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Ethics, evolution and culture

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Abstract Recent work in the fields of evolutionary ethics and moral psychology appears to be converging on a single empirically- and evolutionary-based science of morality or ethics. To date, however, these fields have failed to provide an adequate conceptualisation of how culture affects the content and distribution of moral norms. This is particularly important for a large class of moral norms relating to rapidly changing technological or social environments, such as norms regarding the acceptability of genetically modified organisms. Here we suggest that a science of morality/ethics can benefit from adopting a cultural evolution or gene-culture coevolution approach, which treats culture as a second, separate evolutionary system that acts in parallel to biological/genetic evolution. This cultural evolution approach brings with it a set of established theoretical concepts (e.g. different cultural transmission mechanisms) and empirical methods (e.g. evolutionary game theory) that can significantly improve our understanding of human morality.

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Introduction

Recent years have seen increasing interest in two related fields: "evolutionary ethics" (Richards 1986; Ruse and Wilson 1986; Nitecki and Nitecki 1993; Clayton and Schloss 2004; Boniolo and De Anna 2006) and "moral psychology" (Haidt 2001; Greene and Haidt 2002; Greene 2003; Singer 2005; Doris and Stich 2006; Hauser 2006b; Haidt 2007; Hauser et al. 2008). The former has its origin primarily in sociobiology and philosophy, and the latter in psychology (evolutionary, social and cognitive) and neuroscience. Although comprising a quite diverse range of theoretical positions, all of this recent work is unified by two common themes: (1) an *empirical* basis, in which data from experimental psychology, neuroscience, primatology and anthropology are used to describe and explain people's folk theories, intuitions and beliefs regarding what is right and wrong, rather than taking people's stated beliefs at face value or relying on philosophers' intuitions, introspection or reasoned arguments regarding those beliefs; and (2) an *evolutionary* basis, in which evolutionary principles are used to predict and explain why people hold the ethical norms and beliefs that they do. Although any connection drawn between evolution and ethics once immediately invoked cries of "naturalistic fallacy," it is being increasingly recognised that evolutionary principles can help to explain why people hold the ethical views that they do (a purely descriptive ethics), and that this knowledge can be used to inform, but not solely determine, a normative ethics

also (Wilson et al. 2003; Singer 2005),[1] although we focus here on the former (descriptive) task.

In this paper we fully accept these two principles, that the study of people's everyday ethics or morality must be empirically grounded, and that evolutionary theory can usefully inform that study. Our purpose here is to draw to the attention of ethicists and moral psychologists a wider and richer body of evolutionarily-inspired research, specifically in the "cultural evolution" or "gene-culture coevolution" research tradition. We believe that this theoretical perspective can provide a more inclusive evolutionary science of ethics, moving away from the relatively narrow and gene-centric focus of a certain strand of evolutionary psychology and sociobiology. Although arguments from purely gene-based biological evolutionary theory can explain certain ethical phenomena to some extent, a full understanding of moral norms and changes in those norms can only be achieved by properly considering cultural factors. This can be done by treating culture as an evolutionary system in its own right, and by studying this cultural evolution using similar tools, methods, theories and concepts that biologists use to study biological evolution. Before providing more details of a cultural evolutionary approach to ethics, in the following section we briefly summarise the key assumptions and findings of evolutionary ethics and moral psychology as they currently stand.

Throughout the paper we use the term "moral norm" as a generic term to describe "a rule or principle that specifies actions which are required, permissible or forbidden independently of any legal or social institution" (Sripada and Stich 2006). We think this definition captures the key feature of morality, i.e. evaluations of others' behaviour as right or wrong, good or bad, acceptable or unacceptable. Like Sripada and Stich (2006), we do not clearly distinguish between non-moral norms and moral norms, and leave it for future empirical work to make this distinction.

[1] Wilson et al. (2003) make the point that while descriptive facts about ethical beliefs, such as whether they are the product of natural selection, should not be the *sole* basis for normative theories of ethics, this does not mean that evolutionary origins are *entirely irrelevant* for normative theories. It seems to us that a normative theory that begins with an accurate understanding of why people hold the moral beliefs that they do would be superior to a normative theory that has no grounding in reality. Singer (2005) makes the additional point that ethicists commonly appeal to their own and others' moral intuitions when constructing or criticising normative ethical theories. If these intuitions have an evolutionary basis, as is argued by many moral psychologists, then normative theories are already being influenced by evolutionary history, whether this is explicitly acknowledged or not.

