Prospects for a Dual Inheritance Model of Emotional Evolution

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A common objection to adaptationist accounts of human emotions is that they ignore the influence of culture. If complex emotions like guilt, shame and romantic jealousy are largely culturally determined, how could they be biological adaptations? Dual inheritance models of gene/culture coevolution provide a potential answer to this question. If complex emotions are developmentally 'scaffolded' by norms that are transmitted from parent to offspring with reasonably high fidelity, then these emotions can evolve to promote individual reproductive interests. This paper draws on case studies of emotional development to illustrate how complex emotions satisfy these conditions. Many of the norms and parenting strategies influencing emotional development are absorbed during the early stages of life when a child is in primary contact with its parents and before the onset of complex cognition. These conditions make it likely that emotion-governing norms are transmitted vertically and with relatively little cognitive 'contamination'.

1. Introduction. The complexity and apparent adaptive utility of many human emotions have inspired numerous evolutionary hypotheses about their possible origins and functions. A major stumbling block for these proposals however is the hard-to-deny fact that emotions are significantly influenced by culture. How could a trait be both culturally determined and an adaptation at the same time? Recent developments in evolutionary theory shed light on this question. In particular, dual inheritance models of evolution seem well suited to explaining how human emotions might evolve. In what follows I first outline a basic sketch of dual inheritance systems, and identify three criticisms that have been raised against the attempts to explain other (nonemotional) human traits in these terms. Second, I defend the claim that human emotions satisfy the requirements for a dual inheritance system by considering two case studies of emotional

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development. In the final section I defend this dual inheritance model against the three aforementioned criticisms.

2. Problems and Promise of Dual Inheritance Models. Dual inheritance models of evolution have enjoyed a surge in popularity over recent years (Avital and Jablonka 2000; Sterelny 2003; Boyd and Richerson 2004). Part of the attraction is their potential to account for the evolution of such complex human skills as cooperative hunting, tool making, natural history knowledge, and farming. As Boyd and Richerson argue (2004), many of these skills are not only highly adaptive, they are too complex to have been invented de novo or reinvented time and again each generation. A more likely scenario is that these abilities evolved by a process of gradual modification and selection. Dual inheritance models offer an explanation of how such skills might evolve without presupposing that they are somehow genetically encoded. The key idea is that complex psychological traits are transmitted from parent to offspring via two parallel channels. The computational 'hardware' required for social learning is transmitted genetically and the psychological 'software' that supports a given technology or skill is transmitted culturally. Both modes of inheritance are assumed to be relatively high fidelity but also capable of slight modification over successive generations, as is required for any cumulative process of evolution. Importantly, according to simple dual inheritance models the fitness of a coevolved trait is calculated in terms of the *reproductive* costs and benefits it bestows on its bearers. A new hunting strategy evolves in a population because it enables the individuals who acquire it to obtain more calories and thereby have more (or healthier) offspring to whom they can pass that strategy on. This feature distinguishes dual inheritance models from memetic accounts of cultural evolution. According to memetic models, the fitness of a psychological trait is determined largely by its tendency to spread horizontally (like a virus) from individual to individual regardless of its impact on his or her biological fitness.

While dual inheritance models have been invoked to explain the accumulation of adaptive skills and other forms of "cognitive capital," relatively little has been written on their prospects for explaining the evolution of human *emotions*. However, many of the complex or "higher cognitive" emotions (e.g., guilt, jealousy, shame, pride, embarrassment, and moral disgust) lend themselves to just this sort of framework. As I shall illustrate below, these emotions develop out of innate reactive dispositions that emerge early in life, but which become increasingly cognitively elaborated over the course of an individual's emotional development. This developmental process is governed by social practices (e.g.,

parenting strategies, childhood myths, and rituals) which are culturally transmitted and have apparently evolved for this purpose.

