, the mechanisms to allow an individual to be shaped by the local context are still evolved mechanisms, and thus part of bacterial biology, rather than something that supervenes on it. The mechanisms are still amenable to adaptationist analysis, because the genes for being

malleable to the social environment in this particular way have evidently outcompeted the genes for not being so malleable, or being malleable in some other way. Thus, we can happily pursue a biological explanation for the phenomena without having to deny that the proximate causes of behaviour are social.

These considerations serve to show that considering culture as an evolved characteristic need not imply genetic determinism, or lose the essentially social character of its generation. In the following sections, I briefly examine two major classes of mechanism that have been suggested by evolutionists to underlie cultural variation in humans, with a view to drawing out lessons for the study of human culture. These mechanisms are known as 'evoked' and 'transmitted' culture (Tooby & Cosmides 1992; see also Gangestad *et al.* 2006: 78-9 for some discussion).

Evoked culture

The concept of evoked culture recalls the grasshopper example already discussed. The organism's ancestors have faced a number of different environmental situations through evolutionary history. In some situations, one phenotype is advantageous, and in other situations, another. What selection builds in this instance is a mechanism for seeking and internalizing cues of which of the possible environmental states obtains locally, and calibrating the phenotype accordingly. For the grasshoppers, the two possible states of the local environment are grassy and burnt, and the two phenotypes are green and dark bodies. In other cases, the phenotypes could vary continuously rather than discretely, and could be set by continuously variable rather than categorical cues, but the principle is the same.

Evoked-culture mechanisms can lead to two populations of the same species looking very different simply because their contexts are different. The information on how to build each possible phenotype is built into the organism by selection, as is the menu of which cue should evoke which phenotypic state. The role of the current environment here is to provide the cues. Evoked culture has been compared to a jukebox: there are a number of tracks already stored in the machine, and the environment provides the code for which one is needed.

Evoked culture has been under-explored as a source of inter-population variation in humans, but its potential importance is high. If there is one thing that characterizes the environment of human evolutionary adaptedness, it is that it was not always in the same state. Not only was the human crucible of Pleistocene Africa very temporally labile, with repeated rapid alternations between humidity and aridity, but humans were using several different niches within it, and for tens of thousands of years humans were constantly changing habitats as they colonized new areas (Wells & Stock 2007). Thus, there is abundant scope for humans to have developed the kind of environmentally contingent behaviours that are subserved by evoked-culture adaptations.

For example, it has been known for some time that in populations prone to experience food restriction, the most desired and attractive body sizes for a potential mate are large (Brown & Konner 1987; Ember, Ember, Korotyaev & de Munck 2005; Tovée, Swami, Furnham & Mangalparsad 2006; Wetsman & Marlowe 1999), whereas in affluent Western populations, the preference is consistently for relatively thin bodies (Tovée, Reinhardt, Emery & Cornelissen 1998; Tovée *et al.* 2006). Merely to assert that attractiveness ideals are socially constructed and therefore different across different societies is non-explanatory, for it does not say anything about why the *pattern* – low resources, preference for large bodies; high resources, preference for thin ones – should be as it is.

Nor does it say anything about why *within*-society differences reflect *between*-society differences. The socio-economic groups with least access to resources within Western societies have preferences for larger bodies than those valued by the richer strata (Tovée, Furnham & Swami 2007).

A parsimonious explanation would be that this is evoked culture. Energy expended on depositing fat is energy diverted from other functions, and large bodies make various activities less efficient. Thus, if resources are going to be in continuous and plentiful supply, it optimizes reproductive success to prefer a small body for oneself and one's mate. However, fat reserves have a crucial advantage if the flow of resources is likely to be intermittent, since they permit the buffering of shortage. Thus, in an environment where such shortages are likely, it is advantageous to prefer a fatter body for oneself and crucially – if male – for the mother of one's offspring. To explain the pattern, it is sufficient that there is an evolved mechanism whose function is to shift people's body preferences towards the fatter end when exposed to cues of resource shortage. The collective expression of this shift will be observed as a larger body ideal in cultures under conditions of scarcity. As resources become more reliable and plentiful, the preferences should lawfully shift towards thinner bodies. Thus, the cultural pattern is evoked by the interaction of evolved psychology and local cues.

This explanation is not just parsimonious. It also makes novel predictions. The evolved psychology I have described should be labile and constantly adjusting itself to the current situation. Thus, it might be possible to catch it at work. Nelson and Morrison (2005) allowed male students to indicate their preferred body size either when hungry or after a meal. When hungry, they preferred significantly fatter bodies than when satiated. Similarly, the researchers were able to manipulate participants' feelings of financial adequacy, and when feeling relatively impecunious, the participants again preferred fatter bodies. These are satisfying results. They show that the hypothesized psychology does exist and can be seen at work. This observation validates the explanation of both the intra- and inter-society differences. Most excitingly, the results show that you can make a Western student more like a Hadza forager simply by putting him into a context more like the Hadza's (few resources and periodic hunger), which is a strong demonstration of both the power of context and the psychic unity of humankind.

The evoked-culture explanation is still explicitly Darwinian, because the ability to vary one's mate preferences contingent on food availability is an adaptation that enhances reproductive success. Moreover, the behaviour of individuals in any particular environment can be understood by standard Darwinian cost-benefit analysis, since although the cues are environmental, the behaviours contingent on those cues have been directly subject to the honing power of natural selection. Thus, seeking a mate with ample fat reserves in a population facing periodic food scarcity is a directly adaptive, though non-genetically determined, behaviour.

Evoked-culture-type adaptations can evolve only where each of the different environmental states has been experienced recurrently, and the best behavioural strategy to follow for a given environmental state has recurrently been the same. These conditions are plausible for many types of behaviour, such as the mate preference example given above. Similarly, many of the great dilemmas of human family organization – when to begin reproducing for a woman, how much to invest in offspring as a man, whether to favour sons or daughters in paternal investment – are recurrent through evolutionary

time and have different 'best' answers depending on local conditions. Thus, variation in all of these could be underlain by evoked-culture adaptations.

For example, Holden, Sear, and Mace (2003) show that it makes adaptive sense for people to invest their material resources primarily in their sons as long as the extra benefit of a unit of wealth transferred to a son rather than a daughter outweighs the risk of non-relatedness to son's offspring through adultery. Where these conditions are not met, greater reproductive success is achieved by daughter-biased resource investment. This kind of dilemma will have been experienced recurrently through evolutionary time, and so it is plausible that people will possess evoked-culture-type psychological mechanisms for calibrating their investment according to cues that reveal either local paternity certainty or the marginal value of resources transferred to children. Such an account predicts that both patriliney and matriliney will be widespread in humans, that matriliney will have arisen multiple independent times in cultural history, always under the same kinds of local circumstances, and that switches between the two will occur with changes in the types of resources available.