The current state of evolutionary ethics/moral psychology

Soon after the emergence of sociobiology (Wilson 1975), sociobiologists began to argue that biological evolutionary theory can inform our understanding of people's moral or ethical behaviour (Richards 1986; Ruse and Wilson 1986; see also Singer 1982). Sociobiologists and evolutionary psychologists generally argue that human cognition has been shaped by natural selection to solve recurrent adaptive problems faced during our species' evolutionary past (Barkow et al. 1992; Pinker 1997). Evolutionary ethicists apply this reasoning to morality, arguing that human morality has been shaped by natural selection to solve specific adaptive problems faced by our ancestors. A paradigmatic example used in evolutionary ethics is that of incest taboos: a moral norm prohibiting sex with close relatives, as is found in many societies world-wide, can be given an ultimate evolutionary explanation in terms of inbreeding avoidance, where, due to the mechanics of the diploid genetic inheritance system, the offspring of closely related individuals have a high probability of exhibiting deleterious genetic mutations (Ruse and Wilson 1986). Hence the proximate moral norm—the incest taboo—serves to promote ultimate genetic fitness by protecting against inbreeding depression.

Another commonly cited example is altruism. Altruism towards close kin is explained in terms of the promotion of inclusive fitness, given that close kin share genes and so genes promoting kin-directed altruism will be favoured (Hamilton 1964). Reciprocal altruism—helping others who have helped you in the past—can explain cooperation in small groups of individuals who repeatedly interact (Trivers 1971; Axelrod 1984). More recently, theories have been proposed that draw on group selection—either biological (Sober and Wilson 1998) or cultural (Richerson et al. 2003; Richerson and Boyd 2005) group selection–to explain the existence of widespread non-kin and non-reciprocal altruism that is exhibited by humans. Group selection arguments propose that, during the course of human evolution, selection between small competing groups of people has favoured what Richerson and Boyd (2005) call "tribal social instincts", innate predispositions to help members of one's own group, because these cooperative groups outcompeted groups which were less cooperative and which exhibited internal conflict. *Cultural* group selection models assume that this is made possible by cultural processes such as conformity, which serves to bind groups together and prevent selfish free-riders from exploiting cooperative groups (Henrich and Boyd 1998), and culturally transmitted norms that punish non-cooperators (Boyd et al. 2003).

In parallel to this work, there has also been a surge of research in moral psychology, the empirical study of

people's moral norms, beliefs and behaviour (Haidt 2001; Greene and Haidt 2002; Singer 2005; Doris and Stich 2006; Haidt 2007). This field draws on the methods of experimental social psychology, cross-cultural psychology, cultural anthropology, neuroscience and primatology. The most influential model in moral psychology is probably Haidt's (2001) social intuitionist model. Haidt (2001) distinguishes between moral *judgement* ["evaluations (good vs. bad) of the actions or character of a person that are made with respect to a set of virtues held to be obligatory by a culture or subculture" Haidt 2001, p.817], moral *reasoning* ["conscious mental activity that consists of transforming given information about people in order to reach a moral judgement...(this) process is intentional, effortful, and controllable and ... the reasoner is aware that it is going on" Haidt 2001, p.818] and moral *intuition* ("the sudden appearance in consciousness of a moral judgement, including an affective valence (good–bad, like–dislike), without any conscious awareness of having gone through steps of searching, weighing evidence, or inferring a conclusion" Haidt 2001, p.818). Supported by research from experimental social psychology, Haidt (2001) argues, first, that moral judgement is predominantly caused by initial moral intuitions rather than moral reasoning. Moral reasoning is more accurately seen as the post-hoc rationalisation of those initial moral intuitions and seldom plays a causal role in determining moral judgements. Second, Haidt (2001) emphasises the importance of social and cultural influences on moral intuitions, arguing that one person's post-hoc moral reasoning may influence another person's moral intuitions, and hence their moral judgements. Third, biologically evolved predispositions may also partly determine people's moral intuitions, linking this field with the evolutionary ethics literature discussed above. Recently, Haidt (2007) has argued that moral intuitions may be influenced by five key biologically-derived domains, each with a separate evolutionary origin: (1) harm/care/altruism, originating in kin selection; (2) fairness/reciprocity/justice, originating in reciprocal altruism; (3) ingroup/outgroup dynamics, originating in cultural group selection; (4) authority/respect, originating in hierarchical group relations; and (5) purity/sanctity, originating in defensive disgust reactions.

In related work, Hauser (2006b) and Hauser et al. (2008) have argued that people possess a genetically-specified "moral faculty", akin to the language faculty, following an analogy between language and morality first drawn by Rawls (1971). Hence children are born with a set of moral rules that constitute a "moral grammar", which guides their learning of specific culturally-acquired moral norms. Like the other moral psychology research discussed above, this work primarily draws its support from experimental psychology, primatology and neuroscience. For example, Cushman et al. (2006) found that participants' moral judgements concerning a series of simple trolley problems were determined by three principles (or "grammatical rules") of morality: the *action* principle (harm caused by action is morally worse than equivalent harm caused by omission), the *intention* principle (harm intended as a means to a goal is morally worse than equivalent harm seen as the side-effect of a goal) and the *contact* principle (harm resulting from physical contact is morally worse than equivalent harm that does not result from physical contact). These specific principles stem from previous work in moral philosophy, and complement the broader domains of morality proposed by Haidt (2007).

