ORIGINAL SCIENTIFIC ARTICLE

The Evolution of Morality

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Abstract Here, in textbook style, is a concise biological account of the evolution of morality. It addresses morality on three levels: moral outcomes (behavioral genetics), moral motivation or intent (psychology and neurology), and moral systems (sociality). The rationale for teaching this material is addressed in Allchin (2009). Classroom resources (including accompanying images and video links) and a discussion of teaching strategies are provided online at: http://EvolutionOfMorality.net.

A Biological Approach to Explaining Morality

Animals exhibit a wide range of behaviors. They forage. They defend territory and flee predators. Sometimes they play. They reproduce, at times with spectacular displays. They learn. But perhaps most striking from an evolutionary perspective, they sometimes cooperate or help others, even at a cost to themselves. Why? Morality seems to defy the image of natural selection as "selfish," favoring only traits that benefit the individual in a competitive "struggle for existence." Given the importance of morality for human society, this puzzle is a major challenge for science. How do biologists interpret such behavior? How could morality originate in an evolutionary context?

• *Morality is a form of behavior.*

The first challenge for biologists is characterizing morality in terms amenable to science. Abstract concepts of "right" and "wrong" or virtuous motives and good intentions must be expressed in terms of what can be observed or measured. First, then, *biologists address morality concretely as a form of behavior.* As such, it fits in a context of other behaviors: foraging, mating and nesting, securing territory, play, grooming, and other social interactions.

• *Nonhuman species may exhibit various stages in the evolution of morality.*

Conceptualizing morality as a form of behavior opens the possibility of observing it in other species. Indeed, if complex features evolve gradually, one might well expect to find stages of protomorality, incipient morality, or various precursors in organisms besides humans. An important resource in understanding the evolution of humans and their culture, then, is comparative behavior. Even if the behavior is not strictly genetic, one may still find informative phylogenetic patterns or similarities based on common ancestry. Studies of primate behavior are potentially valuable. Transitions and intermediate stages may be more concretely envisioned or documented.

• *Biologists borrow from other disciplines in characterizing behavior as moral.*

But which behaviors are "moral"? Here, biologists must proceed cautiously. One cannot even identify the relevant behaviors without a working concept of "right" and "wrong" or of "morality." Invoking a value judgment threatens to prejudice the whole endeavor. *The biologist's proper approach is thereby indifferent and fluid, contingent*

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on definitions of ethics identified by others. Biologists may encounter multiple conceptions of what is to be explained. Different benchmark definitions may yield separate complementary explanations. Of course, biologists are accustomed to addressing the "same" phenomenon on multiple levels of organization: molecular and cellular, physiological, populational, ecological, and evolutionary. Biologists have, thus, developed a suite of explanations which apply to different aspects of moral behavior.

• *Philosophers identify at least three frameworks for conceptualizing morality: moral outcomes, moral motives (or intent), and moral systems.*

For guidance, then, a biologist turns to moral philosophers. Yet, even after centuries of reflection and debate, philosophers themselves do not agree on core ethical principles for defining "good." They generally recognize, however, three basic approaches. One approach, consequentialism, focuses on the outcomes themselves. For example, morality is assessed as the greatest good for the greatest number. Good may be defined variously as benefit, happiness, or pleasure. A contrasting approach, deontology, emphasizes instead motives (or reasoning). For example, morality is measured by feelings of sympathy or virtuous intent. Both approaches draw on widely shared intuitions, although they sometimes lead to different moral codes. They have not yet been synthesized. A third, complementary strand of philosophical thought situates morality on yet another level: the concept of a social contract. Morality is characterized primarily by mutual consensus on values. Biologists can inform each perspective, as described below in separate sections (Table 1).

• *Evolution itself does not express or yield values.*

Nature may seem to exhibit its own values. For example, natural selection may seem to "favor" adaptive traits. Survival and reproduction may seem inherent values because they lead to continuity of the lineage. However, historical facts are distinct from values. Effects do not indicate intentions. Patterns of causation do not reflect processes of evaluation. A falling body does not reflect a *value* of gravity. Two charged particles do not reflect a *value* of electrical attraction. In the same way, reproduction and survival do not reflect a *value* of evolution. As exemplified in extinction, species do not "need" to be perpetuated. As exemplified in sterile insect castes and non-

fertile individuals, single organisms do not "need" to reproduce themselves. The language of natural "selection" may easily mislead one to personify nature inappropriately. Recognizing such tendencies may be important in avoiding mistaken impressions.

• *Science is limited to description.*

Biological analysis may enrich our understanding of morality, but it is also limited. Science is not able to discover ethical principles in nature, nor to justify them, nor to evaluate them, say, based on evolutionary history, nor even to develop them based on some presumed universal or "objective" principle of "human nature." Many have tried. All have failed (Farber 1994; Bradie 1994). Rather, the achievable aim is *to explain how organisms such as humans evolved moral capacities to form moral concepts and to act on them in particular environments*. That may also involve *describing how*, as organisms, *they are able to do so* (*neurologically, cognitively, emotionally,* and *socially*). To describe morality as a practice is not to prescribe any particular moral rule. To explain the behavior is not to justify it. Facts and values (is and ought) are conceptually distinct. Charles Darwin (1871), in his own presentation, notably limited the scope of his analysis to the "natural history" of ethics (p. 71). Still, knowing how and why (historically) we value things may fruitfully guide reflections on the process. Having introduced these caveats, then, let us consider what biologists have discovered about morality as an evolved form of behavior.