All of these predictions appear to be supported: matriliney is generally found where there is a high rate of extra-pair sexual activity (Flinn 1981), and where large transferable resources such as cattle are absent (Aberle 1961). As transferable resources increase in abundance during economic development, or cattle are acquired, matriliney tends to be replaced by patriliney (Holden & Mace 2003; Holden *et al.* 2003), presumably as individuals receive cues of the changing affordances of their environment. Thus, the evoked-culture account correctly predicts both culture state and culture change, and also offers a deep understanding of *why* this type of diversity exists (see pp. 233-5).

Another example is paternal investment. Societies differ dramatically in the extent of male investment in their offspring, leading to societies being characterized as father-present or father-absent (Draper & Harpending 1988; Geary 2000). Following Kaplan, Lancaster, and Anderson (1998), I argue elsewhere (Nettle 2008*b*) that men should be expected for adaptive reasons to calibrate their level of investment according to the difference they can make to offspring outcomes. I show that, for contemporary Britain, this leads to lower optimum levels of investment by men in lower socio-economic groups than in higher ones, and lower paternal investment in daughters than in sons, particularly in higher socio-economic strata. These predictions are indeed met, with fathers in higher socio-economic groups more likely to remain present in the household and spending more time and effort with children than men from lower socio-economic groups. Presumably this behavioural variation results from different cues received from the environment about the difference that men can make to their children evoking an evolved psychological flexibility.

If father investment is evoked culture, then, as in the body preferences case, within-society variation may be explained in the same way as between-society variation. That is, societies where general levels of paternal investment are low may be made up of people experiencing the same kinds of cues as low-investing individuals in a generally high-investment society such as contemporary Britain (see Draper & Harpending 1988 and Geary 2000 for discussions and explorations of this idea). The evoked-culture account also gives us a good theory of culture change. Where men start to be able to make more difference, such as, for example, where the rate of exogenous mortality due to disease declines, then there should follow a law-like shift to greater paternal involvement (see Quinlan 2007 for cross-cultural explorations of this prediction).

Evoked culture, then, is a useful concept for explaining both cultural diversity and culture change, both within and between societies. However, it does not capture the totality of what is meant by culture. In evoked culture, there is no tradition, merely a local response to cues, and, moreover, the content of the different behavioural options is pre-designed by genetic evolution. (For this reason, as Sear, Lawson & Dickens 2007 note, it is unclear that evoked culture should really be called 'culture' at all; similar phenomena in other species would just be called environmentally induced plasticity.) Much human cultural behaviour shows a different pattern, with clear, enduring local traditions whose content seems to be created by learning. This is the domain of transmitted culture.

Transmitted culture

Consider cultural domains such as textile design or metaphysical beliefs. Here, societies show patterns whose temporal duration exceeds the life of any individual, which mutate and diversify over time but show some kind of continuity. It is implausible that this is due to evoked culture. Selection cannot have built a menu of all possible types of carpet design or supernatural belief into the individual such that it merely needs to receive a cue of which one is locally appropriate in order to exhibit it phenotypically. Instead, these traits are learned in a deeper sense where learning actually creates, not just calibrates, the phenotypic pattern ('creates' within constraints, of course, since all learning is constrained by the evolved mechanisms that underlie it).

Cultural traditions of this kind exist because (a) humans learn how to do many of the things that they do; and (b) they learn at least partly from others in their social group, whilst others in turn will learn from them. This leads to local traditions of inter-personally transmitted behaviour and thought which differ characteristically from group to group.

The evolutionary issues surrounding such transmitted culture have been thoroughly analyzed and modelled (Boyd & Richerson 1995; Henrich & McElreath 2003; Rogers 1988). It is these models (in particular, from the simple case and summary in Nettle 2006) that I will be drawing on in this section, and for clarity I do so without further citation, the sources having been acknowledged.

First, we must consider why organisms would learn in the first place. Natural selection is a slow process, and to create the optimal behaviour for an environment by assembling fixed genetic patterns would require that a population of organisms experiences precisely the same conditions for many thousands of years and manages not to go extinct in the process. Given that optimal behavioural strategies vary with the environment, and environments vary a lot in both space and time, then under a very wide range of circumstances we should expect selection to equip the organism with mechanisms to learn to solve particular classes of problem in a way that is locally successful. Very often, as with foraging behaviours, for example, selection cannot even build in the full library of possibilities, since this library is unbounded. Instead, it can build in something like criteria for success and mechanisms to create and evaluate behavioural experimentation.

For a social species, a second dilemma emerges. If the more established individuals in the social group are already foraging or making carpets in a particular way, should one imitate what they are doing (i.e. social learning), or should one go out and do original trial-and-error learning for oneself? As ever, the evolutionist tots up costs and benefits. The benefit of social learning relative to individual learning is that it is cheaper.

Trial-and-error learning for oneself will take time and effort, and most early attempts will be poor. Simply copying what others are doing economizes on this process. As for costs of social learning, the main one is that what everyone is doing might not be a good way of solving that particular problem. It may never have been a good way, or it may have been a good way when it was devised, but, owing to the changing environment, may not be good now. Thus a potential downside to social learning is ending up with a pattern of behaviour that does not serve one's interests.

These costs and benefits can be formalized to predict when social learning will and will not be favoured. First, we consider under what conditions social learning would spread when rare. The more costly individual learning is, then, other things being equal, the more social learning is advantageous. This is for the obvious reason that it is the costs of individual learning that social learning saves. However, other things being equal, the faster the environment is changing, then the less useful social learning is. Again, this is for the obvious reason that the faster the change in the environment is, the more likely that the individuals from whom one is learning will be doing something that is already obsolete. Thus, whether a social learning strategy is expected to invade a population of individual learners depends on the balance of the costs of individual learning and the rate of environmental change.

Now we consider a slightly different issue, namely the expected equilibrium proportions of individual and social learning. When social learning is rare, then, subject to the constraints described above, it can provide a substantial advantage over individual learning. This is because the people whom one is imitating are overwhelmingly individual learners who went through the costly trial-and-error process of working out what is best to do in the local environment. However, as the proportion of social learning in the population rises, social learning is to a greater and greater extent copying off other social learners, who in turn copied off other social learners, and so on. The expected length of the chain of social transmission one has to go along actually to reach someone who worked out for him- or herself what was best to do in the local environment increases directly with the frequency of social learning. This means that the risk of copying a behaviour that is in fact obsolete goes up, and, therefore, the advantage of social learning goes down, as social learning becomes more common.

In a population consisting entirely of social learning, it is always better to be an individual learner. It is easy to see why this is the case. A population 100 per cent reliant on social learning would be constrained to copy each other forever, without individual innovation, and thus their behaviour could never be updated to the changing exigencies of the environment. Individuals would do much better in such a case to ignore the consensus and try to work out what to do for themselves, but as this individual learning strategy became more common, it would improve the pay-offs to social learning. The expectation is thus a dynamic equilibrium, where some of the learning in the population is social and some individual. The exact equilibrium point will be set by the costs of individual learning and the rate of environmental change, but the prediction of a mixture of learning types is a general one.