As can be seen from this brief review, the two disciplines of evolutionary ethics and moral psychology have converged to provide a newly synthesised science of morality or ethics (Haidt 2007), one that is both empirically- and evolutionarily-oriented. (NB We do not imply that *all* work in moral psychology has adopted an evolutionary approach, merely that the most influential recent work in the field, such as Singer (2005), Hauser (2006b) and Haidt (2007), has.) We fully accept and support this synthesis, but we would like to point out some shortcomings of this emerging discipline as it currently stands, and suggest possible improvements.

Evolutionary ethics needs culture

Our first criticism stems from that of Haidt (2007), who argued that "morality is about more than harm and fairness" (p.1001). While most research in moral psychology and evolutionary ethics has focused on issues of interpersonal harm and cooperation, often in rather narrow and abstract scenarios such as trolley problems, actual moral norms encompass a much wider range of issues. Moral norms may target actions relating to animal rights, cloning, environmental issues, food taboos, gender and racial (in)equality, genetically-modified (GM) food, neural enhancement and stem-cell research. This has important implications for an evolutionary science of ethics. While the moral norms discussed in the previous section, such as harm and fairness norms or incest taboos, are likely to be influenced to a relatively large extent by gene-based biological evolution, many other moral norms, such as those regarding emerging biotechnology or rapidly changing social conditions, are likely to be influenced to a much greater extent by culture. This is because of differences in the nature of the "environment" that these different norms relate to; in other words, the problems or dilemmas that the norms deal with. When the selective environment has been relatively constant over much of human evolutionary history, such as the dangers of inbreeding or the problem of

free-riders, then we would expect biological evolution to favour human cognition that is highly genetically-predisposed to acquire specific moral norms (such as incest taboos or fairness norms). Such norms should exhibit one or more of the following indicators that they are biological adaptations: they should be relatively domain specific, resistant to attempted modification, cross-culturally universal, influenced by emotions, found to some extent in other species, exhibit a fixed ontogeny, and attributable to specific neural substrates. Incest taboos, for example, are observed universally across cultures (Durham 1991, p. 293), are relatively fixed in the face of attempted modification (Durham 1991, pp. 310–314), and can be observed (in the form of inbreeding avoidance) in many other species (Pusey and Wolf 1996). Similarly, fairness norms are observed cross-culturally (Henrich et al. 2005) and are found in at least a rudimentary form in other great apes (de Waal 1996; Hauser 2006a).

Other norms, on the other hand, may be responses to aspects of the technological or social environment that may be entirely novel or that change extremely rapidly. For example, novel biotechnology such as GM food has emerged only in the last few decades, such that it is impossible that specific genes underlie people's norms regarding such technology. Consequently, the content and distribution of these moral norms are likely to be influenced to a much greater extent by cultural factors.[2] Evidence of the influence of culture might take the form of significant cross-cultural variation and abrupt change over short periods of time. Consistent with this, norms regarding emerging biotechnology show evidence for large cross-cultural differences even in otherwise similar societies (e.g. differences between the US and the EU in the acceptability of GM food: Gaskell et al. 1999) and abrupt change (e.g. the shift that occurred in the UK over a period of a few months from pro- to anti- GM food: Gaskell et al. 2003).

We should be clear here that we are not advocating a simplistic nature-nurture or gene-culture dichotomy, such that particular moral norms can be described as either "genetic" or "cultural". To argue that aspects of moral norms can be explained by appealing to cultural processes does not imply that the norm will not also have a biological/genetic basis. Rather, we are arguing that moral norms (like any aspects of human behaviour) can be explained at multiple levels—ultimate and proximate, biological and cultural—and that an explanation at one of these levels does not negate explanations at other levels (Tinbergen 1963). Rather, we picture a continuum of varying genetic influence over learned behaviour (Gould 1986), with cultural transmission guided or constrained in specific ways by biologically evolved predispositions in memory and cognition (Sperber and Hirschfeld 2004). For example, moral norms regarding food preferences are culturally acquired at the level of the specific food item (Aunger 2000), which may vary from person to person and society to society. Yet food taboos are also affected by a broad, biologically evolved bias that makes food taboos against meat more likely to emerge and persist than food taboos against plants (Fessler and Navarrete 2003), because meat is more likely to harbour diseases. These biological influences on food preferences may also interact with the aforementioned moral norms regarding novel biotechnology. Recent experiments conducted by Schluppi and Weary (2007) show that opposition to GM food is more likely for GM animals than for GM plants. Hence what appear to be entirely culturally-determined norms may be influenced by genetic predispositions to some extent and at some level (We therefore do not agree that norms concerning novel social or technological environments will be free from *all* biological influence, as proposed by Ehrlich [2001]). At an even higher (more ultimate) explanatory level, the capacity to acquire and understand moral norms in the first place almost certainly has a biological basis, in the form of biologically evolved capacities for language and social learning. But these ultimate biological explanations, while correct and valid, cannot explain why a particular person in one society considers it morally wrong to eat pigs and another person in another society considers it morally wrong to eat dogs.