Moral Outcomes (Behavioral Genetics)

• *Cooperation and helping behavior are simple evolutionary puzzles.*

Evolution provides an important context for interpreting moral behavior, interpreted solely in terms of outcomes—regardless of motive or intent. Some behaviors or dispositions—not all—are partly hereditary (innate or instinct). To the degree that they are, they are subject to natural selection. Such behaviors will thus tend to promote an individual's relative fitness. Moral behavior seems an exception. Cooperation or helping may enhance the fitness of another organism. Any behavior that involves a cost (or decreased fitness) to the individual seems ruled out by evolutionary principles. Biologists have solved this puzzle in various ways, as described below.

Table 1 Complementary types of explanations of moral behavior, reflecting multiple philosophical interpretations of ethics

Behavior	Moral philosophy	Biological science
Moral outcomes	Consequentialism	Behavioral genetics
Moral motives/intent	Deontology	Neurophysiology and psychology
Moral systems	Social contract	Sociality and communication

• *Organisms may cooperate when each benefits.*

Behavior that benefits other organisms may sometimes also benefit the individual. In such cases, no conflict arises. For example, mutualisms are common in nature: insect pollination of flowers; animal dispersal of seeds; the ant–acacia symbiosis; and various endosymbionts (bacteria/termites, algae/nudibranchs; mitochondria; chloroplasts). Such interactions between species illustrate how organisms may adapt through mutually beneficial behavior, even where the exchange is not conscious.

The same principle applies for interactions within species. Even if organisms compete for the same resources, they may also establish mutually beneficial relationships. For example, predators (such as wolves, hyenas, or whales) may enhance the chances of capturing prey by acting together. Prey, likewise, may enhance their individual chances of avoiding predation by banding together. Information about food may also be shared when it becomes available in periodic, plentiful batches—as observed among osprey, cliff swallows, weaver birds, crows, honeybees, ants, termites, and others (Allchin 1992). Ultimately, cooperation may enhance fitness, not necessarily diminish it. Benefitting others need not involve individual cost.

• *Some cases of "costly" helping are apparent only.*

Helping that seems to involve cost, therefore, may justify further analysis. Some cases of costly helping are indeed apparent only. Costs that are observed in the short term may be balanced by benefits in the long term.

For instance, when Florida scrub jays (*Aphelocoma coerulescens*) reach reproductive age, they do not always "leave home" and begin their own families. Rather, they help raise their younger siblings: an apparent cost when compared with their own reproductive potential. But the context of reproduction is complex. Outcomes change with a broader perspective. A male scrub jay must have his own territory for foraging and nesting, and territory is limited. Males who stay with their father can help gradually expand the father's territory, which is eventually split between father and son. This way, the son is better able to secure good territory. Females, by contrast, compete for males with the best territories. A female who can wait for opportunity is able to select a better mate. In each case, the scrub jay actually benefits reproductively in the long term by staying at home and helping its parents reproduce in the short term (Woolfenden and Fitzpatrick 1978, 1984). Such reproductive helpers are found widely—in black-backed jackals (*Canis mesomelas*), cichlid fish of Lake Tanganyika (*Lamprologus brichardi*), gray-crowned babblers of Australia (*Pomatostomus temporalis*), carrion crows in Northern Spain (*Corvis corone corone*), and many other species (Emlen 1978; Krebs and Davies 1993, pp 299–302; Clutton-Brock 2002; Baglione et al 2003). In all

cases, as with observed cooperation, benefits are partly shared and ultimately outweigh any costs.

Misleading appearances of costly helping are also vividly exemplified by colony defense in meerkats (*Suricata suricatta*; Clutton-Brock et al. 1999). Meerkats, a type of mongoose found in arid Southern Africa, typically live and forage in groups. Some individuals serve as sentinels, watching for predators and sounding a general alarm if one is spotted. By vocalizing loudly, however, the sentinel seems to alert any nearby predator and put herself at more risk: an apparent costly act. Sustained and careful observation, however, reveals that meerkats guard from safe vantage points, where they can readily escape into a burrow. In addition, sentinels are usually the first to detect the predator, and they hide sooner than most others. Vigilance limits foraging time, however. Meerkats tend to adopt a guard role only when they are well fed. Sentinel behavior can, thus, benefit the individual meerkat while also benefitting others. The same pattern of sentinel volunteering has been observed in the bird, the Arabian babbler (*Turdoides squamiceps*; Wright et al. 2001), and others. The behavior, evolutionarily speaking, seems costly but is indirectly beneficial.

• *Some cases of costly helping are explained by genetic relatedness.*

Considering larger contexts can inform analysis of other cases of costly helping, as well. For example, honeybees, and many wasps and ants, along with the burrowing naked mole rats from Eastern Africa include individuals that do not reproduce. Rather, they contribute to the reproduction of a single individual in a social setting. The failure to perpetuate one's own lineage seems to contradict the principle of natural selection. Yet it is the evolutionary context that also proves significant here. In a broader scope, lineages include collateral relatives and their descendants, who share on average certain percentages of one's heritable traits. Under appropriate circumstances, contributions to their survival and reproduction may well outweigh the individual's. In such cases, costly behavior towards relatives may develop. Natural selection is indirect. The helping traits are preserved and proliferate through relatives, not direct offspring: kin selection. For long-term evolution, a proper measure is thus not individual fitness, but inclusive fitness, the total representation of one's traits in future generations (Hamilton 1964).