The idea that human emotions have been shaped by natural selection is a popular theme in the writings of many psychologists and biologists, beginning with Darwin. These proposals often emphasize the adaptive utility of many human emotions. For example, fear seems well designed for mobilizing a fight or flight response. Guilt and shame have been proposed as internal enforcement mechanisms for motivating adherence to cooperative alliances. Similarly, embarrassment has been suggested as a social signal of one's adherence to cooperative norms. Somewhat more controversially, romantic jealousy has been proposed as a mechanism for monitoring the status of a sexual pair bond and for motivating defensive behaviors when it becomes threatened. Despite their appeal as viable hypotheses, these proposals have run into a theoretical stumbling block. Most if not all of the emotions just mentioned are under the influence of culture—they are not 'innate' in the traditional sense of being largely unlearned. This has led several thinkers to reject evolutionary hypotheses from the outset. Since complex human emotions are not innate, it is argued, they are just not the right sorts of candidates for an evolutionary explanation (Prinz 2004). But for reasons that I discuss below, this argument fails. Dual inheritance models can potentially accommodate the fact that emotions are culturally influenced while at the same time explaining how they might have been shaped by natural selection.

However dual inheritance models raise their own set of challenges. Three criticisms are particularly salient. First, as Kim Sterelny has recently argued (2003, 2008) the same cognitive abilities that are required for the acquisition of cultural information are likely to degrade the fidelity of its transmission. Sterelny points out that imitation learning is required for an individual to acquire a skill by observing its execution. But the greater an individual's capacity for imitation learning, the more prone they will be to draw on individual experience to modify a task. Moreover, a mimic will often have only limited exposure to a model, so some inferential reconstruction of the task will be required (e.g., I know that bow-making had something to do with heating the branch before bending it, but how much heat? For how long?). Thus Sterelny argues that "these very abilities undermine the intergenerational flow of information. For they increase the extent to which an individual's beliefs and behaviour are sensitive to his own experience, and they decrease the extent to which these beliefs and behaviours are the result of blindly copying those of previous generations" (2008, 8). Let's call this the cognitive degradation problem.

Boyd and Richerson attempt to avoid this problem by appealing to the fact that cultural transmission is often not vertical. Some cultural information also flows horizontally (person to person within a generation) and

obliquely (from individuals in the N generation to nonkin in the $N + 1$ generation). Boyd and Richerson argue that horizontal and oblique transmission can compensate for a loss of fidelity, provided that the right sorts of cognitive biases are in place. *Conformist biases* involve the tendency to adopt the most commonly practiced behavior. Thus, an individual of the N generation might sample from multiple "cultural parents" and choose whichever practice is most common. This effectively adds redundancy to a signal thereby making low fidelity traits more likely to be passed on over successive generations. *Content biases* motivate an individual to choose whichever practice is most successful or the one that they find particularly appealing. This form of bias effectively enhances transmission rate by soliciting a high number of mimics. Boyd and Richerson demonstrate mathematically that such biases in the transmission of cultural information can lead to the accumulation of cognitive capital at the population level over successive generations. However, horizontal transmission can also lead to the rapid spread of maladaptive tendencies. It is psychologically unrealistic to suppose that content biases will always lead an individual to choose the most adaptive behavior from a range of alternatives. Some traits will be psychologically appealing but biologically maladaptive, for example, heroine use and abstinence remain attractive to some. Thus, dual inheritance systems that are capable of horizontal and oblique transmission are less likely to support individually adaptive traits than systems that are exclusively linear and high fidelity. Call this the maladaptive meme problem.

A further objection to biased transmission models is that they fail to take into account the biological costs that information transfer imposes on the *model*. As Sterelny points out, sharing valuable information with nonkin of the $N + 1$ generation can be costly to a model if those skills are used to compete against his or her own offspring. Sterelny argues that unless group-level selection is acting on a population, it will be disadvantageous for models to openly share their precious skills with nonrelatives. Call this the costly information problem.