If it is true that a large class of moral norms will necessitate explanations in terms of cultural factors in addition to biological factors, then it is crucial that a science of ethics or morality have a comprehensive and rigorous theory of culture in order to explain why these norms emerge and persist. Currently this does not appear to be the case, as we detail in the following section.

Evolutionary ethics needs a better theory of culture

Several evolutionary ethicists and moral psychologists have invoked the concept of "cultural evolution" to

[2] Models constructed by Boyd and Richerson (1985), Aoki et al. (2005) and Whitehead (2007) support our claim that environmental stability favours genetic control over behaviour, while environmental fluctuation favours learning. Strictly, these models show that rapid environmental change favours *individual* learning rather than cultural transmission, which is favoured at intermediate rates of environmental change. This contradicts our claim that rapidly changing moral norms are primarily culturally transmitted, and suggests instead that they should be acquired through individual learning. However, the efficacy of different moral norms are likely to be costly or difficult to assess through individual learning alone (how might a single member of the public, for example, determine the long-term health risks of GM food from non-GM food?). Other models (Boyd and Richerson 2005, chapters 1–2) suggest that cultural transmission is favoured when individual learning is costly or difficult, supporting our claim that moral norms will be primarily culturally transmitted rather than individually learned.

explain changes in moral norms that are not explicable through biological evolution and/or individual rational deliberation, such as cross-cultural differences or rapid temporal shifts. Haidt (2007), for example, concludes his review of the "new synthesis" in moral psychology by stating that "morality may be as much a product of cultural evolution as genetic evolution" (p.1001). Similarly, Ayala (2006), while accepting a biological origin for the capacity for ethics, goes on to argue that "the moral norms according to which we evaluate particular actions as morally either good or bad ... are products of cultural evolution, not of biological evolution" (p.148). However, appeals such as these to "cultural evolution" rarely go into details concerning precisely what this process entails, or the cultural evolutionary mechanisms whereby different moral norms emerge, change and persist. In this and subsequent sections we hope to make the concept of cultural evolution more explicit, and specifically relate cultural evolutionary theory to moral norms.

Theories of cultural evolution are as old as Darwin's theory of biological evolution. Darwin himself used cultural examples to illustrate his theory of biological evolution (Darwin 1859, 1871; Mesoudi et al. 2004), and several of Darwin's contemporaries applied evolutionary theory to cultural change in disciplines ranging from archaeology (Pitt-Rivers 1875) to linguistics (Muller 1870) to psychology (James 1880). Cultural evolution continued to be written about in the twentieth century under the label of evolutionary epistemology (Campbell 1974; Popper 1979; Plotkin 1982), alongside formal mathematical treatments of cultural evolution and gene-culture coevolution by Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985). In recent years there has been a growth in the number of empirical studies of cultural phenomena that draw on evolutionarily-derived methods (Mesoudi et al. 2006b).

The key idea underlying all of this work is that cultural change is a population process (Richerson and Boyd 2005): cultural traits (ideas, skills, beliefs, norms, attitudes etc.) *vary* in a population, and there is some form of *selection* such that some variants are more likely to be *transmitted* to subsequent generations or time periods than other variants. Applying this variation-selection-transmission heuristic to moral norms yields the proposal that moral norms may *vary* in a population, that they are *selected* according to some criteria or selection pressure, and successful norms are *transmitted* to other individuals through various cultural transmission mechanisms. Understanding the details of this process—why moral norms vary, what the selection criteria for different moral norms are, and how the moral norms are transmitted—can provide explanations for patterns or trends in moral norms that we observe in the world.

Cultural evolutionary theory can enhance evolutionary ethics in two important ways: (1) by providing a set of potential mechanisms (e.g. transmission biases or selection pressures) that might explain the content, distribution and/or changes in moral norms; and (2) by providing a set of established tools and methods for studying moral norms. These two benefits are discussed in the following two sections, respectively.

Mechanisms of cultural evolution

In this section we outline some mechanisms that previous theoretical and empirical work has found to affect cultural evolution, and which may be of use to evolutionary ethicists and moral psychologists in explaining moral norms.