The outcome of kin selection is well illustrated by honeybees (*Apis melifera*). Each hive is typically dominated by one large "queen" bee that reproduces. The other bees are her offspring. While also female, they are sterile and work in the hive supporting their sisters rather than mating on their own. This behavior reflects the bees' distinctive

genetics. The queen is haploid, the female workers (and males) diploid. Paradoxically from a human perspective, workers are more closely related to their sisters (75%) than to their own children (50%)! When a honeybee dies defending the hive, she increases the chances that the queen and her many sisters—the lineage expressing her traits—all continue. Through indirect kin selection, the helping behavior, while costly, increases her inclusive fitness. Many other insects exhibit similar genetics and, not surprisingly, also similar social organization.

Naked mole rats (*Heterocephalus glaber*) also live in colonies with just one much larger reproductive female. Other females become sterile. As mammals, however, the mole rats do not share the honeybees' genomic structure. Yet they do live in family-based groups and are highly inbred. Individuals in the same burrow typically share at least 80% of their genes. Mole rat sociality itself seems an adaptation to patchy food resources in an arid environment (O'Riain and Faulkes 2008). Their striking breeding structure, however, with its costly helping, seems shaped by kin selection (Jarvis 1981; Sherman et al. 1991).

In Belding's ground squirrels (*Spermophilus beldingi*), which inhabit mountain meadows in the western USA, costly helping appears in the alarm calls of sentinels watching for predators. Unlike meerkats, Belding's ground squirrels that raise an alarm are more frequently preyed upon. In this case, the ground squirrels in one area tend to be closely related. They alert—and benefit—mostly their kin. Relatedness among individuals varies, however, and underlies significant differences in calling behavior. Males tend to disperse from their place of birth, while females remain local. Females, thus, have more kin neighbors than males do, and accordingly, they devote more time to the sentinel role. In addition, their alarm calls are more numerous when only close relatives are nearby. While alarm calls in general seem to have evolved based on foraging in the open during the day, the pattern and frequency of sentinel risks in the Belding's ground squirrels seems to reflect kin selection (Sherman 1977; Shelley and Blumstein 2004).

• *Organisms can determine kin relatedness in many ways, sometimes by indirect cues.*

Kin selection can only be effective, of course, if organisms can differentiate kin from non-kin (Grafen 1990). Since they cannot determine each other's genes directly, kinship or degree of genetic relatedness must be perceived indirectly, through vicarious clues (Campbell 1974). The case of Belding's ground squirrels illustrates how locality may function as a substitute when kin tend to inhabit the same area. For example, boobies on the Galápagos Islands (*Sula nebouxii*) recognize their offspring only by location: within a ring of guano that marks their rudimentary nest. If a nestling falls outside the ring, whether accidentally or by being pushed, it is treated as non-kin and is neither cared for nor permitted to return (Gould 1983). Vicarious indicators, thus, do not always function optimally. European cuckoos and American cowbirds, for instance, lay their eggs in the nests of other species, where the host birds raise the chicks as if kin. Such parasitism exploits the limits of an evolved system of kin detection.

Another system for detecting kin indirectly is based on similar traits. Side-blotched lizards in California (*Uta stansburiana*) have three throat colors: orange, yellow, and blue. They establish mutually favorable territories based on the throat visual cues, even when unrelated individuals are mixed. Here, the trait seems to signal genetic similarity, functioning as a substitute for actual genetic relatedness (Sinervo and Clobert 2003). Again, there is a slight displacement between kin and the cue for detecting it: kin selection inevitably involves some probability.

The ability of humans to ascertain kin has been investigated recently with special regard to attitudes towards incest and its avoidance. Primates, including humans, are able to track kin relationships through observed births—for example, younger (but not older) siblings. They use this information in social interactions (even if unconsciously). In other cases, siblings seem to use years of cohabitation, regardless of whether they are actually kin, as a vicarious indicator (Lieberman et al. 2003, 2007). While humans in most cultures tend to associate in family groups, the role or extent of kin selection remains an open question (considered further in the sections below).

• *Some cases of costly helping are explained, alternatively, by reciprocity.*

Kin selection cannot explain every costly act. Behaviors that reduce individual fitness also occur among non-kin. Context, again, is important. Other behaviors between the same organisms may be relevant. Exchanges (as in other cooperative mutualisms) may simply be displaced in time. Namely, the recipient may later *reciprocate*, essentially closing an unstated deal (Trivers 1971).

Such reciprocity, or deferred mutualism, is observed in vampire bats (*Desmodus rotundus*; Wilkinson 1984, 1988, 1990). The bats cannot survive without food more than a few days. But on any given night, 7–30% of the bats fail to find a meal. A bat may then turn to a roostmate and nuzzle its throat. On roughly five of eight occasions, the second bat regurgitates a small amount of blood for the first bat. Such sacrifices are not isolated acts, however. Eventually, the donor bat fails to find food. Because bats frequently return to the same roost, the same behavior can occur again,

with the roles reversed. The "debt" is repaid. Reciprocity, or the potential for such, is critical.