My aim in what follows shall be to defend a simple dual inheritance account of human emotions against the three criticisms just described. My strategy shall be to first consider two case studies of emotional development. These examples provide a vivid picture of the ways that biological and cultural factors act in concert in the production of an emotional phenotype. The examples also highlight some important differences between the acquisition of emotional traits and the transmission of the sorts of complex skills with which dual inheritance theorists are usually concerned. In particular, I argue that emotional traits are (1) acquired early in life, prior to the acquisition of sophisticated cognition, (2) influenced primarily by one's parents and are therefore transmitted linearly,

(3) scaffolded by cultural practices that are unlikely to be modified in light of individual experience. Thus, complex human emotions are especially good candidates for a simple dual inheritance model of their evolution.

3. Guilt and *Metagu*: Two Case Studies in Emotional Development. From an early age children exhibit a range of emotional reactions posited as the developmental precursors to guilt, shame, embarrassment and other complex emotions that develop later in life. By age two the perception of anxiety or distress in others generates a similar state in the observer, which in turn gives rise to a range of 'prosocial' behaviors (e.g., hugs, pats, kisses) in an apparent attempt to alleviate their shared anxiety. Interestingly, Zahn-Waxler (1992) reports that toddlers' own state of anxiety as well as their level of prosociality are influenced by the perception that they caused another person's distress, as opposed to having merely observed its incidental occurrence. The fact that even such young toddlers appear to have a rudimentary sense of responsibility associated with their own bad feelings and conciliatory gestures makes this early affective disposition a good candidate for the developmental precursor to guilt. Of course, such responses do not qualify as full-blown guilt. Mascolo and Fischer (1995) note that not until ages three to four are children able to verbally articulate the link between harmful actions and bad feelings. Without such foresight, it is unlikely that guilt could play a role in deterring a person from engaging in future harmful behaviors. Toddlers also lack an understanding of the norms specifying the conditions under which one ought to feel guilty. Bretherton et al. (1986) note that it is not until at least age five that children fuse their understanding of emotional agency with an appreciation for social norms and conventions. And only some time later that they become sufficiently self-aware to anticipate which behaviors are likely to cause bad feelings in themselves so that they can be avoided. Thus, guilt appears to follow a multistage developmental process that starts out with an 'innate' sensitivity to the distress of others and which becomes increasingly cognitively elaborated as the child matures.

Kochanska (1991) has conducted an elegant study illustrating how different parenting styles influence this developmental process. Toddlers (one and a half to three years) were first rated for their individual anxiety levels. In general, some children are born more anxious than others: they are more reluctant to approach a novel toy or unfamiliar adult, they are more easily distressed by a loud noise, etc. Kochanska then observed toddlers interacting with their parents in a naturalistic setting and took note of two different strategies for dealing with misbehavior. Authoritarian parents tend to issue commands or criticisms without providing

rationalizations—for example, "put that toy back where you found it!" or "don't be so naughty!" Perspective-taking parents encourage the child to consider how their actions impact others—for example, "how do you think that made Johnny feel?" or "what if that was your toy?" Finally, Kochanska surveyed the same population of children five to six years later for their tendency to experience guilt. Interestingly, she discovered an interaction effect between toddlers' early anxiety levels and the parenting styles they encountered. Low anxiety children displayed an average level of guilt-proneness regardless of which parenting style they encountered. However, high anxiety children who encountered the authoritarian style exhibited lower than average levels of guilt. High anxiety toddlers who encountered the perspective taking style exhibited higher than average levels of guilt later in life. One thing that this study makes clear is that the development of guilt involves more than just the internalization of norms once one has reached a certain level of cognitive sophistication. The development of guilt involves both a biological and a cultural contribution, and appears to begin even before children acquire an explicit sense of agency or can draw a conscious link between their actions and their future feelings.

