

The difference of being human: Morality

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In *The Descent of Man, and Selection in Relation to Sex*, published in 1871, Charles Darwin wrote: "I fully ... subscribe to the judgment of those writers who maintain that of all the differences between man and the lower animals the moral sense or conscience is by far the most important." I raise the question of whether morality is biologically or culturally determined. The question of whether the moral sense is biologically determined may refer either to the *capacity* for ethics (i.e., the proclivity to judge human actions as either right or wrong), or to the *moral norms* accepted by human beings for guiding their actions. I propose that the capacity for ethics is a necessary attribute of human nature, whereas moral codes are products of cultural evolution. Humans have a moral sense because their biological makeup determines the presence of three necessary conditions for ethical behavior: (i) the ability to anticipate the consequences of one's own actions; (ii) the ability to make value judgments; and (iii) the ability to choose between alternative courses of action. Ethical behavior came about in evolution not because it is adaptive in itself but as a necessary consequence of man's eminent intellectual abilities, which are an attribute directly promoted by natural selection. That is, morality evolved as an exaptation, not as an adaptation. Moral codes, however, are outcomes of cultural evolution, which accounts for the diversity of cultural norms among populations and for their evolution through time.

biological evolution | cultural evolution | human uniqueness | moral norms | moral sense

Humans are animals and have evolved from ancestors that were not human. But our "bodily frame," as well as the capacities that stem from it, show also that we are a unique kind of animal, a unique kind of ape, with distinctive features, of which the moral sense is one and, if we are to agree with Darwin, the most important one (ref. 1, p. 67). As Steven Pinker has written, "Morality is not just any old topic in psychology but close to our conception of the meaning of life. Moral goodness is what gives each of us the sense that we are worthy human beings" (ref. 2, p. 34). In this essay, I will examine morality as a consequential attribute among those that determine "the difference of being human." At issue, of course, stands the evolutionary origin of morality.

Human Uniqueness

Two conspicuous human anatomical traits are erect posture and large brain. We are the only vertebrate species with a bipedal gait and erect posture; birds are bipedal, but their backbone stands horizontal rather than vertical (penguins are a trivial exception) and the bipedalism of kangaroos lacks erect posture and is drastically different from our own. Erect posture and bipedal gait entail other morphological changes in the backbone, hipbone, and feet and others.

Brain size in mammals is generally proportional to body size. Relative to body mass, humans have the largest brain. The chimpanzee brain has an approximate volume of 300 cm³; a gorilla's is slightly larger. The human adult brain is more than three times larger, typically between 1,300 cm³ and 1,400 cm³. The brain is not only larger in humans than in apes but also much more complex. The cerebral cortex, where the higher cognitive functions are processed, is in humans proportionally much greater than the rest of the brain when compared with apes.

Erect posture and large brain are not the only anatomical features that distinguish us from nonhuman primates, even if

they may be the most obvious. Other notable anatomical differences include the reduction of the size of the jaws and teeth and the remodeling of the face; reduction of body hair and changes in the skin and skin glands; modification of the vocal tract and larynx, with important implications for spoken language; opposing thumbs that allow precise manipulation of objects; and cryptic ovulation, which may have been associated with the evolution of the nuclear family, consisting of one mother and one father with their children.

Humans are notably different from the apes and all other animals in anatomy, but also and no less importantly in their functional capacities and behavior, both as individuals and socially. Most fundamental are the advanced intellectual faculties, which allow humans to categorize (see individual objects as members of general classes), think in the abstract and form images of realities that are not present (and, thus, anticipate future events and planning future actions), and reason. Other distinctive functional features are self-awareness and death awareness; symbolic (creative) language; tool making and technology; complex and extremely variable forms of cooperation and social organization; legal codes and political institutions; science, literature, and art; and ethics and religion (3).

Humans live in groups that are socially organized, and so do other primates. But primate societies do not approach the complexity of human social organization. A distinctive human social trait is culture, which may be understood here as the set of non-strictly biological human activities and creations. Culture in this sense includes social and political institutions, ways of doing things, religious and ethical traditions, language, common sense and scientific knowledge, art and literature, technology, and in general all of the creations of the human mind. Culture "is a pool of technological and social innovations that people accumulate to help them live their lives" (ref. 4, p. 65). The advent of culture has brought with it cultural evolution, a superorganic mode of evolution superimposed on the organic mode, which has, in the last few millennia, become the dominant mode of human evolution. Cultural evolution has come about because of cultural change and inheritance, a distinctively human mode of achieving adaptation to the environment and transmitting it through the generations (3, 5–9).