Transmitted culture is clearly very important in humans, as the distinctive cultural traditions of different populations vividly attest. Moreover, in language, humans have a powerful system for making it even more efficient, since language removes the need even for direct observation of one's social models. Instead, one can simply talk to them about how the world is and what should be done (Nettle 2006). Why would humans have invested so much more in transmitted culture than other species have? In part, as

for evoked culture, one can point to the changeability of their environments and the diversity of their ecological niches. This explanation is not sufficient, however. Other widespread African primates, such as baboons, share these features and have not developed transmitted culture to the same degree as humans have. A more unique human situation is the knowledge-intensiveness of our way of life. Humans extract resources from their environments in a dazzling array of different ways, but what all of these ways share is that they require a lot of knowledge to do them well (Kaplan, Hill, Lancaster & Anderson 2000). Humans eschew simple folivory and frugivory, and instead coax high-quality resources from their ecosystems by such diverse means as hunting, trapping, domesticating, burning, damming, digging, planting, and fermenting. Whereas for folivory, it is plausible to argue that the costs of working out for oneself the best way to do it is rather low, all of the human extractive activities take a lot of expertise to do well. Thus, in general terms, the costs of individual learning are high for humans, and so we might expect extensive reliance on social learning and thus transmitted culture.

It might seem that the models of transmitted culture place us back within the existing division of labour between evolution and the social sciences (pp. 223-4). That is, they seem to say that evolution has produced a capacity for cultural learning as an adaptation in humans – has made them, in effect, depend on ‘extra-genetic’ inputs from the social environment – and because this adaptation is powerful enough to produce arbitrarily great learned differences in behaviour from population to population, evolutionary theory makes no further predictions about how humans will actually behave. A different kind of approach, one based on culture history, is needed instead. This conclusion is wrong. Although there is considerable common ground between the evolutionary theory of transmitted culture and traditional ideas of social and cultural anthropology, there are also some differences.

First, the evolutionary theory predicts not that humans will be malleable to social learning in an undifferentiated way, but rather that reliance on social learning will appear predictably in domains of activity where the environment is somewhat stable and the costs of individual learning are high. For example, many societies show enduring traditions of taboo against certain classes of food. These can be understood as the product of social learning, which has become widespread in this domain because in particular environments, particular food classes persistently contain pathogens, and the costs of learning about these through individual trial-and-error can be high. However, food taboos are not arbitrary in their distribution. Fessler and Navarrete (2003) show that, across societies, they are overwhelmingly concentrated around meats and animal products. This makes sense given the theoretical models. Animals contain live pathogens from which one could contract a damaging long-term infection. Thus, the cost of trial-and-error learning for oneself is potentially very high. Fruits, by contrast, are pathogen-free, and even where they are toxic, the consequences are brief malaise at most. Thus, the costs of individual learning about fruits are rather low, and there is no reason to expect people to develop social learning adaptations for this domain. In accordance with this prediction, social traditions of taboo surrounding fruit are not widely attested ethnographically. Thus, which domains will show enduring cultural traditions and which will not can be predicted from the general theoretical framework.

Second, the evolutionary framework does not show that humans will learn just anything through culture. Because there is always a mixture of individual and social learning at equilibrium, and individual learning is always directed at improving

outcomes for individuals, the chances that the population is doing something that is good for individuals' reproductive success in that environment are substantial. Thus, many of the patterns of behaviour we see that are transmitted through culture will still be understandable as Darwinian adaptations, and reverse-engineered in the standard way. In fact, we can derive a specific expectation from the models about how often this will be the case. McElreath and Boyd (2007: 214) show that the proportion of the time that a population exhibits a behaviour optimal from the point of view of reproductive success is simply a function of the cost of individual learning relative to the benefit that having the right behaviour produces. Where the cost of learning is low, there will be enough individual learning going on to keep the population doing the best thing in the context, and the behaviour will look like a standard Darwinian optimal strategy, and will change rapidly as the environment changes. The more costly individual learning is, the less of it there will be at equilibrium, the more of the time the culture will perpetuate behaviour patterns that do not optimize reproductive success, and the greater the cultural lag will be in response to environmental change.

These are interesting and largely unexplored predictions. They make sense of the fact that meat taboos can endure for hundreds of years even if they have outlived any hygienic functions (Aunger 1994), whereas no enduring traditions surrounding fruit are observed. In some domains of human life, such as augury of the future, there are highly enduring and irrational-seeming cultural traditions, whereas in other domains people seem much more responsive to empirical experience. It may be that the cultural traditions appear exactly where it is hard to have enough experiences of the right kind to be able to learn effectively for oneself.

To posit that humans have evolved the capacity for extensive transmitted culture, then, is not to posit that humans have evolved a kind of generalized ability to be indoctrinated, and thus that human cultures can vary arbitrarily and without assignable limit. It is instead to predict that humans will use social learning to improve their average reproductive success given the evolutionary novelty of their environments. It does not exclude the possibility that cultural lags and non-adaptive traits will appear. However, it makes predictions about the types of domains where these will and will not be found, and predicts that even in the most inscrutable of domains, culture will eventually be propelled in the direction of an adaptive change by individual learning.

Lessons for the social sciences: the 'added value' of the evolutionary approach

Many social scientists might respond to the foregoing review of evolutionary origins of cultural variation by questioning what they have learned which is new. Social scientists already know that people respond to changes in the distribution of resources and the pattern of incentives by shifting their behaviour, and already know that cultural inheritance can lead to persistent traditions that are sometimes useful for individuals and sometimes not. What, then, is actually gained by embracing the Darwinian framework?

I would argue that there is a lot to be gained, but before saying why, I would point out that the debate about the role of Darwin's theory is not unique to the attempt to cross the biological-social science divide. Similar issues arise within biology. Although biologists generally accept that the Darwinian framework is the unifying paradigm of their discipline and the ultimate explanation for the properties of living organisms, this does not mean that it explicitly informs all their working practices on a day-to-day basis. Cellular and molecular biologists in particular spend much of their time simply

trying to describe the mechanisms they look at and their responses to various forms of perturbation. Although the mechanisms must have evolved, this fact imposes sufficiently loose constraints on their possible details that careful laboratory work proceeds largely on its own terms (see Dunbar 1996: 28 on this point). By the same token, adopting a Darwinian framework in the social sciences will never obviate the need for good ethnographic, sociological, and cross-cultural data of the type that social scientists are so skilled at producing.

What Darwinism can do for social science, then, is the same as what it can do for cellular and molecular biology, namely leave its methods intact, but add the additional layer of asking the ultimate *why* question. It is answering this *why* question, the question of ultimate causation, which is the unique and revolutionary contribution of Darwinian theory (Dennett 1995). In this section, I suggest a number of benefits to social scientists of considering the Darwinian ultimate question alongside their traditional more proximate concerns.