Turning to our second example, in her influential ethnography of the Ifaluk of Micronesia the anthropologist Catherine Lutz describes an emotion—*metagu*—quite similar to what Westerners would identify as guilt or shame. Lutz describes *metagu* as the primary inhibitor of misbehavior in children and adults. A well-socialized member of Ifaluk society is expected to experience this emotion in the presence of a respected elder, or in response to another person's "justifiable anger." Lutz explains that, "Good people on Ifaluk are those who anticipate 'justifiable anger' of others (especially elders), are metagu of their own wrongdoing, and hence behave in a calm, nonagressive manner" (1983, 253–254). Failing to exhibit this emotion under the appropriate circumstances is unthinkable in Ifaluk society, thus there is social pressure on parents to instill this emotion from an early age. Interestingly, Lutz notes that the Ifaluk themselves view *metagu* as something that emerges naturally in children, but which requires careful cultivation though the enforcement of norms and, periodically, through explicit rituals. From the first year of life children are expected to exhibit *metagu* in the presence of an adult visitor to the home. For example, when a visitor enters the house children are expected to adopt a subordinate posture and to avoid direct contact. Lutz explains that, "children who do not appear metagu have their attention drawn to the stranger in an attempt to elicit this emotion" (1983, 254). If this strategy proves unsuccessful or if children fail to exhibit *metagu* in other social settings, parents will resort to the following ritual:

> The most striking way in which metagu is socialized is through the use of a special type of ghost (tarita) which is said to kidnap and eat children. This ghost is impersonated by one of the women of the child's household, who covers and disguises herself with cloths. The ghost, which normally resides within the wooded interior of the island, is called by parents to come and take the child if she or he misbehaves. The ghost is most frequently called if the child has aggressed against a peer, of if the child begins to wander away from the house. Appearing menacingly at the edge of the house compound, the ghost causes young children to leap into the arms of any nearby adult. The label metagu is used in profusion to describe the child's reaction, and the ghost is then told by one of the adults present that "the child will no longer misbehave" and that it should therefore go away. (1983, 255)

These accounts of the tactics parents employ in scaffolding the development of *metagu* betray a complex interaction between biological and cultural factors. It is well established that toddlers possess an affective disposition to become frightened by strangers, often looking to their parents as a "social reference" to determine whether they should approach or avoid the unfamiliar person. The Ifaluk have apparently adopted cultural practices that harness this aversive tendency in the development of *metagu*. As Lutz explains, the child who does not immediately display an aversive response when a stranger enters the house has their attention drawn to the visitor in an attempt to elicit this response. If that doesn't work, parent's stage a frightening ritual that effectively enhances the threatening stimulus (what ethologists would consider a superstimulus) thereby ensuring that the fear response is engaged. It is also significant that parents proceed to use the word "*metagu*" profusely while the child is recoiling in fear. This practice presumably establishes a direct association in the child's mind between this term and the appropriate aversive response. Once this association has been established it could facilitate the further cognitive elaboration of *metagu*. On future occasions when a child encounters this term (e.g., while being instructed on how the *metagu* individual ought to behave) the mere mention of *metagu* might trigger a "somatic marker" (a low-level physiological response) in the subject, leading her to associate norm violations with a strong, negative emotional episode (Damasio 1994). Interestingly, Lutz herself offers a similar interpretation of the socialization of *metagu*: "Adults link the child's early developmental avoidance reaction to strangers to other dangerous situations (such as straying from the household) which the child does not yet perceive as such" (1983, 257).

However, Lutz goes on to emphasize only the cultural aspects of this

socialization process. A more accurate model of *metagu*'s development ought to recognize the interaction between biological and cultural factors. Both the innate aversive response to strangers and the social norms and rituals that exploit this disposition contribute to *metagu*'s development.