Moral Behavior

I will define moral behavior for the present purposes as the actions of a person who takes into account in a sympathetic way the impact the actions have on others. A similar definition is advanced, for example, by David Copp in *The Oxford Handbook of Ethical Theory* (ref. 10, p. 4): "[W]e can take a person's moral beliefs to be the beliefs she has about how to live her life when

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In this essay, the author draws extensively from his work, "What the Biological Sciences Can and Cannot Contribute to Ethics," chap. 18, pp. 316–336, in Ayala FJ and Arp R, eds. *Contemporary Debates in Philosophy of Biology* (Wiley-Blackwell, Malden, MA, 2010).

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she takes into account in a sympathetic way the impact of her life and decisions on others.” Altruism may be defined in a similar way as, for example, “unselfish regard for or devotion to the welfare of others” (11). Altruism, however, is usually taken to imply some cost to the altruist for the benefit of others, and this is the sense in which I will use “altruism” here. Moreover, “altruism” is often predicated on the behavior of social insects and other animals, in which no intentionality is involved but rather comes about as a result of genetically determined behaviors. This is biological altruism, or altruism_b, in contrast to moral altruism, or altruism_m (12).

I will use the term “ethical behavior” as a synonym of “moral behavior,” and “morality” and “ethics” as synonyms of each other, except when explicitly noted or contextually obvious that they are used with a somewhat different meaning. Some authors use “morality” or “virtue ethics” in a broader sense that would include good feelings in regard to others and exclude inappropriate thoughts or desires, such as entertaining sexual desires for somebody else’s wife or wishes that something harmful would happen to others. So long as these thoughts or desires are not transformed into actions, they will not be included in my use of “morality.” Actions that may be thought to be evil or sinful in some moral systems, such as masturbation or eating pork, will not be included either in my use of “morality,” so long as the actions have no consequences for others.

Theories of Morality

People have moral values; that is, they accept standards according to which their conduct is judged as either right or wrong, good or evil. The particular norms by which moral actions are judged vary to some extent from individual to individual and from culture to culture (although some norms, such as not to kill, not to steal, and to honor one’s parents, are widespread and perhaps universal), but value judgments concerning human behavior are passed in all cultures. This universality raises two related questions: whether the moral sense is part of human nature, one more dimension of our biological make-up; and whether ethical values may be products of biological evolution rather than being given by religious and other cultural traditions.

When philosophers consider theories of morality they distinguish between metaethics, normative ethics, and practical ethics (10). Theories of metaethics seek to justify why we ought to do what we ought to do. They are the primary concern of philosophers, who favor different theories, such as “divine command” (God’s commanding is what makes a particular kind of action moral); “moral realism” (there are moral facts; our moral judgments are made valid or not by the moral facts); “utilitarianism” (the moral value of an action is determined by the expected benefit to the largest number of people); “positivism” (there are no objective rational foundations for morality, but rather moral norms are determined by social agreement or, in the individual, by emotional decisions); “libertarianism” (moral values are measured by the extent to which they maximize personal freedom and limit the role of the state to the protection of individual freedoms); and several others.

Normative ethics refers to the rules or laws that determine what we ought to do. Practical ethics considers the application of moral norms to particular situations, which often involve conflicting values: will abortion be justified to save the life of the mother?

In practice, humans justify the set of moral norms they follow on several, not only one, metaethical doctrines. Thomas Aquinas, the 13th century Christian theologian whose authority is highly respected up to the present, says that some moral laws come from divine authority (worship only one God), others from natural law (do not kill, do not commit adultery), and still others from civil authority (respect private property, pay taxes).

Aristotle and other philosophers of classical Greece and Rome, as well as many other philosophers throughout the centuries, held that humans hold moral values by nature. A human is not only *Homo sapiens*, but also *Homo moralis*. For the last 20 centuries, the foundations of morality were an important subject for Christian theologians, as in the case of Thomas Aquinas, but also for philosophers, such as, in the 18th and 19th centuries, Hume, Kant, and others familiar to Darwin, including notably William Paley (*The Principles of Moral and Political Philosophy*, 1785; ref. 13) (Fig. 1) and Harriet Martineau (*Illustrations of Political Economy*, 1832–1834; ref. 14).

The theory of evolution brought about the need to reconsider the foundations of morality. We do not attribute ethical behavior to animals (surely, not to all animals and not to the same extent as to humans, in any case). Therefore, evolution raises distinctive questions about the origins and tenets of moral behavior. Is the moral sense determined by biological evolution? If so, when did ethical behavior come about in human evolution? Did modern humans have an ethical sense from the beginning? Did Neandertals hold moral values? What about *Homo erectus* and *Homo habilis*? And how did the moral sense evolve? Was it directly promoted by natural selection? Or did it come about as a by-product of some other attribute (such as rationality, for example) that was the direct target of selection? Alternatively, is the moral sense an outcome of cultural evolution rather than of biological evolution?