Reciprocity can occur at various levels of costs and consequences. Grooming is not critical to survival, but it occurs frequently in many primate species, even among unrelated individuals. It is typically reciprocated by later grooming or other social "favors." In one study of food sharing in a chimpanzee troop, based on over 7,000 observed interactions, exchange was ultimately balanced for each chimp pair (de Waal 1989). Among black hamlet fish of the Caribbean (*Hypoplectrus nigricans*), the exchange involves reproduction. The fish are hermaphroditic; they can both spawn and fertilize. The energy investment in eggs is much greater than in sperm, however, so the reproductive cost to the fish that lays eggs is greater. What fosters reciprocity? Here, any laying of eggs is limited, and successive matings depend on the alternation of male and female roles (Krebs and Davies 1993, p. 285). Here, as elsewhere, repeated encounters allow reciprocity.

As these examples may indicate, arrangements of reciprocity can be fragile, susceptible to cheaters. Each organism cannot always depend on the other to fulfill its end of the "bargain." Such relationships have been modeled using computers for repeated encounters among individuals using various postures of cooperating or "defecting." An individual that "reciprocates" by doing whatever the other individual has done (whether to cooperate or not) seems to be strategically most effective (Axelrod 1984). Such simulations underscore the possible relevance of social interactions, addressed below.

Moral Motivation or Intent (Neurophysiology and Psychology)

Explaining moral outcomes alone does not address what many consider most fundamental to morality: moral sentiments. An alternative approach to morality focuses on feelings or reasoning at the level of mental phenomena rather than on genetics (Sober and Wilson 1998). In ordinary terms, morality may be less *what* you do so much as *why* you do it: are your motives or intentions "good," regardless of the actual outcome? Adopting this perspective introduces a whole new set of biological questions and explanatory aims—and corresponding methods.

Mental phenomena pose a challenge for science. They are not directly observable. Philosophers have relied conventionally on introspection. In our daily lives, we also make judgments about what other persons think, believe, or intend or why they act. Both methods can be informative; yet they are also limited and possibly misleading, especially with animals. One common error is to *anthropomorphize* animals or to interpret them idealistically in human terms.

Biologists must take care in documenting or mapping behavior as a clear relationship between stimulus and response. They learn from psychological, anatomical, and physiological studies, especially using recently developed neurological imaging technologies.

• *Darwin proposed the moral sense as an inevitable outcome of four elements: social instinct, memory, language, and habit.*

In describing the evolution of humans in *Descent of Man*, Darwin (1871) prominently addressed mental and moral abilities. Following cultural discourse at the time, he focused on what he called the moral sense, or conscience, notably reflected in the emotion of remorse. "Why do we feel moral duty?" Darwin wondered. First, Darwin observed that animals could evolve societies, structured (he assumed) by a social instinct. Second, with multiple instincts, behavior might not always accord with social benefit. But memory, Darwin thought, would help resolve such conflicts as the organism learned to regulate its instincts, making the social instinct primary. Third, the use of language would allow organisms to communicate their needs clearly to one another. Fourth, repetition would lead to habit and a spontaneous sense of what one "ought" to do. While incomplete and flawed in some respects, Darwin's early sketch remarkably identified many relevant variables and processes, discussed further below.

• *Nonhuman organisms exhibit sympathetic concern for both kin and nonrelated individuals.*

The first significant question in investigating the evolution of moral motives is whether other species, especially those closely related to humans, also express such motives. Many relevant cases are documented. Some of the most striking examples come from unexpected observations, rather than formal scientific study. For example, in 1996, Binti Jua, a female gorilla at the Brookfield Zoo outside Chicago, rescued a 3-year-old child that had fallen into her enclosure. Binti Jua cradled the unconscious boy, just as she did her own child, growled at another gorilla who approached her, and then carried the boy about 20 meters to a door where the zookeeper could retrieve the boy, all while her own daughter clung to her back (Bils and Singer 1996; Anonymous 1996). The incident echoed a similar case at England's Jersey Zoo in 1986 with a male gorilla named Jambo. While one might want to dismiss these cases as mere stories, primatologist Frans de Waal (1996b, 2005) defends their significance in the context of similar, more systematic observations of sympathy among primates in captivity and in the wild (both episodes were recorded on home video).

De Waal (de Waal 1996a; de Waal and Aureli 1996) has highlighted numerous other cases. For example, he

describes Mozu, a snow monkey born without hands or feet in a free-ranging troop in Japan. Mozu could not climb. Still, the other members of Mozu's troop did not move in the trees above her at a pace that would leave her behind, despite their ability to do so. They seemed tolerant of Mozu's handicap. Such observations add weight to the notion that moral sentiments are rooted in human ancestry.

In an effort to understand the nature of such apparent sympathy, Jules Masserman et al. (1963) investigated how macaques responded to other monkey's suffering in a laboratory environment. How would they behave if they knew that securing food would give an electric shock to another monkey? Masserman's monkeys often prolonged their hunger rather than administer a painful stimulus. One monkey refrained from taking food for 12 days. Responses showed several patterns. Self-starvation was more likely in monkeys that had themselves experienced electroshock as a subject. Sacrificial behavior was not biased towards members of higher dominance rank but was slightly stronger for cagemates (although not statistically significant). Visual contact, even without auditory cues, seemed sufficient to induce the response. The monkeys' behavior seemed to reflect an understanding of another's pain, as well as strong aversion to causing such suffering (experimental ethics have since become stricter and no one has replicated this important early study in primates).

Mice, too, seem to show signs of proto-empathy in expressing feelings modified by the feelings of others. Experimentally, they exhibit increased sensitivity to mild pain when cagemates (but not unfamiliar mice) also experienced noxious stimuli at the same time. Again, visual contact seems important in communicating an emotional state and triggering a corresponding, even if not directly sympathetic, response (Langford et al 2006).