These examples paint a suggestive picture of how complex human emotions might evolve in accordance with a simple dual inheritance model. Kochanska's study illustrates that individual genetic differences in toddlers' anxiety levels impact their susceptibility to different parenting styles. Assuming that parenting styles are transmitted socially from parent to offspring, it is easy to imagine how modifications to either the genetically or the culturally transmitted component of this phenotype might impact an individual's fitness. In a socioecological environment that places a premium on cooperation, for example, guilt prone individuals might enjoy a selective advantage. This selection pressure could result in an increase in the frequency of the anxiety-prone genotype, in the perspective taking parenting style, or both. Similarly, in Ifaluk society an individual who fails to develop *metagu* would likely incur a fitness cost associated with social ostracism, for example, by encountering difficulties in finding a mate or failing to receive cooperative social benefits. Admittedly, these "how possibly" scenarios are speculative. A more detailed understanding of the social and biological implications of individual differences in guilt and *metagu* would provide insight into whether these emotions have in fact undergone evolution by natural selection. However, there is fairly strong evidence that dually-inherited emotions have evolved in some nonhuman animals. Certain artificially selected strains of mice exhibit extremely high anxiety levels when placed in novel contexts. Cross-fostering experiments reveal that this emotional disposition is transmitted in part via a behavioral channel: the biological offspring of low anxiety mice develop the high anxiety phenotype when reared by high anxiety adults (Meaney 2001). More detailed studies reveal that whether a rodent develops the high anxiety phenotype depends specifically on the amount of "anogenital licking" and "arched-back nursing" that it receives from its mother during the first week of life. These maternal behaviors are socially acquired and highly heritable. Their occurrence is significantly less common in low anxiety than in high anxiety strains, yet they can be readily adopted and passed on by the offspring of low anxiety mice as a result of cross fostering. Thus, artificial selection for fear in mice appears to have resulted in the evolution of a maternal 'parenting style' that scaffolds the development of this emotional disposition. In humans, the opportunities for such nongenetic influences on emotional development are even greater, given our extended period of infant dependency and the degree to which we are steeped in cultural traditions. It would therefore be surprising if selection had not retained some of our cultural traditions for

their fitness enhancing influence on emotional development. With this proposal in mind, let us turn to the three objections (mentioned earlier) to simple dual inheritance models.

4. How Emotional Traits Differ from Complex Skills. Recall that the cognitive degradation problem arose out of a sort of catch-22: the same cognitive prerequisites required for imitative learning are likely to degrade the fidelity with which a trait is culturally transmitted. This occurs, according to Sterelny, because sophisticated social learners can be expected to modify previously acquired skills in light of their individual experiences. Notice that this argument assumes that the acquisition of the phenotype in question—a valuable skill—involves a sophisticated learning process. In this respect emotional development differs from skill acquisition. Emotional development involves no sophisticated learning abilities. Rather, complex emotions are scaffolded by parenting norms and rituals that exert their influence long before children have acquired the ability to reflect on their own experiences. By the time an individual has reached an age of self-reflection, it will be too late to undue those influences without considerable effort. Therefore, cognitive degradation does not threaten the transmission of emotional phenotypes.

But perhaps this argument is too quick. What happens when the child matures and it becomes time for her to scaffold the emotional development of her own children? Dual inheritance models require that the adult reproduces the same cultural practices that were influential on her own development. However, by this time the individual will possess the cognitive resources to reflect on her actions and to modify the relevant parenting techniques accordingly. Won't fidelity be lost?

In considering this objection it is important to become clear on why Sterelny thinks that cognitive sophistication will lead to degradation in a cultural tradition. Presumably, in the case of a social skill, modifications are motivated by feedback: differences in the execution of a skill that have an identifiable bearing on its outcome will inspire an individual to make permanent changes. I propose that people are less likely to tinker with emotion-governing traditions for four closely related reasons. First, in the case of emotional development there is a significant time delay (a matter of several years) between the point where a parenting strategy begins to be employed and the time when it manifests itself in the offspring's emotions. Children begin to encounter a particular parenting style at infancy, they do not develop full-blown guilt until after age five. With such a time lag, it will be difficult for an individual to develop hypotheses about which aspects of a parenting strategy influenced particular aspects of emotional development. The feedback process is just too slow to be amenable to trial and error. Second, connections between a parenting