Darwin and the Moral Sense

Darwin’s most sustained discussion of morality is in chapter III of *The Descent of Man* (ref. 1, pp. 67–102). The keystone significance of morality in human distinctness is clearly asserted by Darwin in the first sentence, already quoted, of chapter III: “I fully subscribe to the judgment of those writers who maintain that of all the differences between man and the lower animals the moral sense or conscience is by far the most important” (ref. 1, p. 67). Darwin (Fig. 2) had started gathering the contemporary literature on human moral behavior much before the publication



Fig. 1. William Paley (1743–1805). English theologian who taught at the University of Cambridge, United Kingdom, and author of *The Principles of Moral and Political Philosophy* (1785). His best known work is *Natural Theology, or Evidences of the Existence and Attributes of the Deity* (1802). Image source: www.nndb.com/people/526/000096238/.

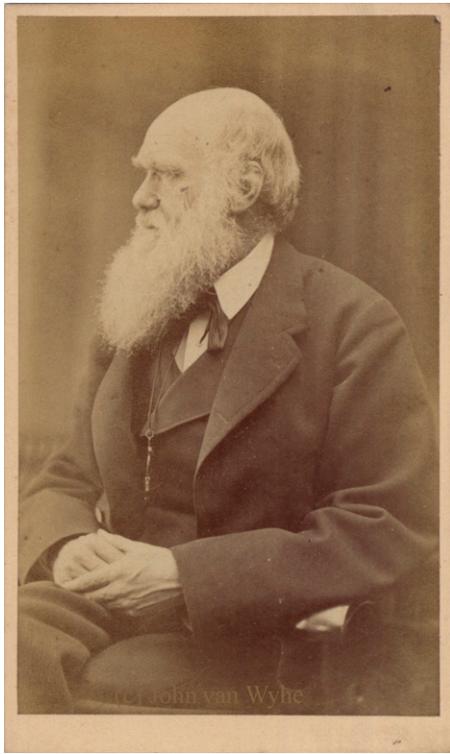


Fig. 2. Charles Robert Darwin (1809–1882). Photograph by Oscar Gustave Rejlander, ca. 1871, the year Darwin published *The Descent of Man*. Image source: http://commons.wikimedia.org/wiki/File:Charles_Darwin_photograph_by_Oscar_Rejlander,_circa_1871.jpg.

of *The Descent of Man* in 1871 (Fig. 3); indeed, we know from his notebooks that Darwin was reading the contemporary philosophical literature about moral behavior in 1837, only a few years after returning from his trip on the *HMS Beagle* (1826–1831). Treatises that he read early on include the aforementioned *Moral and Political Philosophy* by Paley (13), which he had already encountered while a student at Cambridge University, and the multivolume *Illustrations of Political Economy* by Harriet Martineau, published more recently, in 1832–1834 (14). These two authors, like other philosophers of the time, maintained that morality was a conventional attribute of humankind, rather than a naturally determined human attribute, on the grounds of an argument often advanced nowadays by philosophers and anthropologists: the diversity of moral codes.

The proliferation of ethnographic voyages had brought to light the great variety of moral customs and rules. This diversity is something Darwin had noticed when comparing the prevailing English and European norms of morality with those of South American Indians and other native populations elsewhere. But Darwin would eventually develop a more complex and subtle theory of the moral sense than his contemporaneous authors; a theory that, implicitly at least, recognized moral behavior as a biologically determined human universal but with culturally evolved differences. For Darwin, the ethnographic diversity of moral customs and rules came about as an adaptive response to the environmental and historical conditions, unique in every different place, without necessarily implying that morality was an acquired, rather than natural, human trait.

A variable adaptive response could very well derive from some fundamental attribute, a common substrate, unique for the whole human race but capable of becoming expressed in diverse directions. Darwin did not attribute the universality of morality to supernatural origin but rather saw it as a product of evolution by natural selection. The presence of a universal and common

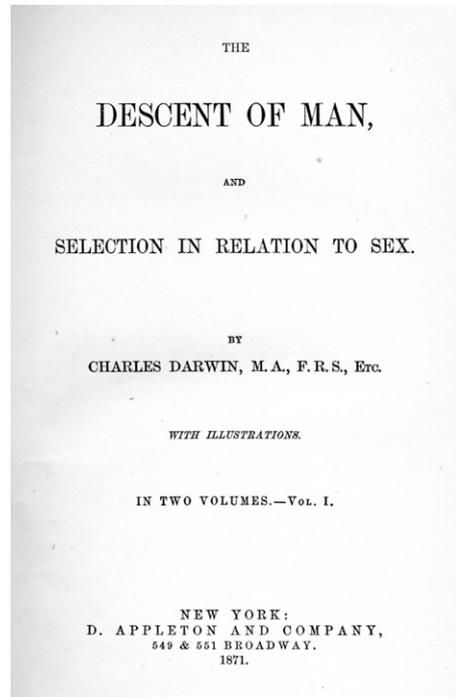


Fig. 3. Cover page of Darwin's *The Descent of Man and Selection in Relation to Sex*, first American edition, published by Appleton and Company, New York, in 1871, the same year in which his first English edition was published by John Murray, London.

foundation, endowing humans with an ethical capacity, was for Darwin compatible with different cultures manifesting different stages of moral evolution and with different sets of moral norms.