The first of these is that Darwinian theory concerns the big questions, such as why humans have culture, whether cultural traditions benefit or oppress individuals, why some societies are matrilineal and some patrilineal, why societies change over time, and so on. As Barnard (2008: 232) points out, these are the kinds of questions that invariably draw us into disciplines such as anthropology in the first place, but are all too easily lost sight of in the detail of descriptive and proximate research. The big questions are always *why* questions and thus amenable to Darwinian analysis. The Darwinian move thus raises the big questions anew and provides a powerful explanatory lens, as we have seen for the case of matriliney and patriliney (see p. 229).

The second added value is in terms of fleshing out and adding to aspects of existing accounts. For example, many traditions in anthropology such as cultural ecology and historical materialism have taken it as an axiom that humans respond to changes in the pattern of distribution and control of resources by changing their behaviour. In itself, this leaves unanswered *why* they would do this (the big question, see above), but also *how* those environmental conditions are mapped into the behaviour of the individual – how material conditions get under the skin, so to speak. Evolved psychological mechanisms which calibrate themselves by environmental cues provide the bridge, and in cases such as the Nelson and Morrison (2005) hunger study (p. 228), we can actually isolate and study these mechanisms, resulting in new predictions, for example about within-society variation.

In similar vein, social constructionists have argued that people are to a significant extent formed by the discourses and cultural practices to which they are exposed. The theory of transmitted culture (pp. 230-3) gives an ultimate account of why this might be. However, social constructionists have also been keen to argue that people are not complete cultural dupes. If they were, there could be no accounting for cultural change, or for the ways that people resist and seek to alter social discourses that they perceive as antithetical to their interests. The theory of transmitted culture shows why this must always be the case, since individual and social learning coexist in dynamic equilibrium, with individual learning driving culture change. The theory also makes the novel prediction that those aspects of human life which will have the most monolithic and laggard of cultural traditions are those where the cost or difficulty of finding out for oneself is the highest.

The third added value of evolutionary approaches is that evolutionary biologists have developed a large library of tools for generating predictions and testing

hypotheses in particular situations. Many of these can be applied to different types of data from those for which they were originally designed, and without implying that the proximate mechanisms are the same between biological and social applications. What these models provide above all is an improvement over purely verbal models in the ability to test between the predictions of competing hypotheses. It is the ability to choose between competing hypotheses on the basis of their predictions – rather than, for example, simply the amount of data available – which determines the speed of progress in science. Phylogenetic models, game theory, optimality modelling, and many other tools in the Darwinian toolbox can be of use to the social sciences in this regard (see, e.g., Holden & Mace 2003 and Holden *et al.* 2003 for the use of phylogenetic and optimality methods on social science problems and data).

The final added value of Darwinizing is that attention is drawn to new arenas of cultural diversity. For example, it was primarily Darwinian thinking (e.g. Trivers 1971) that drew attention to the class of situation known as a social dilemma – where there is a conflict between the optimal course of action if the behaviour of others is already fixed, and the optimal course of action if there is a chance of altering the behaviour of others. Experimental settings such as the prisoner's dilemma, dictator, and ultimatum games were devised to tap into human intuitions about how to behave in this regard. It turns out that behaviour in these situations varies substantially across cultures, for reasons that are not yet well understood (Henrich *et al.* 2005). Thus, a whole domain of human cultural variation has been discovered by researching a scenario that the Darwinian theory leads us to expect will be an interesting one.

Note that none of these potential benefits of adopting a Darwinian framework entails the 'reduction' of social science to biology, the claim that everything that humans do is adaptive, or any kind of genetic determinism. They merely require social scientists to be open to understanding biological ideas and techniques, and accepting that the Darwinian accounting of ultimate costs and benefits, whilst not the only kind of inquiry to be undertaken, is a valid one.

Lessons for evolutionists: the adaptiveness of human behaviour

If there are lessons from evolutionary theory for social scientists, there must also be lessons for evolutionists from the fact of cultural diversity. In this section, I review some implications for evolutionary psychology of the prevalence of evoked and transmitted culture.

The first lesson is that simple human universals, immune to socio-cultural variation, are likely to be rather rare or restricted in scope. Some early evolutionary psychologists focused on allegedly universally occurring patterns such as the male preference for women with a waist-to-hip ratio of 0.7 (Singh 1993). However, further research has revealed a more interesting situation where body preferences vary dramatically from culture to culture (pp. 227–8). Similarly, although Buss's (1989) original thesis that women universally value resources in their potential mates more than men do in theirs remains uncontradicted, much of the interest in recent years has shifted to how local conditions such as the economic roles available to men and women, the disease ecology, and the sex ratio might evoke locally different mating preferences (Eagly & Wood 1999; Gangestad *et al.* 2006; Pollet & Nettle 2008).

It is important to stress that these evoked-culture accounts are no less Darwinian or adaptationist than are accounts hypothesizing pancultural universals. The theoretical edifice of evolutionary psychology was never reliant on behaviour being

cross-culturally invariant, a point that is often misunderstood. Instead, as Tooby and Cosmides (1992) are at pains to point out, it is psychological mechanisms that are universal, but the evolved function of those mechanisms is to take input from the environment and calibrate behaviour accordingly. Thus, the idea that evolutionary psychology has had to retreat from a strong Darwinian claim of panculturality to a weaker 'interactionist' (Eagly & Wood 1999) position is a mischaracterization. Local variation is just as much a product of evolution as pancultural patterns are.

The general evolutionary expectation, then, is for mechanisms to have evolved flexibility, for reasons mentioned above, such as the great diversity of environments that human ancestors have lived in. Thus, behaviour will tend to vary as local conditions vary. Consequently, taking US undergraduates as behavioural representatives of *Homo sapiens* will not be good science. However, US undergraduates are good representatives of US undergraduates, a population as worthy of study as any other, and the point is that Darwinism may help us understand why they do what they do, without making any claims that other populations in different environments would necessarily do the same.

A crucial issue for evolutionary psychology is what the balance of evoked and transmitted culture is in determining behavioural variation. This is because evoked and transmitted culture produce adaptive behaviour to different degrees and under different circumstances. Behaviours which are the product of evoked culture are generally adaptive in the environments in which they occur to the extent that those environments resemble environments that have been recurrently experienced ancestrally. Thus, in environments that are not too novel, the behaviours so produced can be analysed as strategies to maximize reproductive success, and the straightforward accounting of costs and benefits, for example using optimality modelling (Parker & Maynard Smith 1990), is useful. This is the basic approach of human behavioural ecology (Winterhalder & Smith 2000), and human behavioural ecologists have been happy to concede that under conditions of modernity, for example, people do not always make fitness-maximizing decisions (Kaplan, Lancaster, Bock & Johnson 1995).