strategy and its impact on emotional development are often nonrational and contrary to folk-psychological expectations. Who would have expected that an authoritarian approach would result in *lower* than average guilt levels in anxious children? Surely not the parents who employ it! Similarly, in the case of rodents the links between parental behaviors and an offspring's emotional development are detectable only with careful experimentation. Nonrational connections between cultural practices and their developmental outcomes make the parenting process difficult to reverse engineer and therefore less likely to be tinkered with. Of course, this does not mean that some modifications will not occur. Some people will invent novel ideas about how their children should be raised that will impact emotional development. But these changes will be effectively random, on par with random genetic mutations. Third, as Kochanska's study further suggests, the influence of a given parenting style on emotional development is not uniform across different genotypes. There is therefore no guarantee that adopting the style of another apparently successful parent will produce similar results in one's own offspring. Again, the existence of such gene/environment interactions might not preclude a parent from occasionally adopting another's style. However, if horizontally acquired parenting strategies are rarely successful when applied to genotypes with which they have not coevolved, this could deter the evolution of a metapractice that encourages such parental borrowing. The fourth and final reason for expecting parents to be less inclined to tinker with emotion-norms than with complex skills is that the former are more culturally diffuse than the latter. Hunting, for example, is a relatively discrete practice with a specific context and duration. By contrast, the norms that scaffold emotional development are more pervasive: they are embedded in the stories that we tell our children, in our expressive reactions to their misdemeanors, and in the explicit rules that we lay down. Modifying such a pervasive system of norms would require widespread tinkering and considerable conscious effort. Altering a hunting or farming technique appears simple by comparison, requiring only the adoption of a new tool or planting a different crop. Thus, the fact that parental strategies are (*a*) temporally distanced from their effects, (*b*) unpredictable in their outcomes, (*c*) variable in their interactions with different genotypes, and (*d*) highly culturally diffuse militates against their cognitive degradation.

The maladaptive meme problem also seems less likely to arise in the case of emotion-governing traditions. Recall that the threat of maladaptive cultural traditions spreading viruslike through a population is made possible by the existence of horizontal and oblique transfer. The more horizontal and oblique transmission taking place in a system, the greater the threat. When it comes to cultural traits that require sophisticated cognition for their acquisition, horizontal transmission seems likely be-

cause by the time an individual is in a position to acquire them (when he or she has the requisite motivation, coordination, attention span, etc.) he will be interacting with numerous adults and peers in the community. By contrast, emotional dispositions are laid down before most children have left the home or had much exposure to people besides their parents. Therefore, emotionally significant traditions will be more likely follow a vertical (parent to offspring) pattern of inheritance. So long as the transmission process occurs with reasonably high fidelity, emotional traits will evolve in ways that benefit individual lineages. For similar reasons the expensive information problem does not arise in the case of emotion-governing practices. If a parents' influence is restricted primarily to their own children, the fitness costs associated with teaching a 'good idea' to a nonkin member do not arise. Nor is it necessary to appeal to group selection to explain how adaptive emotional traditions evolve.

5. Conclusion. Emotional traits resemble complex skills in their complexity and in their apparent adaptive value. The practices and rituals that regulate emotional development are unlikely to have sprung de novo out of the mind of some insightful individual. It is more likely that these traits evolved over successive generations by a process of gradual selection. Dual inheritance models provide an explanation of how such culturally influenced traits might have evolved. Examples of emotional development reveal that guilt, shame, and probably other complex emotions develop out of innate dispositions that are cognitively elaborated through their interaction with culturally sustained practices. Adaptive modifications to either the genetic or the culturally transmitted component of these complex traits could potentially be favored by natural selection. Emotions are unlike complex skills, however, in that they are acquired without the use of imitative learning and when toddlers are interacting primarily with their parents. Nor will adults be motivated to tinker with the social scaffolding apparatus required for the development of an emotion. The significant time lag between cultural cause and emotional effect, the nonrational nature of these developmental systems, their sensitivity to different genetic backgrounds, and their culturally diffuse nature make parental practices difficult to reverse engineer. Therefore, the cultural component of an emotion should be transmitted primarily vertically with relatively high fidelity. This is precisely what is required for a dual inheritance system to operate effectively.

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