Fig. 4. Theodosius Dobzhansky (1900–1975), a principal author of the modern theory of evolution. The *In the Light of Evolution* (ILE) Sackler colloquium series is named after Dobzhansky's well-known statement, "Nothing in biology makes sense except in the light of evolution."

Darwin's two most significant points concerning the evolution of morality are stated early in chapter III of *The Descent of Man*. The two points are (i) that moral behavior is a necessary attribute of advanced intelligence as it occurs in humans, and thus that moral behavior is biologically determined; and (ii) that the norms of morality are not biologically determined but rather a result of human collective experience, or human culture as we would now call it.

After the two initial paragraphs of chapter III of *The Descent of Man*, which assert that the moral sense is the most important difference "between man and the lower animals" (see quotation above), Darwin states his view that moral behavior is strictly associated with advanced intelligence: "The following proposition seems to me in a high degree probable—namely, that any animal whatever, endowed with well-marked social instincts, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well developed, or nearly as well developed, as in man" (ref. 1, pp. 68–69). Darwin is affirming that the moral sense, or conscience, is a necessary consequence of high intellectual powers, such as exist in modern humans. Therefore, if our intelligence is an outcome of natural selection, the moral sense would be as well an outcome of natural selection. Darwin's statement further implies that the moral sense is not by itself directly promoted by natural selection, but only indirectly as a necessary consequence of high intellectual powers, which are the attributes that natural selection is directly promoting.

In the ensuing paragraph of chapter III, before proceeding to a discussion of how morality might evolve, Darwin makes an important distinction: "It may be well first to premise that I do not wish to maintain that any strictly social animal, if its intellectual faculties were to become as active and as highly developed as in man, would acquire exactly the same moral sense as ours . . . [T]hey might have a sense of right and wrong, though led by it to follow widely different lines of conduct" (ref. 1, p. 70). According to Darwin, having a moral sense does not by itself determine what the moral norms would be: which sorts of actions might be sanctioned and which ones would be condemned.

Darwin's distinction between the moral sense or conscience on the one hand, and the moral norms that guide the moral sense or conscience on the other, is fundamental. It is a distinction I will now elaborate. Much of the post-Darwin historical controversy, particularly between scientists and philosophers, as to whether the moral sense is or is not biologically determined has arisen owing to a failure to make that distinction. Scientists often affirm that morality is a human biological attribute because they are thinking of the predisposition to make moral judgments: that is, to judge some actions as good and others as evil. Some philosophers argue that morality is not biologically determined but rather comes from cultural traditions or from religious beliefs, because they are thinking about moral codes, the sets of norms that determine which actions are judged to be good and which are evil. They point out that moral codes vary from culture to culture and therefore are not biologically predetermined.

Moral Judgment vs. Moral Norms

The question of whether ethical behavior is biologically determined may, indeed, refer to either one of the following two issues. First, is the capacity for ethics—the proclivity to judge human actions as either right or wrong—determined by the biological nature of human beings? Second, are the systems or codes of ethical norms accepted by human beings biologically determined? A similar distinction can be made with respect to language. The question of whether the capacity for symbolic creative language is determined by our biological nature is different from the question of whether the particular language we speak—English, Spanish, Chinese, etc.—is biologically determined, which in the case of language obviously it is not.

I propose that the moral evaluation of actions emerges from human rationality or, in Darwin's terms, from our highly developed intellectual powers. Our high intelligence allows us to anticipate the consequences of our actions with respect to other people and, thus, to judge them as good or evil in terms of their consequences for others. But I will argue that the norms according to which we decide which actions are good and which actions are evil are largely culturally determined, although conditioned by biological predispositions, such as parental care to give an obvious example.

Moral Behavior as Rational Behavior

The moral sense refers first and foremost to our predisposition to evaluate some actions as virtuous, or morally good, and others as evil, or morally bad. Morality, thus, consists of the urge or predisposition to judge human actions as either right or wrong in terms of their consequences for other human beings. In this sense, humans are moral beings by nature because their biological constitution determines the presence in them of the three necessary conditions for ethical behavior. These conditions are (i) the ability to anticipate the consequences of one's own actions; (ii) the ability to make value judgments; and (iii) the ability to choose between alternative courses of action. These abilities exist as a consequence of the eminent intellectual capacity of human beings.

The ability to anticipate the consequences of one's own actions is the most fundamental of the three conditions required for ethical behavior. Only if I can anticipate that pulling the trigger will shoot the bullet, which in turn will strike and kill my enemy, can the action of pulling the trigger be evaluated as nefarious. Pulling a trigger is not in itself a moral action; it becomes so by virtue of its relevant consequences. My action has an ethical dimension only if I do anticipate these consequences.