Cultural transmission rules

A large body of theoretical work suggests that the manner in which knowledge is transmitted from individual to individual may have distinct and identifiable effects at the population level (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985, 2005; Feldman and Laland 1996). Cavalli-Sforza and Feldman (1981) distinguish between vertical (from biological parents), oblique (from the parental generation) and horizontal (within-generational) cultural transmission. Cultural traits that are transmitted vertically will generally be more conservative and change more slowly than horizontally transmitted traits, and vertically transmitted traits are more likely to be biologically adaptive than horizontally transmitted traits given that vertical cultural transmission parallels genetic inheritance. A general prediction for ethics might be that rapidly changing moral norms, such as those related to novel biotechnology, are primarily horizontally transmitted, whereas more slowly changing norms, such as incest taboos, are biologically adaptive and are primarily vertically transmitted (genetically and/or culturally).

Various biases in horizontal cultural transmission have been identified and modelled. Conformist cultural transmission is exhibited when individuals are disproportionately more likely to adopt the cultural trait that is most frequent in the population. The prevalence and importance of conformity has been confirmed by a large body of experimental work in social psychology (Bond and Smith 1996; Cialdini and Goldstein 2004), while mathematical models suggest that conformist transmission may increase the speed at which cultural traits spread and reduce variation in those traits within groups of interacting individuals (Boyd and Richerson 1985; Henrich and Boyd 1998). Other biases involve preferentially copying individuals with certain indicator traits, such as success, prestige, age or health (Henrich and Gil White 2001). Models suggest that prestige bias can lead to runaway

selection for increasingly elaborate or extreme cultural traits (Boyd and Richerson 1985), analogous to runaway sexual selection in biological evolution. Another transmission bias involves copying another member of the population at random. This random copying has been shown to result in a distinct "power law frequency distribution," which features a small number of very popular traits and a large number of relatively uncommon traits (Bentley et al. 2004).

The key point here is that different transmission biases—e.g. conforming to the majority, copying successful individuals or copying individuals at random—can generate distinct population level patterns. Conformity may reduce variation in moral norms within groups, prestige bias can cause moral norms to become increasingly extreme over time (i.e. generate group polarization: Isenberg 1986; Sunstein 2002), while random copying can cause a small number of moral norms to predominate in a population. If we can identify such patterns in sociological or ethnographic data concerning the distribution of or changes in moral norms, we might infer which bias was responsible for that distribution or change. For example, rapid changes in moral norms, such as the shifts in public opinion regarding GM food noted above, might be driven at least in part by group polarisation, while stable intergroup differences in norms between otherwise similar regions (e.g. the US and the UK) might be maintained by conformity.

Cultural selection biases

The content of moral norms and beliefs may be affected by biases in memory and cognition that favour the transmission of certain kinds of information. As proposed by Sperber and Hirschfeld (2004) for culture in general, and Nichols (2002) for moral norms in particular, these biases can serve as "attractors" that cause moral norms to converge on specific values. Sperber and Hirschfeld (2004) proposed that many of these biases constitute biologically evolved predispositions, and we can draw on the existing evolutionary ethics work discussed above to predict what these values might be. For example, while large variation in sex taboos is theoretically possible, biologically evolved biases in learning will favour those taboos prohibiting sexual relations with close relatives (Durham 1991). Nichols (2002) used etiquette manuals to show that disgust-evoking moral norms are more likely to survive over time than moral norms that do not evoke disgust (recall that disgust is one of Haidt's (2007) five biologically evolved moral domains).

There is a good deal of overlap here between the existing evolutionary ethics work reviewed above and this aspect of cultural evolution, where biologically evolved preferences may serve as the selective environment in which moral norms culturally evolve. However, the cultural evolution approach diverges in emphasising how these biases are only one of several mechanisms that may affect population-level cultural dynamics, such as the transmission biases noted above. So rather than simply assuming that morality will converge on a biologically-relevant set of values, as evolutionary psychologists and evolutionary ethicists commonly do, we can instead see biologically evolved attractors as one influence of many on moral norms. If, for example, prestige bias causes the runaway selection of a certain norm, and conformist transmission eliminates all other norms before biological influences can favour other more biologically adaptive norms, then a population may end up with a biologically maladaptive moral norm, contrary to the predictions of evolutionary ethics. Extreme and blanket opposition to stem cell research in the United States, despite its huge potential health benefits, might be an example of a runaway, conformity-driven, biologically maladaptive moral norm.