Concern towards others may occur in more positive contexts, as well. Common marmoset monkeys (Callithrix jacchus) are cooperative breeders and strongly interdependent socially. When given an opportunity (with no personal reward) in a laboratory setting, they provide food to other individuals, even without reciprocity or genetic relatedness (Burkart et al 2007). Unsolicited, other-regarding behavior may thus occur without the more sophisticated cognitive structures found in chimps and humans and without explicit reciprocation.

• *Humans and some other primates exhibit moral sentiments at a very early age.*

One way to assess foundational human motivation is to observe behavior before possible learning or training. Human infants (age 18 months), for example, frequently help adults in simple problematic tasks in a lab setting—without being asked and without reward. Young chimps, too (ages 3 to 4.5 years), exhibit the same behavior, at least

when they are able to understand the incomplete task (Warneken and Tomasello 2006). A macaque (or rhesus monkey, *Macaca mulatta*) of a captive troop, only a few months old, was also observed hugging another younger member who had just been assaulted sexually by one of the adult males: apparent unsolicited consolation (de Waal 1996a). Simple moral tendencies seem innate in humans and other primates, at least early in life. The question remains how such feelings evolved and whether the social environment was relevant historically (see section below).

• *Moral thinking and feeling has a neurological basis.*

Evolutionary understanding is typically informed by analysis of structure and function. To further understand moral behavior, then, biologists consider the anatomy and physiology of the brain and nervous system (Pfaff 2007).

Perhaps the most fascinating case is a man who lost some his social and moral bearing due to an unusual brain injury: a railroad worker in the nineteenth century named Phineas Gage. Gage was using his tamping iron to compact an explosive charge when it detonated prematurely and sent the 1.5-inch-wide rod up under his cheek bone, through his brain, and out the top of his skull. Gage remarkably survived, but he had lost some of his brain, and with it, some of its function. Whereas before the accident Gage had been "quiet and respectful," afterwards he became "fitful, irreverent, indulging at times in the grossest profanity (which was not previously his custom), manifesting but little deference for his fellows." The attending physician profiled the dramatic change, noting that "the equilibrium or balance, so to speak, between his intellectual faculties and animal propensities, seems to have been destroyed" (Harlow 1868, pp. 339, 340).

One can easily overstate the correspondence, as was done at the time by one enthusiast for phrenology, a theory now abandoned in disrepute. Persuaded that there were discrete personality traits that mapped onto the surface of the skull, he imagined that in Gage's brain, "the iron had passed through the regions of the organs of BENEVOLENCE and VENERATION…hence his profanity, and want of respect and kindness" (Macmillan 2000, quote on p. 350). Avoiding such speculative and unsubstantiated extreme claims, one can still hope to identify how certain areas of the brain may be associated with different dimensions of moral mental activity, as illustrated broadly in Gage's case.

In recent years, neurological imaging techniques especially have proven useful in monitoring brain activity of subjects in the midst of moral thinking. For example, the ventromedial prefontal cortex shows activity when subjects view images that evoke moral impressions but do not require any actual moral judgment. This area has been proposed as part of a network involving feelings related to social interactions. People with damage to this area (such as

Phineas Gage) are less able to integrate emotional information into judgments that also involve an analysis of costs and benefits, and their conclusions reflect a corresponding bias. By comparison, when moral reflection turns to interpreting and assessing other people's intentions, the key brain area seems to be the right temporoparietal junction. When moral problems become personal, the medial frontal gyrus becomes more active. More abstract or hypothetical problems, by contrast, tend to activate the dorsolateral prefontal cortex and other areas. When such different forms of thinking conflict, as one often finds in moral dilemmas, activity rises in the anterior cingulate cortex—perhaps serving a mediator role. Thinking in terms of a single "moral organ" thus seems inappropriate. As initially sketched by Darwin, multiple faculties seem involved, distributed throughout the brain. Indeed, all regions active in moral thinking have been implicated in other nonmoral mental processes. None seems devoted exclusively to moral thinking (Damasio et al 1994; Greene and Haidt 2002; Miller 2008).

Neuroimaging studies show significantly that actual moral reasoning involves *both* emotion and logic. Philosophers have long debated which is (or should be) primary in moral judgment. In practice, as least, both seem to be relevant (Greene and Haidt 2002).

• *Moral behaviors may be learned as part of an open behavioral program.*

A focus on neural processes, especially in contrast to genetics, emphasizes the importance of open behavioral programs. Not all behavior is innate, or closed, with narrow predetermined stimulus-response patterns. With appropriate neural structures, learning is possible. The flexibility afforded by learned behavior allows organisms to respond to local environments, which may change during an organism's lifetime or vary from organism to organism within the same species. Evolution may thus favor the brain's potential for behavioral plasticity and for placing "values" on certain responses. Moral behavior—or immoral behavior—may be partly (or even largely) learned and shaped by local social environments.

Open behavior systems lead to a new level of organization: the psychological. To achieve plasticity, a learning system needs to be decoupled from particular inherited behaviors. Organic evolution can then act only at the level of the whole learning system. Fitness is determined by how well the system in its entirety performs, not whether each and every behavior, gauged separately, enhances survival and reproduction. Individual acts thus become relatively insulated from direct natural selection. In addition, learning has the potential to modify, or regulate, innate behavior or dispositions. The psychological level thereby becomes emergent, exhibiting new interactions and properties rela-

tively independent of lower level functions (genetic and physiological) and able in part to influence them.