The ability to anticipate the consequences of one's actions is closely related to the ability to establish the connection between means and ends; that is, of seeing a means precisely as a means, as something that serves a particular end or purpose. This ability to establish the connection between means and their ends requires the ability to anticipate the future and to form mental images of realities not present or not yet in existence.

The ability to establish the connection between means and ends happens to be the fundamental intellectual capacity that has made possible the development of human culture and technology. An evolutionary scenario, seemingly the best hypothesis available, proposes that the remote evolutionary roots of this capacity to connect means with ends may be found in the evolution of bipedalism, which transformed the anterior limbs of our ancestors from organs of locomotion into organs of manipulation. The hands thereby gradually became organs adept for the construction and use of objects for hunting and other activities that improved survival and reproduction; that is, which increased the reproductive fitness of their carriers. The construction of tools depends not only on manual dexterity, but on perceiving them precisely as tools, as objects that help to perform certain actions; that is, as means that serve certain ends or purposes: a knife for cutting, an arrow for hunting, an animal skin for protecting the body from the cold. According to this evolutionary scenario, natural selection promoted the intellectual capacity of our bipedal ancestors because increased intelligence facilitated the perception of tools as tools, and therefore their construction and use, with the ensuing improvement of biological survival and reproduction.

The development of the intellectual abilities of our ancestors took place over several million years, gradually increasing the ability to connect means with their ends and, hence, the possibility of making ever-more complex tools serving more diverse and remote purposes. According to the hypothesis, the ability to anticipate the future, essential for ethical behavior, is therefore closely associated with the development of the ability to con-

struct tools, an ability that has produced the advanced technologies of modern societies and that is largely responsible for the success of humans as a biological species.

The second condition for the existence of ethical behavior is the ability to advance value judgments, to perceive certain objects or deeds as more desirable than others. Only if I can see the death of my enemy as preferable to his survival (or vice versa) can the action leading to his demise be thought of as moral. If the consequences of alternative actions are neutral with respect to value, an action cannot be characterized as ethical. Values are of many sorts: not only ethical but also aesthetic, economic, gastronomic, political, and so on. But in all cases, the ability to make value judgments depends on the capacity for abstraction; that is, on the capacity to perceive actions or objects as members of general classes. This makes it possible to compare objects or actions with one another and to perceive some as more desirable than others. The capacity for abstraction requires an advanced intelligence such as it exists in humans and apparently in them alone.

I will note at this point that the model that I am advancing here does not necessarily imply the ethical theory known as utilitarianism (or, more generally, consequentialism). According to the so-called “act consequentialism” the rightness of an action is determined by the value of its consequences, so that the morally best action in a particular situation is the one, the consequences of which would have the most benefit to others. I am proposing that the morality of an action depends on our ability (*i*) to anticipate the consequences of our actions, and (*ii*) to make value judgments. But I am not asserting that the morality of actions is exclusively measured in terms of how beneficial their consequences will be to others.

The third condition necessary for ethical behavior is the ability to choose between alternative courses of actions. Pulling the trigger can be a moral action only if you have the option not to pull it. A necessary action beyond conscious control is not a moral action: the circulation of the blood and the process of food digestion are not moral actions. Whether there is free will is a question much discussed by philosophers, and the arguments are long and involved (e.g., refs. 15–18). Here, I will advance two considerations that are common-sense evidence of the existence of free will. One is personal experience, which indicates that the possibility to choose between alternatives is genuine rather than only apparent. The second consideration is that when we confront a given situation that requires action on our part, we are able mentally to explore alternative courses of action, thereby extending the field within which we can exercise our free will. In any case, if there were no free will, there would be no ethical behavior; morality would only be an illusion. A point to be made, however, is that free will is dependent on the existence of a well-developed intelligence, which makes it possible to explore alternative courses of action and to choose one or another in view of the anticipated consequences (Fig. 4).

Adaptation vs. Exaptation

I will now consider explicitly two issues that are largely implicit in the previous section. The moral sense, as I have proposed, emerges as a necessary implication of our high intellectual powers, which allow us to anticipate the consequences of our actions, to evaluate such consequences, and to choose accordingly how to act. But is it the case that the moral sense may have been promoted by natural selection in itself and not only indirectly as a necessary consequence of our exalted intelligence? The question in evolutionary terms is whether the moral sense is an adaptation or, rather, an exaptation. Evolutionary biologists define exaptations as features of organisms that evolved because they served some function but are later co-opted to serve an additional or different function, which was not originally the target of natural selection. The new function may replace the

older function or coexist together with it. Feathers seem to have evolved first for conserving temperature, but were later co-opted in birds for flying. The beating of the human heart is an exaptation used by doctors to diagnose the state of health, although this is not why it evolved in our ancestors. The issue at hand is whether moral behavior was directly promoted by natural selection or rather it is simply a consequence of our exalted intelligence, which was the target of natural selection (because it made possible the construction of better tools). Art, literature, religion, and many human cultural activities might also be seen as exaptations that came about as consequences of the evolution of high intelligence.