Where behaviour is largely a product of transmitted culture, the dynamics are somewhat different. Behaviours which are a product of transmitted culture are not appropriately understood as strategies that would have been adaptive in some Pleistocene hunter-gathering past. The extent to which they are currently adaptive will depend not on the ancestral familiarity of the environment, but on the costs of individual learning (see McElreath & Boyd 2007). Where these are low, individuals will generally be doing whatever best serves their current reproductive interests, and again the accounting of fitness costs and benefits is appropriate. Where learning costs are high, however, traditions may persist for long periods that are not particularly useful for solving anyone's adaptive problems. Thus, cultures will be more as traditionally viewed by socio-cultural anthropologists, that is, determined by their own history and to some extent arbitrary, rather than as seen by economists, that is, the emergent property of individuals all following their self-interest.

Crucially, evoked and transmitted culture make different predictions about culture change. If a population is transplanted to a different environment, then those aspects of their behaviour which are evoked by the environment should update within a generation. On the other hand, to the extent that their behaviour depends upon

transmitted culture, there will be an effect of tradition that may, if the costs of individual learning are high, persist for a long period. The world of evoked culture, then, is much more like that of Marxist social theory, with material conditions driving culture change, whereas that of transmitted culture is much more like that of social constructionism, with ideas passed on through discourse having an enduring influence on people.

It is an open question how much of culture is evoked and how much is transmitted. There are also hybrid possibilities. For example, under conditions of competition for mates, men may universally be motivated to enter status competition (evoked culture), but the local form that status competition takes (praise-singing, jousting, potlatch, wrestling) could be transmitted. There may also be other mechanisms not well covered by either of these possibilities. However, the potential diversity of predictions from these evolutionary theories of culture should alert evolutionary psychologists to the fact that embracing Darwinism *per se* does nothing to abolish the complexity of existing social science. Darwinism is a broad meta-theory that can motivate many different predictions about behaviour depending on what kinds of evolved mechanisms and selection pressures are assumed. In the end it will be careful empirical work and nuanced theorizing that will sort out which of the various possibilities is the correct one in particular cases (Sear *et al.* 2007).

Conclusions

I hope to have demonstrated that there is no conflict between being a Darwinian and accepting that human behaviour is culturally variable. The notions of evoked and transmitted culture are powerfully explanatory, and compatible with elements of historical materialism and cultural ecology, on the one hand, and social constructionism, on the other. They dovetail neatly with traditional ideas from social science, which means that the Darwinian *why* question and all it entails can be smoothly incorporated into social science without violating its existing intellectual commitments or thematic concerns. On the other hand, evolutionists have to accept that the world is too complex for them simply to read off the behaviour of a population and hypothesize why that behaviour might have been good for ancestral foragers in Pleistocene Africa. Human behaviour is more variable, and actually more interesting, than that position implies.

Social science has a rich library of information about human behavioural diversity. Biological science has a rich toolkit of theories and methods for testing hypotheses about the sources of this variation. It should not be a question of evolution replacing social science, or social science attempting to establish itself as an autonomous zone free of biological constraints. Rather, I see it as akin to the marriage of Beatrice and Benedick in Shakespeare's *Much ado about nothing*. The two have a great deal to offer each other, but cleverness, fear of change, and a certain competitive tendency keep them sniping at each other instead. It is time for well-meaning friends to engineer their union.

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Par-delà l'opposition nature-culture : la variation culturelle comme caractéristique évolutionnaire

Résumé

Les explications du comportement opposent deux écoles de pensée, privilégiant les explications par l'évolution (biologique) et par le social ou la culture. Dans cet article, l'auteur tente de résoudre cette dichotomie en montrant que les organismes sont sensibles aux influences sociales et culturelles parce qu'ils ont acquis au cours de leur évolution des mécanismes qui leur confèrent cette sensibilité. Il étudie deux classes d'explications évolutionnistes des variations culturelles, celle de la culture « évoquée » et celle de la culture « transmise », et avance que ces deux types de mécanismes enrichissent et renforcent les comptes-rendus existants, tout en permettant de nouvelles prédictions. L'article suggère qu'il existe une grande compatibilité mutuelle et qu'il y a beaucoup à gagner des échanges entre sciences sociales et naturelles.

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Not whether but how: a comment on Nettle's 'Beyond nature versus culture'

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It should not be necessary for Daniel Nettle to assure an anthropological audience that 'to endorse the central ideas of evolutionary psychology (and Darwinism more generally) need in no way imply genetic determinism or de-emphasize the importance of culture' (p. 224). But mutual misunderstanding has long characterized the debates over the applicability of the Darwinian conception of heritable variation and competitive selection to the study of human behaviour. It has taken longer than it should for it to be generally accepted that cultural evolution is continuous with biological evolution, and that the mechanisms of cultural selection are analogous, but not reducible, to those of natural selection. One reason has been a persistent exaggeration of the dichotomies heredity/environment and individual/society, on which Nettle comments to good effect. But evolutionary psychology and dual-inheritance theory are now here to stay. The question is no longer whether, but how, they can be put to use in the explanation of the data in the ethnographic record.

It is not, however, an easy question to answer. The evoked/transmitted distinction captures the essential difference between the acting out of information inherited genetically and of information acquired exosomatically by imitation or learning. But it becomes progressively more difficult to apply as the behaviour studied moves away from such topics as mate choice or parental investment in the direction of the multifarious attitudes, beliefs, and consequential life-styles observed in populations which are both sub-culturally differentiated and open to external cultural influences. The models which have served population geneticists so well cannot be directly applied by anthropologists aware that memetic inheritance is as often blended as particulate; that unlike our genes, our attitudes and beliefs are constantly changing during the course of our lives; and that the mutations without which social learning and frequency dependence would lead to cultural inertia are not random in the sense that genetic drift is random. That does not remove them into a world of cultural creationism. But it does mean that comparative ethnography is confronted with not only a formidably wide range of culturally acquired behaviour patterns but an equally wide range of unique path-dependent cultural-evolutionary sequences.

Consider the data on lethal interpersonal violence culminating in warfare. It is known that killers are universally more likely to be young adult males than either older

males or coeval females. But it is also known that populations which are not genetically different and share a common ecological environment can have significantly higher or lower rates of lethal violence than each other. And it is also known that charismatic big-men, war-leaders, and conquerors can make their followers significantly more pugnacious than they would otherwise have been. So how is the observer seeking to explain the differences between populations to assign the correct weights to evoked culture (young men instinctively responding to attack or threat to themselves and their comrades or kin), transmitted culture (warrior norms of aggressiveness and bravery inculcated by parents, mentors, and peer-groups), and the personal influence of exceptional individuals?