Other aspects of the selective environment in which moral norms emerge may not stem from specific biologically evolved mental domains, but rather constitute incidental side effects of human cognition. For example, Norenzayan and Atran (2004) argued that information that is "minimally counterintuitive", i.e. that violates certain rules of folk physics, folk biology and folk psychology but not excessively so, is more memorable and therefore transmitted with greater fidelity than information that is entirely intuitive or entirely non-intuitive. This effect is normally used to explain the persistence of supernatural concepts. Ghosts, for example, violate certain laws of folk physics (e.g. they can pass through solid objects like walls), yet in terms of folk psychology they behave quite intuitively: they have many of the same motivations and desires (e.g. for revenge) that ordinary, living people possess. Such beliefs that violate some rules of folk physics and psychology but not excessively so have been found experimentally to be more memorable than similar beliefs that violate no rules or that violate too many rules (Norenzayan et al. 2006). The same cognitive principle might also explain the different levels of acceptance of different moral norms. For example, GM technology—specifically, the transfer of genes between individuals of different species and xenotransplantation—the transfer of organs between individuals of different species—may be opposed by many because they are seen to violate the folk biological law that species are inviolable and have essences that cannot (or should not) be mixed (Atran 1998). Organ transplantation between two people, on the other hand, would be relatively more acceptable, because while it violates the folk psychological concept that different

individuals are separate entities and have separate bodies, it does not violate the folk species concept. Experiments using a similar design to those of Norenzayan et al. (2006) might test this hypothesis by measuring people's reactions to scenarios that violate different folk principles to greater and lesser degrees.

Cultural drift and cultural founder effects

Just as aspects of biological evolution can often be explained using purely stochastic (random) processes rather than selection (Gould and Lewontin 1979), cultural evolution too can be affected by stochastic factors. As noted above, random copying—the cultural analogue of genetic drift (Cavalli-Sforza and Feldman 1981) – can generate a distinct population-level pattern in culture. Founder effects constitute a more extreme example of drift. In biological evolution, a founder effect occurs when a small number of individuals establish a new colony and, purely by chance (or "sampling error"), that small founder population has different genetic characteristics to the larger population from which it came. Given that evolution can only work with the variation available in an inter-breeding population, this sampling error will constrain subsequent evolution in that group. Similarly, cultural evolution may exhibit founder effects when small groups are formed which by chance have certain cultural characteristics (e.g. a majority of members opposed to an ethical issue), and this sampling error influences subsequent cultural evolution. An historical example of this phenomenon might be the Puritan founding colonies of the United States, which were particularly religious compared to the European societies from which they originated, and which might explain present-day differences between the US and Europe in the strength of religious attitudes (Wald and Calhoun-Brown 2007). Furthermore, cultural founder effects may be magnified by the aforementioned conformity bias, where a group majority disproportionately sways a group minority. An awareness of conformity-driven cultural founder effects may be particularly important when public policy is determined partly through small focus groups, as is commonly used in "deliberative democracy" approaches (e.g. Luskin et al. 2002). Experimental studies that simulate jury decision-making (MacCoun 1989; Devine et al. 2001) confirm that the decisions of juries are often variable and strongly influenced by conformity, such that in over 90% of juries the initial majority opinion becomes the eventual unanimous verdict (Devine et al. 2001, p. 623). If the same occurs for moral judgement, then the adoption of moral norms may similarly be strongly influenced by conformity-driven founder effects. This element of random starting conditions reinforced by conformity might explain the aforementioned international differences in moral norms such as opposition to GM food.

Methods of cultural evolution

Given the parallels between biological and cultural evolution, we can often draw on the methods of evolutionary biology, suitably modified where appropriate, to analyse cultural change (Mesoudi et al. 2006b). These methods can be used to identify which of the cultural mechanisms listed above (or others) are involved in moral norm change. Mesoudi et al. (2006b) listed eight branches of an evolutionary science of culture. As not all of these are directly relevant to moral norms, and some more than others, we group them slightly differently here.

Evolutionary game theory

Evolutionary game theory (Gintis 2000) is a formal, mathematical approach to modelling strategic social interactions, where an individual's behaviour is assumed to be a fitness-relevant response to other individuals' actions, and these responses are subject to an evolutionary process of selection and replication. In biology, evolutionary game theory is typically used to model the cooperative and competitive frequency-dependent interactions between individual animals (Maynard Smith 1982). Evolutionary game theory is also suited to studying cultural evolution (Gintis 2007), where strategies are different norms or beliefs.

As Danielson (2007) notes, evolutionary game theory is particularly suited to the study of ethics, given that many moral dilemmas are frequency dependent. That is, the most effective moral behaviour will crucially depend on the behaviour of others. Cooperative norms have been extensively studied using evolutionary game theory, given that whether cooperation is beneficial or costly depends on whether other individuals reciprocate (Danielson 1992, 2002; Binmore 1998; Skyrms 1996). Many other ethical problems are likely to be frequency dependent, making evolutionary game theory potentially useful for studying a wide range of practical problems. For example, pro-environmental behaviours such as reducing one's carbon emissions will only be effective if others also agree to reduce emissions (Danielson 1993).

Gene-culture coevolution models

Mathematical models variously known as gene-culture coevolution, dual inheritance or cultural evolution models (Feldman and Laland 1996) use mathematical modelling techniques originating in population genetics to track changes in frequencies of cultural traits (and sometimes also genes) over successive generations and in response to various transmission rules and selection pressures. These models are typically more detailed than game theoretic

models, for example containing more details regarding specific transmission mechanisms (genetic and/or cultural).