Organisms with open behavior accordingly achieve a degree of autonomy (Murphy and Brown 2007). The consequences for interpreting morality are profound. For example, autonomous organisms may make authentic choices (not strictly dictated by heredity). Emergence and autonomy provide a biological context for interpreting many major philosophical concerns: intention, agency, and free will—which are only meaningful at the mental, or psychological, level (Hofstadter 1979; Sterelny 2001).

Autonomy also leads to individual identity. Even organisms with identical brains may behave uniquely, due to different learning histories or environments. Cultural variation is also possible. Organisms [with open behavior] have the potential to develop a wide range of values, whether moral or immoral, not determined strictly, or exclusively, by their genes.

• *Cooperation and helping behavior may be intentional.*

Organisms with open behavior programs may thus engage in cooperative and helping behavior, quite apart from genetic reasons. For example, chimpanzees in a novel laboratory setting that enables them to work together to secure food collaborate. Given a choice, they recruit chimps with the best history of cooperation, indicating their understanding of cooperative behavior (Melis et al. 2006). Similar behavior has also been documented in the crow-like rooks of Europe (*Corvis frugilegus*; Holden 2008; Seed et al. 2008). Biologically, one distinguishes sharply between genetic and psychological levels of helping (Sober and Wilson 1998).

Cooperation at the psychological level is still susceptible to cheating or defection. However, the problem is transformed because individual organisms have the potential to learn. The ability of organisms to interact leads biologists to consider the social level more fully.

Moral Systems (Sociality and Communication)

A third important perspective on moral behavior addresses the interactions of organisms and their social organization (including what philosophers call an implicit social contract). For example, behavioral genetics does not solve the problem of selfish behavior spreading in groups where innate reciprocity might arise. Psychological level considerations alone leave open the question of what may be learned and in what contexts. Relationships that emerge at the social level can shape behavior in ways that resolve these uncertainties. As Darwin suggested in 1871, human behaviors may well be shaped by "the wishes, approbation, and blame of his fellow-men" (p. 86).

The most profound challenge to explaining moral behavior seems the threat of cheaters. Selfish individuals may proliferate by "free-riding" at the cost of sharers. Economists encounter this problem when they discuss public goods, intended to be distributed evenly, but freely available for anyone to take a disproportionate share. Philosopher Garret Hardin (1968) suggested that many environmental problems develop because individuals will tend to overuse or spoil a shared "commons" (public lands, rivers, oceans, air) at everyone else's expense—resulting in what he called the tragedy of the commons. Problems seem inherent in any group trying to establish a pattern of sharing behavior. Ultimately, selfishness seems always to subvert cooperation. It may well seem an inescapable consequence of the process of natural selection.

The problem arises, however, only when individuals act independently of each other. In a social setting, blind interactions can rarely be assumed. For example (as described below), individuals may learn to interact selectively: only with individuals that reciprocate or that are known publicly as reliable cooperators—or they may identify and punish violators. Social level interactions dramatically alter the prospects for moral behavior.

• *Organisms may cooperate selectively with reciprocators.*

Organisms may guard against loss to cheaters by limiting their interactions. Consider again the case of vampire bats. Their observed system of blood exchange seems stable, undisrupted by potential free-riders. Why? Here, the bats tend to roost in the same colony, a very simple social organization which forms a context for sustainable reciprocity. The bats do not share blood unconditionally. They are more likely to provide food for a bat that has fed them on a previous occasion or that is a frequent roostmate. The bats can recognize distinct individuals and remember past events. They learn to identify cheaters. A bat that does not repay previous "favors" does not get endless handouts. Bats that cheat ultimately do *not* benefit. Defection is thereby limited (Wilkinson 1984, 1988, 1990). Selective interaction leads to network reciprocity, a social cluster of cooperators insulated against invasion by selfish individuals (Nowak and Sigmund 2005).

• *Social organisms may enforce cooperation through rewards and punishment.*

Organisms may also actively punish noncooperators. For example, in a free-ranging (semi-captive) colony of macaques, or rhesus monkeys (*Macaca mulatta*), on an island off Puerto Rico, individuals call to the group when they find food. Individuals that fail to call are frequently discovered and, here, actively punished. They are more likely to be bit, hit, chased, or rolled. Cheaters ultimately eat less food. There are costs to deception (Hauser 1992).

Cooperation enforced through punishment yields strong reciprocity. Such punishment has also been observed in the cooperative breeding of fairy wrens and in the shared nesting of paper wasps (*Polistes fuscatus*; Clutton-Brock and Parker 1995). In these cases, interactions at the higher social level regulate behavior, or stimulus-response patterns, at the individual level.

Punishment seems important in human culture and evolutionary history. When Darwin began considering the evolution of morality, he reflected on a possible role for the "fear of others acting in unison" and "the fear of punishment" (*M Notebook*, p. 151; Darwin 1871, p. 92). However, punitive behavior cannot be assumed. It costs extra effort or resources. Humans, nonetheless, accept personal cost to ensure group benefits in anonymous experimental situations. Moreover, others respond to their punitive actions (Fehr and Gächter 2002). A norm of cooperation can be learned and enforced through punishment.