It is a methodological commonplace that anthropologists cannot do experiments on minds and cultures in the way that biologists can do experiments on organisms and species. Sometimes, it is possible to observe what happens when a culturally homogeneous population moves into a different ecological environment, or when two or more culturally heterogeneous populations move into the same ecological environment. Sometimes, it is possible to use phylogenetic models to trace the vertical transmission of mutant memes by homologous descent. But perhaps the most promising current approach is cross-cultural game-theoretic experimentation of the kind carried out by Joseph Henrich and co-workers in fifteen different small-scale societies. Nettle, in citing that study, comments that the cross-cultural variations which the researchers report 'are not yet well understood' (p. 235). But their findings invite explanations of just the kind that anthropologists should be well qualified to provide. Where, for example, generous offers in the Ultimatum Game are significantly more often refused than rational-choice theory predicts, this becomes much less surprising if the culture turns out to be one where gift-giving is interpreted as an attempt by the donor to place an unwelcome obligation on the donee. This is surely an area of research where there is much to be gained from active cooperation between evolutionary psychologists and cultural anthropologists.

A further complication is the dispute between behavioural ecologists and memeticists about how far adaptive cultural mutations can be biologically maladaptive, and vice versa. Should memes – whatever exactly they are – be seen as replicators whose reproductive success depends on their spreading like viruses among the more culturally susceptible members of the population, or as by-products of natural selection acting on their forebears' genes? Can their rate of diffusion be enhanced by their environment sufficiently for them to be unconstrained by the pressure to maximize their carriers' reproductive fitness? Such questions are critical to the burgeoning neo-Darwinian literature on the anthropology of religion. To what extent is behaviour informed by distinctive traditions of metaphysical beliefs, sacralizing attitudes, and ethical norms evoked by environmental cues acting on innate susceptibilities and dispositions? Anthropologists and psychologists are a long way from agreement on what kind of evidence will settle what Nettle rightly calls the 'crucial issue' of 'what the balance of evoked and transmitted culture is in determining behavioural variation' (p. 236).

Explanation of variation becomes more difficult still when not only have the people observed been (as Nettle puts it) 'to a significant extent formed by the discourses and cultural practices to which they are exposed' (p. 234), but also their behaviour has been determined by institutionalized intra- and inter-societal differences in economic, ideological, and political power. As anthropologists are increasingly drawn into such areas long familiar to sociologists as imperialism, industrialization, bureaucracy,

political parties, formal education, and so on, they have to take account of the selective pressures which favour one over another set of social, as distinct from cultural, practices. Information affecting phenotypic behaviour is now encoded in rules underwritten by formal sanctions to which those in subordinate roles have no choice but to conform whatever the genes in their bodies and the memes in their minds. It is still part of the same continuous process of variation and selection of information affecting phenotype. But social selection operates at a different level and through different mechanisms from cultural selection, and it raises both theoretical and methodological issues which need also to be addressed as part of the collaboration between the social and biological sciences which Nettle persuasively recommends.

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Evolution in anthropology: a comment on Nettle's 'Beyond nature versus culture'

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Evolution has had a poor press within conventional social/cultural anthropology, pretty much since the turn of the twentieth century, when Boas and Durkheim argued that biology was not really relevant to cultural facts. At the time, this was undoubtedly a valid position, since biology had not fully engaged with the behavioural or cognitive worlds. However, one consequence of the social sciences turning their collective back on biology at this particular point was that they did so before biology had resolved its own confusions over the evolutionary processes. As a result, the form of evolutionary thinking that the social sciences took with them was eighteenth century and pre-Darwinian in its thinking – a view of evolution infused with the *scala natura* conception of a progressive unfolding of traits that led inexorably to ever greater perfection. Unfortunately, all this was later undermined by the Darwinian revolution, a revolution that did not finally gain wide acceptance within biology until well into the twentieth century.

Daniel Nettle's careful and erudite analysis of why anthropology and its cognate disciplines should take evolution seriously makes an important contribution to the process of rebuilding disciplinary bridges. Since I strongly endorse his approach (see, e.g., Dunbar 2003; 2008), I do not want to waste journal space by simply repeating what he has said. Instead, I just want to make two points that I think are important since they concern confounds that still inadvertently get in the way of *rapprochement*.

The first point I want to emphasize is the conceptual framework that organismic biologists refer to as Tinbergen's *Four Whys*. Tinbergen (1963) pointed out that when biologists ask why something is the case, they might in fact be asking any one of four different kinds of questions. Conventionally, these are function, mechanism, ontogeny, and phylogeny. Function refers to the evolutionary goal of a trait, as indexed by its effect on genetic fitness (not to be confused with teleological explanations); mechanisms identify explanations at the cognitive, behavioural, or anatomical levels that make it possible for an organism to achieve this functional goal; ontogeny refers to the process of development from egg to adult that makes it possible for an organism to have that trait (the nature-vs-nurture part); and phylogeny refers to the historical sequence whereby the trait was acquired within a biological lineage. Although invariably attributed to the ethologist Niko Tinbergen, in fact these separate kinds of biological

investigation were first explicitly articulated by the polymath Greek philosopher Aristotle in his biological works in the fourth century BC (Huxley 1930).

The two important points that Aristotle (and later both Huxley and Tinbergen) made are that these explanations are logically independent of each other (an answer to any one of them does not commit us to a particular answer on any of the others), and that all of them are equally important (we cannot have said to understand a phenomenon until we have answered all four kinds of questions). Of particular importance for our present concerns is the fact that a functional explanation in terms of the way a particular trait allows an organism to maximize its genetic fitness does not imply that the trait is genetically determined in any crude sense: the latter is a question about ontogeny, and a functional explanation can be supported as easily by trial-and-error-learning or social learning (cultural transmission) as by a genetically determined behavioural programme. Even though the term 'gene' appears in both functional and ontogenetic explanations, the meaning of the word is different: genes in the functional sense are not the same kind of thing as genes in the developmental sense. For evolutionary biologists, genes in the functional sense are really strategies, and can therefore be behaviourally very flexible. Nor should these explanations be confused with explanations about motivation (which are properly explanations of mechanism). Unfortunately, we are so used to thinking teleonomically about our own behaviour that a statement about 'selfish genes' has repeatedly been mistaken for an explanation at the motivational (i.e. mechanisms) level rather than the functional level. Biologists do not (usually!) confuse these levels of explanation, and being able to slide seamlessly between explanatory levels without confusing them is an important hallmark of modern evolutionary biology.

The second of my points concerns the role that evolutionary theory plays in biology, and therefore should play in anthropology. Thanks mainly to the clear separation between Tinbergen's *Four Whys*, evolutionary theory's primary role has been as a framework theory that helps bridge between biological (sub-)disciplines that would not normally have much in common (behaviour, ecology, genetics, physiology, cell biology, anatomy, palaeontology, etc.). Even if biologists working in different disciplines do not always see eye to eye with each other (behavioural biologists constantly bemoan the way genetics dominates everything in contemporary biology), none the less they can now engage intellectually with each other, and many important new research programmes have developed within biology during the last few decades as a result. An example is the area known to practitioners as 'evo-devo' (evolutionary developmental biology), where exciting new ideas in developmental biology have been worked out in the last decade within an explicitly evolutionary framework.