We saw above how these models have been used to identify the population-level signatures of different micro-evolutionary mechanisms, such as cultural transmission biases or cultural drift, and also to model cultural group selection (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). Such models might also be used to model changes in specific moral norms. Mesoudi and Laland (2007) modelled the influence of both genes and culture on moral norms regarding mating and marriage, finding that the cultural beliefs held in certain South American societies in "partible paternity", that children can have more than one father, favour the evolution (genetic and/or cultural) of more polygamous mating behaviour. This example illustrates that even moral norms that are directly related to biological fitness—how many husbands/wives one may have—can be influenced by culture, and highlights the need to treat culture as an ultimate arbiter of moral behaviour and not necessarily subordinate to genetic evolution.

Experimental simulations

Although theoretical models are useful for understanding the cultural evolution of moral norms, experimental work is also needed to verify the assumptions and findings of those models (Mesoudi 2007). The same is true in evolutionary biology, where experimental simulations of biological evolution in the lab have provided significant insights into both the mechanisms of genetic inheritance (Hartl and Clark 1997) and large-scale macroevolutionary phenomena (Elena and Lenski 2003).

While moral psychologists have begun to conduct experimental investigations into moral norms (e.g. Cushman et al. 2006), these studies have so far been restricted to single individuals reacting to material prepared by the experimenters (e.g. trolley problems), and have not addressed the social/cultural influence of other individuals. As such, it is not known whether cultural processes such as conformity can cause moral judgement to diverge from this individual (non-social) moral judgement. Social psychologists have studied social influence by running experiments using groups of participants and manipulating how participants interact with one another. Classic social psychology studies have shown that decisions and attitudes are often strongly affected by social influence, to the extent that socially-influenced judgements can be entirely inconsistent with individual non-social judgements (e.g. Asch 1951; Milgram 1974). More recently, cultural transmission experiments have examined when and why people employ different cultural transmission rules such as conformity (McElreath et al. 2005) and prestige bias (Mesoudi and O'Brien 2008), and others have tested for selection biases that cause certain kinds of information to be more successfully transmitted along chains of people (e.g. Mesoudi et al. 2006a). Such methods might be used to simulate the transmission of different moral norms along chains of participants, in order to compare their fidelity. We might predict that norms for which people are biologically predisposed (e.g. incest taboos, meat taboos or fairness norms) are more likely to persist than biologically-irrelevant norms. More elaborate experimental designs might test the prediction made above that moral norms may diverge between groups due to cultural founder effects and converge within groups due to conformity. This can be done by studying the extent to which moral norms diverge in multiple replicate groups of randomly assigned participants all presented with the same moral dilemmas (Mesoudi and Danielson 2007), just as biologists simulate biological evolution in replicate groups of bacteria (Lenski and Travisano 1994). If moral judgements in each group consistently converge on biologically-relevant or rational values, then cultural processes likely have little influence. On the other hand, if different groups exhibit different moral norms then this divergence might be attributed to conformity driven founder effects.

Phylogenetic Analyses

Phylogenetic methods are used in biology to distinguish between traits that have been inherited from a common source from traits that have independently evolved at separate times and in separate lineages (Harvey and Pagel 1991). This allows biologists to uncover historical relationships between different species and identify general patterns of biological macroevolution. Phylogenetic methods can be used to address the same questions in cultural evolution (Mace and Holden 2005; Lipo et al. 2006). Cultural traits most commonly analysed using these methods concern language (Gray and Atkinson 2003) and archaeological artefacts (O'Brien and Lyman 2003). The same methods might also be used to analyse the origin and history of moral beliefs and moral norms: if two societies both hold the same moral norm, we can use phylogenetic methods to determine whether this is because they both inherited it from a common source (suggesting vertical cultural transmission and/or genetic inheritance), or because they both invented it independently (suggesting convergent cultural evolution to a similar selective environment). A possible test-case might involve food taboos: for example, did the moral norm prohibiting the eating of pork that is observed in both Islam and Judaism emerge before the two religions split into separate lineages (i.e. they inherited the taboo from a common ancestor), or did the taboo emerge independently in the two religions after they split into separate lineages? Phylogenetic analyses are ideally suited to address such questions.

Other methods

Ethnographic field studies, cross-cultural psychology experiments and sociological public opinion research can provide the cross-cultural data that is needed for cultural phylogenies of moral norms, paralleling biological field studies and biogeographical surveys which are used to obtain data on the geographical distribution of species and biological traits. As well as providing between-society cross-cultural data, ethnographic studies can also be used to study the cultural transmission of moral beliefs within societies, such as Aunger's (2000) study of food taboos in the Congo. The cultural analogue of molecular genetics involves studying how culturally acquired information is stored in the brain using neuroimaging methods; researchers such as Greene et al. (2001) are already using these methods to study the neural basis of morality. The cultural analogue of paleobiology (the historical study of past biological evolution) is history or archaeology (the study of past cultural evolution), which can be used to study changes in moral norms over extended time periods. Nichols (2002) illustrated how historical records can be used to track changes in moral norms.