The second issue is whether some animals, apes or other nonhuman primates, for example, may have a moral sense, however incipient, either as directly promoted by natural selection or as a consequence of their own intelligence.

The position that I will argue here is that the human moral sense is an exaptation, not an adaptation. The moral sense consists of *judging* certain actions as either right or wrong, not of choosing and carrying out some actions rather than others. It seems unlikely that making moral judgments would promote the reproductive fitness of those judging an action as good or evil; *acting* in one way or another might be of consequence in promoting fitness, but passing *judgment* by itself would seem unlikely to increase or decrease adaptive fitness. Nor does it seem likely that there might be some form of “incipient” ethical behavior that would then be further promoted by natural selection. The three necessary conditions for there being ethical behavior are manifestations of advanced intellectual abilities.

It, indeed, rather seems that the target of natural selection was the development, which happened mostly through the Pleistocene, of advanced intellectual capacities. This was favored by natural selection because the construction and use of tools, made possible by advanced intelligence, improved the strategic position of our biped ancestors. In the account I am advancing here, once bipedalism evolved and after tool-using and tool-making became practiced, those individuals more effective in these functions had a greater probability of biological success. The biological advantage provided by the design and use of tools persisted long enough so that intellectual abilities continued to increase, eventually yielding the eminent development of intelligence that is characteristic of *H. sapiens*.

A related question is whether morality would benefit a social group within which it is practiced and, indirectly, would also benefit individuals who are members of the group. This seems likely to be the case, if indeed moral judgment would influence individuals to behave in ways that increase cooperation, or benefit the welfare of the social group in some way; for example, by reducing crime or protecting private property. That is, the moral sense that had evolved as an exaptation associated with high intelligence could eventually become an adaptation, by favoring beneficial behaviors.

Group Selection in Human Populations

I have asserted that patterns of actions beneficial to the tribe or social group might, in humans, be favored by natural selection. This brings up the issue known as “group selection.” Evolutionists generally contend that group selection based on altruistic behavior is not an evolutionarily stable strategy. Altruistic behavior within an animal population would benefit the population itself, so that a population consisting of altruists would do better than a population consisting of selfish individuals. This would be group selection: the population as a whole benefits from the behavior of its individuals. But this state of affairs is not evolutionarily stable in an animal population. The reason is that mutations that favor selfish over altruistic behavior will be favored by natural selection, because the behavior of an altruistic individual implies a cost. The altruistic individual as well as the

rest of the population will benefit from the behavior of the altruist. A selfish individual also benefits from the behavior of the altruist, but the selfish individual does not incur the cost implied by the altruistic behavior. Thus, selfish behavior will be favored within the population. Natural selection will thus eliminate genetically determined altruistic behaviors.

Of course, it is admitted that it might be the case that populations with a preponderance of altruistic alleles would survive and spread better than populations consisting of selfish alleles. This would be group selection. But typically there are many more individual organisms than there are populations; and individuals are born, procreate, and die at rates much higher than populations. Thus, the rate of multiplication of selfish individuals over altruists in a given population is likely to be much higher than the rate at which altruistic populations multiply relative to predominantly selfish populations.

There is, however, an important difference between animals and humans that is relevant in this respect. Namely, the fitness advantage of selfish over altruistic behavior does not necessarily apply to humans, because humans can *understand* the benefits of altruistic behavior (it benefits the group but indirectly it benefits them as well) and thus adopt altruism and protect it, by laws or otherwise, against selfish behavior that harms the social group. As Darwin wrote in *The Descent of Man*: “It must not be forgotten that, although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another” (ref. 1, chap. V, p. 159).

The theory of sociobiology advances a ready answer to the second question raised above, whether morality occurs in other animals, even if only as a rudiment. The theory of kin selection, they argue, explains altruistic behavior, to the extent that it exists in other animals as well as in humans. I will propose, however, that moral behavior does not exist, even incipiently, in non-human animals. The reason is that the three conditions required for ethical behavior depend on an advanced intelligence—which includes the capacities for free will, abstract thought, and anticipation of the future—such as it exists in *H. sapiens* and not in any other living species. It is the case that certain animals exhibit behaviors analogous with those resulting from ethical actions in humans, such as the loyalty of dogs or the appearance of compunction when they are punished. But such behaviors are either genetically determined or elicited by training (conditioned responses). Genetic determination and not moral evaluation is also what is involved in the altruistic behavior of social insects and other animals. Biological altruism (altruism_b) and moral altruism (altruism_m) have disparate causes: kin selection in altruism_b, regard for others in altruism_m.