The important lesson for social scientists, as Nettle observes, is that incorporating an evolutionary framework into what they do does not suddenly make them stop doing conventional social science. The Darwinian revolution (if we may so call it in this context) is not a replacement revolution, but rather a synthesizing revolution. Indeed, the history of evolutionary biology over the past half-century has emphasized time and again how important it is that the various disciplines continue to work within their own natural paradigms, for these provide the grist to the evolutionary mill. Without the hard-won observational work of the anthropologist, sociologist, demographer, historian, economist, and so on, there is nothing for an evolutionary approach to be applied to. And experience in biology tells us that this has to be a two-way process, with each partner benefiting from the insights offered by the other.

That said, of course, the one thing that an evolutionary approach does bring with it is a stringent sense of rigorous hypothesis-testing. Some social anthropologists will find that challenging insofar as they will want to argue that anthropology is properly a qualitative discipline, and not an empirical pseudo-science. I do not agree. All disciplines, whether they belong to the conventional sciences, the social sciences, or the humanities, are, of necessity, empirical at heart: they seek to describe and explain the world we live in, even if they do it imperfectly. In one sense, even good novelists aspire to that. Indeed, a good case can be made that what makes good novelists great is precisely their astute understanding – based on close observation of real life as it is lived – of the (evolutionary) forces that underpin everyday human behaviour (Dunbar 2005). But a subject's value in this respect is greatly enhanced by the intellectual discipline that an empirical hypothesis-testing framework imposes. Such an approach obliges us to confront our assumptions about the world and allows no room for casual thinking. This is a hard taskmaster for all of us, but disciplines that embrace it benefit enormously. An evolutionary framework offers that opportunity, and anthropology can and should seek to capitalize on it.

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Cultural variation and social complexity: a comment on Nettle's 'Beyond nature versus culture'

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Daniel Nettle's paper is a valuable, clearly argued contribution to the *rapprochement* of social and evolutionary anthropology. Nettle's distinction between evoked and transmitted culture, and his emphasis on the emergent properties of systems, are particularly helpful for social anthropology. The discovery that the parameters of the Ultimatum Game are set by the degree to which, in any culture, individuals rely on each other to reduce risk was an important step in the reconciliation of the two disciplines.

I anticipate that many social anthropologists will none the less continue to think that evolutionary or adaptive explanations fail to do justice to the complexity of social interaction. This has its roots in the foundational debate between Durkheim and Tarde on explanation in social science. Tarde argued that '[w]e may call it social evolution when an invention quietly spreads through imitation' (1969 [1888]: 184). The inventor was an individual with a special psychology, but his environment merely facilitated the transmission of a new idea from one individual to the next by imitation. Tarde's approach was taken up by writers such as Cavalli-Sforza and has recently been reincarnated in Dawkins's 'meme' (Dawkins 1976: 189).

While this may provide a useful model for transmitted culture, Tarde's ideas were strenuously opposed in his own time by Durkheim, whose axioms (as Nettle notes) are still accepted by sociologists and social anthropologists. Durkheim explained the Industrial Revolution as the consequence of a collective social process, rather than a series of individual inventions. 'Darwin says that in a small area, opened to immigration, and where, consequently, the conflict of individuals must be acute, there is always to be seen a very great diversity in the species inhabiting it' (Durkheim 1933 [1893]: 266). When rural communities expanded, they came into competition for resources and responded, analogously, by adapting specialized economies. Durkheim, in other words, took an ecological approach to explaining social change.

A similar debate is active within evolutionary biology. The Tarde-like approach taken by Dawkins is implicitly challenged by the notion of evolutionary fitness landscapes advocated by Kauffman. Kauffman writes, 'In co-evolutionary processes, the fitness of one organism or species depends upon the characteristics of the other organisms or species with which it interacts, while all simultaneously adapt and change' (1993: 33). Both co-evolution and niche construction are aspects of the complexity of

human social evolution. Co-evolution occurs whenever different individuals or species change the selective pressures acting on each other. Symbiosis, parasitism, and predation all have parallels in human society, and can influence human biological evolution. Niche construction occurs where individuals modify their environment, thereby changing selection pressures on their offspring.

Durkheim's thesis concerning the emergent properties of social systems is neatly illustrated by Nettle's example of the social bacteria, 'where the outcome of the behaviour is dependent on what other individuals are doing' (p. 226). More problematic, for evolutionary biologists, is Durkheim's theory that the group acts to suppress individuals' deviation from the norms (1962 [1895]: 2), which appears to commit the group-selection fallacy. The classic example of a fallacious group-selection argument was the hypothesis that some male grouse forgo mating in order to prevent over-exploitation of moorland resources. If this disposition to celibacy was genetically determined, it would quickly be eliminated from the population. Durkheim's argument was that as soon as the individual deviated from the norms of society, collective forces pulled him/her back into line. However, an evolutionary approach to collective resource management and to reciprocal altruism shows their success depends on participants' ability to detect and punish cheaters or free-riders, *because it is in their individual self-interest* to sustain cooperation.

The opposite scenario is illustrated by Helbling's re-analysis of Yanomamo warfare. Helbling argues that the Yanomamo, on the borders of Brazil and Venezuela, are trapped by their lack of overall leadership, and the difficulty of defending their crops against attack from neighbouring villages, in a version of the Prisoner's Dilemma where villages that renege on alliances cannot subsequently be punished, because their erstwhile allies are dead (Helbling 1999; and see Layton 2006).

Niche construction (Odling-Smee, Laland & Feldman 1996) is illustrated by the evolution of language (and here I think Nettle is too kind to Barkow, Cosmides, and Tooby). There is no point in having a 'language acquisition module' unless there are other people to talk to. Once verbal communication begins, a social niche is constructed that favours selection for those who have the genetic capacity to speak. The more individuals can exchange verbal information, the richer the niche, that is, the speech community, becomes. Recent work by Barton (2006) and by Shultz and Dunbar (2007) examines ways in which the creation of a social niche may have shaped brain evolution. On the other hand, the acceptance by some of an innovative behaviour may impede its acceptance by others. If some farmers adopt more efficient machinery, they may be able to squeeze those using less efficient techniques out of the market niche before they can afford to buy the new equipment, eliminating the benefits of social learning (Layton 2000).

Many social anthropologists may be more interested in compiling the good ethnographic descriptions of social complexity that Nettle commends than in explaining limits on variation. The rich complexity of human social systems may seem dazzling compared to the apparently simple and limited explanations for social behaviour offered by evolutionary theorists, but it is this very complexity that shapes much of the fluctuating human adaptive environment. Natural selection *can* explain the limits to cultural variation, for example the tendency for livestock herders in Africa to practise patrilineal inheritance and horticulturalists matrilineal inheritance, or the relative reliance of social and individual learning, examples that Nettle discusses. The evolutionary critique on social theory demonstrates that cultural variation is not independent of the

laws of biology, while social theory can demonstrate the complexity of the environment in which human adaptation takes place.