Summary

A cultural evolution framework brings with it a set of established methods, many derived from evolutionary biology, that can be used to study the cultural evolution of moral norms. Many of these methods are already being used, such as evolutionary game theory, which has become a well-established tool for studying morality (Danielson 2002). The added benefit of adopting a cultural evolutionary framework is that each of these usually separate disciplines and methods can be integrated. For example, ethnographic data and survey research can be used in phylogenetic analyses, and experimental simulations can be used to test the assumptions and findings of theoretical models. This cross-disciplinary transfer of ideas and methods has been instrumental in fostering the success of evolutionary biology (following the 'evolutionary synthesis': Mayr and Provine 1980). A similar synthesis is being forged in the social sciences for cultural evolution (Mesoudi 2008), and this can significantly improve our understanding of human morality.

Conclusions

In this paper we have argued that evolutionary ethics and moral psychology can be enhanced by adopting an evolutionary approach to culture. A more accurate understanding of morality can be achieved by drawing on the theoretical concepts ("Mechanisms of cultural evolution") and empirical methods ("Methods of cultural evolution") of cultural evolution. The adoption of an explicit and rigorous theory of cultural evolution is made all the more important given that many moral norms, particularly those related to novel or rapidly changing aspects of the technological and social environment, are influenced to a greater extent by cultural factors than are moral norms traditionally considered by evolutionary ethicists, which are better explained by appealing to genetic factors alone.

Another evolutionary approach to human behaviour not yet discussed, human behavioural ecology (Smith and Winterhalder 1992; Winterhalder and Smith 2000), may also prove to be useful in studying moral norms. While modern evolutionary psychology tends to focus on cognition (rather than behaviour) and assumes that human cognition is adapted to the Pleistocene environment of 10,000–2 million years ago (and not necessarily to current environments), human behavioural ecologists tend to focus less on proximate cognitive processes and instead examine whether human behaviour is biologically adaptive (i.e. maximises survival and reproduction) in current environments. Certainly, many moral norms might be found to be biologically adaptive responses to local ecological or social conditions. For example, Henrich et al. (2005) found that certain cross-cultural variability in fairness norms can be explained as adaptive responses to local social/economic conditions (e.g. people who must cooperate in order to obtain food have norms that emphasise fairness more strongly than people who do not need to cooperate in order to survive). However, this is not always the case, and many cultural differences, including in fairness norms, cannot be attributed to local ecological or social conditions (e.g. Gurven et al. 2008). Moreover, even if a moral norm *were* shown to be biologically adaptive, this does not preclude the possibility that it is culturally transmitted and influenced by cultural processes such as conformity. Indeed, we would expect that most of the time conformity will maintain biologically adaptive behaviour (Boyd and Richerson 1985). As noted above, however, cultural evolutionary theory can additionally explain the biologically maladaptive cases. Nevertheless, human behavioural ecology offers a valuable set of methods for determining whether moral behaviour is biologically adaptive under specific ecological conditions, and may prove a useful complement to evolutionary/moral psychology work that focuses more on beliefs and intuitions rather than overt behaviour, given that beliefs and behaviour may not always match.

Our proposal that cultural evolutionary theory should be used to study morality is perfectly consistent with recent

work in moral psychology and evolutionary ethics. Most evolutionary ethicists already accept the importance of culture in explanations of moral beliefs (e.g. Ruse and Wilson 1986); all we are proposing is a theory of how "culture" is conceptualised (as a separate evolutionary process) and empirically studied (using methods adapted from evolutionary biology). The same is true for moral psychology. Haidt's (2001) social intuitionist model emphasises that moral intuitions are influenced by other people's moral reasoning, allowing for the operation of the kinds of cultural mechanisms outlined above, such as conformity. Hauser's (2006b) linguistic analogy centres on the assumption that our capacity for morality, like our capacity for language, is genetically specified. Yet linguists have also used cultural evolutionary concepts and methods to explain changes in the *content* of specific languages (Croft 2000; Mufwene 2001; Oudeyer and Kaplan 2007). We suggest exactly the same for morality: while there may exist a biologically evolved moral faculty, this allows the content of morality—the actual moral rules and norms—to themselves evolve, forming a separate cultural evolutionary inheritance system. This cultural inheritance system coevolves with the genetic inheritance system. We believe that this gene-culture coevolutionary perspective on morality offers a significant improvement on existing evolutionary approaches to ethics and morality.

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