Mind to Morality

The capacity for ethics is an outcome of gradual evolution, but it is an attribute that only exists when the underlying attributes (i.e., the intellectual capacities) reach an advanced degree. The necessary conditions for ethical behavior only come about after the crossing of an evolutionary threshold. The approach is gradual, but the conditions only appear when a degree of intelligence is reached such that the formation of abstract concepts and the anticipation of the future are possible, even though we may not be able to determine when the threshold was crossed. Thresholds occur in other evolutionary developments—for example, in the origins of life, multicellularity, and sexual reproduction—as well as in the evolution of abstract thinking and self-awareness. Thresholds occur in the physical world as well; for example, water heats gradually, but at 100 °C boiling begins and the transition from liquid to gas starts suddenly. Surely, human intellectual capacities came about by gradual evolution.

Yet, when looking at the world of life as it exists today, it would seem that there is a radical breach between human intelligence and that of other animals. The rudimentary cultures that exist in chimpanzees (19, 20) do not imply advanced intelligence as it is required for moral behavior.

A different explanation of the evolution of the moral sense has been advanced by proponents of the theory of “gene–culture coevolution” (5, 21–24). It is assumed that cultural variation among tribes in patriotism, fidelity, sympathy, and other moralizing behaviors may have occurred incipiently in early hominid populations, starting at least with *H. habilis*. This cultural variation may have, in turn, selected for genes that endowed early humans with primitive moral emotions. Primitive moral emotions would in turn have facilitated the evolution of more advanced cultural codes of morality. Repeated rounds of gene–cultural coevolution would have gradually increased both the moral sense itself and the systems of moral norms. That is, the evolution of morality would have been directly promoted by natural selection in a process whereby the moral sense and the moral norms would have coevolved.

The gene–culture coevolution account of the evolution of morality is, of course, radically different from the theory I am advancing here, in which moral behavior evolved not because it increased fitness but as a consequence of advanced intelligence, which allowed humans to see the benefits that adherence to moral norms bring to society and to its members. The extreme variation in moral codes among recent human populations and the rapid evolution of moral norms over short time spans would seem to favor the explanation I am proposing. Gene–culture coevolution would rather lead to a more nearly universal system of morality, which would have come about gradually as our hominid ancestors gradually evolved toward becoming *H. sapiens*.

Empathy, or the predisposition to mentally assimilate the feelings of other individuals, has recently been extensively discussed in the context of altruistic or moral behavior. Incipient forms of empathy seem to be present in other animals. In humans, increasing evidence indicates that we automatically simulate the experiences of other humans (ref. 25, chap. 5, pp. 158–199). Empathy is a common human phenomenon, surely associated with our advanced intelligence, which allows us to understand the harms or benefits that impact other humans, as well as their associated feelings. Empathic humans may consequently choose to behave according to how their behavior will impact those for whom we feel empathy. That is, human empathy occurs because of our advanced intelligence. Humans may then choose to behave altruistically, or not, that is morally, or not, in terms of the anticipated consequences of their actions to others.

The question remains, when did morality emerge in the human lineage? Did *H. habilis* or *H. erectus* have morality? What about the Neandertals, *Homo neanderthalensis*? When in hominid evolution morality emerged is difficult to determine. It may very well be that the advanced degree of rationality required for moral behavior may only have been reached at the time when creative language came about, and perhaps in dependence with the development of creative language. When creative language may have come about in human evolution is discussed in ref. 3.

Moral Codes

I have distinguished between moral behavior—judging some actions as good, others as evil—and moral codes—the precepts or norms according to which actions are judged. Moral behavior, I have proposed, is a biological attribute of *H. sapiens*, because it is a necessary consequence of our biological makeup, namely our high intelligence. But moral codes, I argue, are not products of biological evolution but rather of cultural evolution.

It must, first, be stated that moral codes, like any other cultural systems, cannot survive for long if they prevalently run in outright conflict with our biology. The norms of morality must be by

and large consistent with human biological nature, because ethics can only exist in human individuals and in human societies. One might therefore also expect, and it is the case, that accepted norms of morality will often, or at least occasionally, promote behaviors that increase the biological fitness of those who behave according to them, such as child care. But the correlation between moral norms and biological fitness is neither necessary nor indeed always the case: some moral precepts common in human societies have little or nothing to do with biological fitness, and some moral precepts are contrary to fitness interest.

How do moral codes come about? The short answer is, as already stated, that moral codes are products of cultural evolution, a distinctive human mode of evolution that has surpassed the biological mode, because it is a more effective form of adaptation: it is faster than biological evolution and it can be directed. Cultural evolution is based on cultural heredity, which is Lamarckian, rather than Mendelian, so that acquired characteristics are transmitted. Most important, cultural heredity does not depend on biological inheritance, from parents to children, but is transmitted also horizontally and without biological bounds. A cultural mutation, an invention (think of the laptop computer, the cell phone, or rock music) can be extended to millions and millions of individuals in less than one generation.