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Beyond nature versus culture: a response to comments

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I am grateful to the three correspondents for thoughtful and supportive comments on my paper. I detect considerable convergence in our views on both the promise and the difficulty of an adequate integration of Darwinian ideas into social science. I will not respond here point by point, since the commentaries raise deep, open questions that would require at least another full article to address. Nor do I wish to burden the reader with repetition of points already made in the main article. Instead, I would like to conclude briefly by pointing out some key ways in which the problems that evolutionary social scientists face are actually very similar to the problems that evolutionary biological scientists face. That is, the difficulties which strike us in applying something as simple as the theory of evolution to something as complex as human social life are in fact the very same difficulties which we encounter when applying that same theory to something as complex as organic life more generally. This point may help to bring social and biological researchers together. It is not that the one faces complexities and difficulties of a different order than the other faces; rather, both face great complexities, and the challenges in the two cases are often parallel.

Dazzling diversity

The comments remind us that the human ethnographic record is one of dazzling diversity. Populations in similar ecologies with similar population densities and production systems are organized in strikingly different ways, ways that could not be predicted *a priori* and which depend to a considerable extent on historical contingency. But before we conclude that '[t]he rich complexity of human social systems may seem dazzling compared to the apparently simple and limited explanations ... offered by evolutionary theorists' (Layton, p. 248), let us remind ourselves that the very same point could be made in respect of all organic life. Over 70 million years, a single mammalian ancestor has given us over 5,000 radically different ways of making a living, from 30 millimetre bumblebee bats, to 30 metre blue whales. Some mammals have gone down the road of speed, some of size, some of arboreality, some of flight; some have gone for numerous and frequent offspring and fleeting sexual relations, others for extended pair bonds and few offspring with extended care. Males may be larger than females and adorned, or the same size, or smaller; seasonality may be dealt with by storage, or

migration, or hibernation, or being large, or being small. Although this dazzling variation – all of which occurs within one rather small branch on the tree of life – is constrained by ecology, it is not exhausted by it. Indeed, within similar habitats or the very same one, one may find many different mammals making their livings in quite different ways. Different lineages have different histories, and these gave them different affordances, different paths across what became effectively different fitness landscapes.

Thus, the contrast between the simplicity of the theory and the complexity of the record is not a peculiarity of social science. It is the very heart of what evolution always produces. Darwin's is precisely a theory of how a few simple forces, applied to a contingent and stochastic world, a world in which history matters, produce dazzling diversity from homogeneous origins. This is the meaning of the famous 'tangled bank' passage which concludes the first edition of *The origin*:

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us (Darwin 1996 [1859]: 360).

Complexity of outcome is not an obstacle to applying evolutionary theory, but rather a sign that this is a case where an appropriately nuanced evolutionary theory is needed.

The comparative method

In view of the above, it is easy to despair at the possibility of prediction, of generalization, in both evolutionary social science and evolutionary biology. The outcomes seem so variable, so unpredictable *a priori*, that there appears little point in trying to do anything more than describe what is there. However, this counsel of despair can be easily avoided if one is appropriately clear what it is that one is trying to do. Prediction of the exact evolutionary path that any particular lineage (culture) will take is indeed more than one could hope for. However, an understanding of the dynamics of evolution allows predictions to be made at a comparative level instead. For example, lineages facing high rates of mortality will tend to invest in early and frequent reproduction, and often small adult size ('fast' life history), compared to those facing lower mortality rates, which will tend to evolve a slower life history of large size, fewer births, and later age at sexual maturity. This prediction is made by theory, and amply confirmed by comparative data across species (Promislow & Harvey 1990). There may be many, contingent, unpredictable, reasons *why* mortality is high or low in a particular time and place – the indrii, for example, experiences low mortality by being big and happening to live in Madagascar, where there are no large carnivores, whereas bats experience low mortality because they can fly – but the point is that we can make 'if-then' hypotheses which are amenable to test with comparative data: *if* (for whatever reason) mortality is high, *then* early reproduction is likely to evolve. As well as differences *between* species, this very same principle powerfully explains differences in age at reproduction *within* the human population, whether it be the contrast between pygmy and non-pygmy populations in Africa and Asia (Migliano, Vinicius & Lahr 2007), or the difference across poor and affluent neighbourhoods in Chicago (Wilson & Daly 1997). That the reasons for the mortality differences are so diverse, and the proximate mechanisms by which adaptation is achieved multifarious (genetic selection, cultural transmission, individual cost-benefit calculation), makes no difference to the elegance and generality of the functional explanation.

The lesson of this is that evolutionary hypotheses are often best tested using comparative evidence from many cultures rather than within any single culture (see, for some examples, Fincher, Thornhill, Murray & Schaller 2008; Holden & Mace 2003; Low 1988; Quinlan 2007; Schaller & Murray 2008). This is equally true for biologists, but for social scientists it constitutes a change of emphasis from usual ethnographic practice, where individual researchers concentrate on just one culture, about which they wish to understand everything, rather than a question, which they test across all cultures. Evolutionary biologists are satisfied if they can explain even a small portion of the variation across many taxa, whereas ethnographers want to understand deeply how the various components of one culture fit together. However, the gains from trade between the two approaches are very high here. There can only be good cross-cultural databases if there are good ethnographers of every culture, just as there can only be good cross-species databases if there are good descriptions of each species. Thus, a fruitful collaboration between ethnographers and evolutionists lies in the creation and exploration of comparative data on human cultural and social organization, with the richness of ethnographic data, and the hypothesis-generating power of evolutionary theory.

Diversity of mechanism is not diversity of function

A final point to make about the diversity of the ethnographic record is that diversity of mechanism is not diversity of function. This echoes Dunbar's point about the need to differentiate functional explanations (why is *X* retained in the form it is?), mechanistic ones (how does *X* work?), and historical or phylogenetic ones (where did *X* come from?). These distinctions are not always made clearly in social science, but they are crucial, not least because different mechanisms with different historical origins can serve the same function. The wings of birds and those of bats, for example, have arisen in quite different ways, at different times, from different substrates. However, given the fundamental aerodynamic pressures on flight, the functional reasons for their current shapes can be studied without regard to this difference in their origins. Similarly, human societies organize, for example, the provision of public goods using different traditions or institutions which were moulded out of different socio-cultural raw materials. However, regardless of what they were built from, or how they hold their normative power, they are moulded by the same fundamental conflicts and possible solutions well described by evolutionary theory (West, Griffin & Gardner 2007). Thus, we should be wary of rejecting common functional hypotheses for patterns of behaviour just because their phenomenology, proximate mechanism, or historical origin is demonstrably diverse. Tinbergen's four whys are just as useful for social science as they are for biology more generally, and indeed they might become a useful interface for reconciling explanations not just between biology and social science, but amongst the various human sciences (psychology, sociology, anthropology, history, economics) as well.

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