Punishment of selfish behavior seems present in all human cultures. They include not only different nations on different continents and Oceania but also cultures with widely divergent environments, economies (from foraging and pastoralism to industrialism), and residence patterns (from nomadic to sedentary; Heinrich et al. 2006; Hermann et al. 2008). Most important, perhaps, negative sanctions are found in small mobile hunter-gatherer cultures—similar to our Paleolithic ancestors—where they help maintain egalitarian societies (Boehm 1999).

Selective interaction and punishment may combine. When given the option, human subjects prefer to join groups functioning cooperatively through sanctions over groups where they are "free" to be selfish but can reap only limited benefits (Güreck et al. 2006). Cooperative groups are thus not necessarily at a relative disadvantage. Indeed, mathematical models indicate that being able to choose between such groups (or not join either) may have been critical to the origin of punishment-based cooperation (Hauert et al. 2007). As suggested by Hardin (1968), the tragedy of the commons may be solved by "mutual coercion, mutually agreed upon." Again, social-level dynamics can affect how individuals act.

• *Organisms may benefit from social information.*

Another social response to cheaters is to gather information about how other organisms behave—whether they are trustworthy cooperators, say—and to act accordingly. For example, one small cleaner fish (*Labroides dimidiatus*) has a mutualism with large fish. The small fish eat parasites on the large fish. Occasionally, however, they "cheat" and feed on the host's mucus or nip a bit of its flesh. Other potential host fish (or "clients"), however, can observe such behavior. Such host fish show a preference for cleaner fish that are demonstrably "honest." Accordingly, cleaner fish

cheat less when bystanders are present (Bshary and Gutter 2006). Social "eavesdropping" also seems to keep defection from cooperation in check.

Many animals, including humans, seem to collect information on the behavior of other organisms. Observed organisms, in turn, seem to modify their behavior when visual clues, such as a pair of eyes, indicate that they are being watched. Observers may then "spy" from concealed vantage point to detect unbiased behavior. The value of the social information is reflected in the responses and counter-responses (Dally et al. 2006; Milinski and Rockenbach 2007).

Ultimately, social information allows image scoring or evaluating of other organisms' behavior patterns. Reputation can matter. Cooperation can be guided by status, or reputation, rather than instances of direct reciprocity. Indirect reciprocity can evolve in a group with image scoring (Nowak and Sigmund 1998, 2005)—and can also effectively solve the problem of the tragedy of the commons (Milinski and Rockenbach 2007).

• *Variations in social and cognitive contexts shape helping and cooperative behavior.*

While helping and punitive behaviors seem universal among humans, they do vary across cultures. Punishment occurs more readily, for example, in societies with stronger norms of cooperation (Heinrich et al 2006; Hermann et al. 2008). Social context affects cooperative behavior. Most monkeys do not help others unless there is a personal benefit. One might tend to attribute their behavior to limited cognitive skills (when contrasted with great apes). Yet, common marmosets (*Callithrix jacchus*) in experimental situations do retrieve food for others, even with no clear benefit to themselves. Unlike closely related species, however, the marmosets breed cooperatively. Their social system (here, shared with the great apes) seems to provide a context that fosters the helping behavior (Burkart et al. 2007).

As noted earlier, both chimps (primates) and rooks (birds) can recruit helpers to perform joint tasks. But their behaviors also differ, as do their social organizations. Rooks do not seek or achieve cooperation as frequently as chimps. Their social organization is also simpler. They form single mating pairs that tend to remain for life. Chimps, by contrast, shift mating partners and must also negotiate political allegiances in an unstable dominance hierarchy. The degree of cooperation in each case reflects the respective social demands. In addition, cooperation among individual pairs of rooks reflects their mutual tolerance in other social encounters. Overall, the cooperative behavior is closely linked to the social context (Seed et al. 2008).

The behavioral difference between early humans and their closest primate relatives also seems based on social organization. Chimps compete for both food and mates,

even within social groupings. Their societies are marked by linear dominance hierarchies. Pairs sometimes form coalitions and significantly alter the balance of power. Larger coalitions appear temporarily, but they too are limited in scope. Chimp cooperative behavior is also limited and often politically oriented. Altruism is rare. Early humans (around 100,000 years ago) were able to level these hierarchies. Communication skills facilitated the coordination of large coalitions that could effectively check the authority of dominant individuals. Weapons, once developed for hunting, likely contributed further to equalizing power. Egalitarianism emerged, and with it, moral norms that could shape further biological evolution. Human morality, too, seems to reflect how the species is organized socially (Boehm 1999).

• *Effective communication enhances the social function of moral behavior.*

Social coordination among organisms, in general, is enabled and further facilitated by communication. Moral behavior is no exception. In sketching the possible roots of moral responses, Darwin (1871) noted the role of organisms being able to interpret the needs of others in order to assist them. Darwin underscored the role of language, but he also understood the role of less complex means. For example, emotions are typically expressed externally, through anatomically distinct postures or facial configurations. They offer important clues about the internal mental states of other organisms. Darwin followed *Descent of Man* with a whole volume exploring *The Expression of Emotions in Humans and Other Animals* (Darwin 1872/1965). Contemporary studies continue to document the importance of the body and even of particular muscles in expressing emotions, as well as in feeling and perceiving them among others (Niendenthal 2007).

One of the most challenging communication tasks—sometimes even with language—is interpreting the intention of others. This is a further dimension of managing social information relevant to moral responses—for example, in deceiving others or in detecting such deception. Being able to interpret, or "mirror," another mind appears to be quite a sophisticated cognitive skill. The abilities of other primates and mammals in doing this are still being debated (Zimmer 2003; Miller 2005; Pennisi 2006).