In chapter V of *The Descent of Man*, entitled, “On the Development of the Intellectual and Moral Faculties during Primal and Civilized Times,” Darwin writes: “There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase” (ref. 1, pp. 159–160).

Darwin is making two important assertions. First, that morality may contribute to the success of some tribes over others, which is natural selection in the form of group selection. Second, Darwin is asserting a position of moral optimism, namely that the standards of morality will tend to improve over human history precisely on grounds of group selection, because the higher the moral standards of a tribe, the more likely the success of the tribe. This assertion depends on which standards are thought to be “higher” than others. If the higher standards are defined by their contribution to the success of the tribe, then the assertion is circular. But Darwin asserts that there are some particular standards that, in his view, would contribute to tribal success: patriotism, fidelity, obedience, courage, and sympathy.

Moral Norms and Natural Selection

Parental care is a behavior generally favored by natural selection that may be present in virtually all codes of morality, from primitive to more advanced societies. There are other human behaviors sanctioned by moral norms that have biological correlates favored by natural selection. One example is monogamy, which occurs in some animal species but not in many others. It is also sanctioned in many human cultures, but surely not in all. Polygamy is sanctioned in some current human cultures and was more so in the past. Food sharing outside the mother–offspring unit rarely occurs in primates, with the exception of chimpanzees—and, apparently, in capuchin monkeys (26, 27)—although even in chimpanzees food sharing is highly selective and often associated with reciprocity. A more common form of mutual aid among primates is coalition formation; alliances are formed in fighting other conspecifics, although these alliances are labile, with partners readily changing partners.

One interesting behavior, associated with a sense of justice, or equal pay for equal work, has been described by Sarah Brosnan and Frans de Waal (26, 27) in the brown capuchin monkey, *Cebus paella*. Monkeys responded negatively to unequal rewards in exchanges with a human experimenter. Monkeys refused to participate in an exchange when they witnessed that a conspecific had obtained a more attractive reward for equal effort. Is the capuchin behavior phylogenetically related to the human virtue of justice? This seems unlikely, because similar behavioral patterns have not been observed in other primates, including apes, phylogenetically closer to humans. Cannibalism is practiced by chimps, as well as by human cultures of the past. Do we have a phylogenetically acquired predisposition to cannibalism as a morally acceptable behavior? This seems unlikely.

The interpretation of the capuchin monkeys’ behavior as an incipient sense of justice (26) has been challenged by other investigators. Silberberg and collaborators (28) have shown that the capuchins rejected a reward whenever a more desirable reward was visible to them, not just whenever the more desirable reward was offered to other individuals.

Schiff and de Waal (29) observed also that chimpanzees rejected a reward when they observed another chimpanzee obtaining a more attractive reward for equal exchange with the human experimenter, although the tolerance for inequity increased with the social closeness among the chimpanzees. However, this interpretation of inequality rejection has also been challenged in the case of the chimpanzees. The chimpanzees’ rejection may be attributed to a breach in their expectations, rather than to a sense of equality (30, 31).

Moral codes arise in human societies by cultural evolution. Those moral codes tend to be widespread that lead to successful societies. Since time immemorial, human societies have experimented with moral systems. Some have succeeded and spread widely throughout humankind, like the Ten Commandments, although other moral systems persist in different human societies. Many moral systems of the past have surely become extinct because they were replaced or because the societies that held them became extinct. The moral systems that currently exist in humankind are those that have been favored by cultural evolution. They were propagated within particular societies for reasons that might be difficult to fathom but that surely must have included the perception by individuals that a particular moral system was beneficial for them, at least to the extent that it was beneficial for their society by promoting social stability and success (25, 32). Cultures, of course, do not evolve as completely differentiated units. Rather, cultures often incorporate elements from other cultures. “Far from being self-preserving monoliths, cultures are porous and constantly in flux. Language . . . is a clear example” (ref. 4, p. 66).

The norms of morality, as they exist in any particular culture, are felt to be universal within that culture. Yet, similarly as other elements of culture, they are continuously evolving, often within a single generation. As Steven Pinker has pointed out, western societies have recently experienced the moralization and amoralization of diverse behaviors. Thus, “smoking has become moralized . . . now treated as immoral . . . At the same time many behaviors have become amoralized, switched from moral failings to lifestyle choices. They include divorce, illegitimacy, working mothers, marijuana use and homosexuality” (ref. 2, p. 34). Acceptance by individuals or groups of particular sets of moral norms is often reinforced by civil authority (e.g., those who kill or commit adultery will be punished) and by religious beliefs (God is watching, and you’ll go to hell if you misbehave). But it is worth noticing that the legal and political systems that govern human societies, as well as the belief systems held by religion, are themselves outcomes of cultural evolution, as it has eventuated over human history, particularly over the last few millennia (33).

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