Communication and language are also integral, of course, to sharing desires and ideas about ideal behavior and thus to moral discourse. In the context of organisms with open behavior programs, language also contributes significantly to the transmission of culture and to the learning of moral norms. Moral systems may thus not only emerge socially but also perpetuate themselves culturally, apart from specific genes or individual behavior patterns (Richerson and Boyd 2005).

• *Social interactions may affect individual learning and biological fitness*.

Moral systems not only exhibit a degree of autonomy at the social level but also provide an environment in which individuals learn and natural selection acts. First, when an organism (with an open behavior program) ventures into trying new social behaviors, the environment of other group members will be part of reinforcing them, positively or negatively. Successful (or failed) reciprocities and punishment (or rewards), for example, will shape what is learned. Appropriate social contexts will tend to foster helpful or cooperative behavior. Further learning through observation and imitation will then tend to amplify socially successful behavior.

Second, social interactions provide an environment for biological selection as well. Innate dispositions—such as extending sympathy beyond kin, an unschooled tendency to try helpful behavior, or readiness to punish (see above)—may enhance survival and reproduction in certain social environments. Social environments may also promote general traits that enhance social or moral behavioral abilities, such as improved language skills ("reading" emotions, interpreting signals, articulating needs, etc.), perceptual skills in differentiating group members, or memory. Indeed, anthropological evidence indicates that we have inherited many such tendencies and skills from our primate and early hominid ancestors (Boehm 1999; Richerson and Boyd 2005). Society and morality may ultimately be forces in evolution as much as they are products of it.

Summary and Application

• *Biologists can explain morality on multiple levels*.

As genetic behavior, moral outcomes are explained alternately by kin selection or reciprocity. As a psychological motive or intent, morality is explained by open learning systems shaped by emotion and reasoning from experience. As a social system, morality is explained by mutual accountability among individuals or by selective interaction based on social information. Processes at each level provide a context in which the others function.

• *Higher levels of organization limit reductionistic explanations of behavior*.

Understanding how morality as a behavior is explained on multiple levels is valuable for correcting some widespread but misleading popular beliefs about evolution and culture. Many persons portray evolution as nothing more than a fiercely competitive "struggle for existence." They render nature and culture alike as governed by an unqualified "survival of the fittest." Such conclusions are based on the mistaken doctrine of biological determinism, the flawed assumption that all behavior reduces simply to genes (Gould 1981; Lewontin et al. 1984; Lewontin 1993; Rose 1997). Such a view disregards the relevance of learned behaviors at the psychological level and the regulation of behavior by interactions at the social level. Biological determinism fails by not acknowledging the role of emergence, the appearance of new dynamics at higher levels of organization (Holland 1998; Camazine et al. 2001). Interactions at these levels may generate new relationships and new properties. They may create a system that functions on its own principles and can modify how component parts act. For example, social punishment limits individual "selfishness." Learning can disarm any genetically based defection. Psychology and sociology, as distinct fields, thus complement standard biology in studying behavior.

Once one becomes aware of mutualisms between species, reciprocities among individuals within a species, and the potentials of open behavioral programs, the view of natural selection as universally "selfish" is clearly too narrow. Kin selection among Belding ground squirrels or honeybees may inform our understanding of the evolution of morality, but it does not map or determine human behavior. Human psychology establishes its own values. Human society establishes its own laws. Humans are not enslaved by some stereotyped "law of the jungle" (despite the premise of some "reality" television shows!).

• *Cultural bias may generate error in science, with adverse effects beyond science*.

As a flawed doctrine, biological determinism also has significant political overtones not justified by science. Characterizing society as "merely" biological implies that any social organization—disparity in wealth, for example—is inherent in nature and cannot be changed. The appeal to nature obscures how human interaction or politics—at the social level—contributes to the outcome. Biological determinist claims function socially to preserve the status quo: to protect power and acquired wealth and to peripheralize moral analysis. Further, the appeal to science and its authority implies that the view is proven and cannot be challenged, further concealing the role of human politics.

Biological determinism ultimately tries to present certain values as based on facts of nature. Accordingly, it also reflects another error, the naturalistic fallacy: the effort to find or extract values from the facts of nature. This error has a long history, going back at least to Herbert Spencer in the late 1800s. He claimed that laissez-faire social ideology was based on his biologized psychology and sociology and on Darwinian evolution (Spencer 1851, 1852a, b, 1864; Moore 1903). The same

error is found today when someone argues that some value or moral principle is justified because a certain trait is (so they claim) universal, or innate, or reflects "human nature." But frequency does not establish value. Such appeals typically indicate that the scientist is trying to inscribe his or her own cultural prejudice into the "facts" of nature: a threat to sound science called the naturalizing error (Allchin 2008). Facts of nature may surely inform moral reasoning and justification. But nature does not yield values on its own.

• *Biologically, humans have multiple moral potentials*.

Morally, humans have multiple behavioral potentials. Despite some predispositions, they do not seem bound by their genes to be either selfish or cooperative. They exhibit the emotional and cognitive tools for both. Evolution seems to have generated sometimes conflicting motives. Processes at different levels of organization, especially, may foster contrary tendencies. Perhaps this is why philosophers and others, even after many centuries, continue to debate the nature of morality. Ultimately, it seems, humans exercise their cognitive and emotional potential by finding their own ethical trajectory, both individually and collectively.

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