MICHAEL RUSE and EDWARD O. WILSON

(1) For much of this century, moral philosophy has been constrained by the supposed absolute gap between *is* and *ought*, and the consequent belief that the facts of life cannot of themselves yield an ethical blueprint for future action. For this reason, ethics has sustained an eerie existence largely apart from science. Its most respected interpreters still believe that reasoning about right and wrong can be successful without a knowledge of the brain, the human organ where all the decisions about right and wrong are made. Ethical premises are typically treated in the manner of mathematical propositions: directives supposedly independent of human evolution, with a claim to ideal, eternal truth.

While many substantial gains have been made in our understanding of the nature of moral thought and action, insufficient use has been made of knowledge of the brain and its evolution. Beliefs in extrasomatic moral truths and in an absolute is/ought barrier are wrong. Moral premises relate only to our physical nature and are the result of an idiosyncratic genetic history—a history which is nevertheless powerful and general enough within the human species to form working codes. The time has come to turn moral philosophy into an applied science because, as the geneticist Hermann J. Muller urged in 1959, 100 years without Darwin are enough.¹

(2) The naturalistic approach to ethics, dating back through Darwin to earlier pre-evolutionary thinkers, has gained strength with each new advance in biology and the brain sciences. Its contemporary version can be expressed as follows:

Everything human, including the mind and culture, has a material base and originated during the evolution of the human genetic constitution and its interaction with the environment. To say this much is not to deny the great creative power of culture, or to minimize the fact that most causes of human thought and behaviour are still poorly understood. The important point is that modern biology can account for many of the unique properties of the species. Research on the subject is accelerating, quickly enough to lend plausibility to the belief that the

¹ H. J. Muller is quoted by G. G. Simpson in *This View of Life* (New York: Harcourt, Brace & World, 1964), 36.

Philosophy 61 1986

human condition can eventually be understood to its foundations, including the sources of moral reasoning.

This accumulating empirical knowledge has profound consequences for moral philosophy. It renders increasingly less tenable the hypothesis that ethical truths are extrasomatic, in other words divinely placed within the brain or else outside the brain awaiting revelation. Of equal importance, there is no evidence to support the view—and a great deal to contravene it—that premises can be identified as global optima favouring the survival of any civilized species, in whatever form or on whatever planet it might appear. Hence external goals are unlikely to be articulated in this more pragmatic sense.

Yet biology shows that internal moral premises do exist and can be defined more precisely. They are immanent in the unique programmes of the brain that originated during evolution. Human mental development has proved to be far richer and more structured and idiosyncratic than previously suspected. The constraints on this development are the sources of our strongest feelings of right and wrong, and they are powerful enough to serve as a foundation for ethical codes. But the articulation of enduring codes will depend upon a more detailed knowledge of the mind and human evolution than we now possess. We suggest that it will prove possible to proceed from a knowledge of the material basis of moral feeling to generally accepted rules of conduct. To do so will be to escape—not a minute too soon—from the debilitating absolute distinction between *is* and *ought*.

(3) All populations of organisms evolve through a law-bound causal process, as first described by Charles Darwin in his Origin of Species. The modern explanation of this process, known as natural selection, can be briefly summarized as follows. The members of each population vary hereditarily in virtually all traits of anatomy, physiology, and behaviour. Individuals possessing certain combinations of traits survive and reproduce better than those with other combinations. As a consequence, the units that specify physical traits—genes and chromosomes—increase in relative frequency within such populations, from one generation to the next.

This change in different traits, which occurs at the level of the entire population, is the essential process of evolution. Although the agents of natural selection act directly on the outward traits and only rarely on the underlying genes and chromosomes, the shifts they cause in the latter have the most important lasting effects. New variation across each population arises through changes in the chemistry of the genes and their relative positions on the chromosomes. Nevertheless, these changes (broadly referred to as mutations) provide only the raw material of evolution. Natural selection, composed of the sum of differential survival and reproduction, for the most part determines the rate and direction of evolution.²

Although natural selection implies competition in an abstract sense between different forms of genes occupying the same chromosome positions or between different gene arrangements, pure competition, sometimes caricatured as 'nature red in tooth and claw', is but one of several means by which natural selection can operate on the outer traits. In fact, a few species are known whose members do not compete among themselves at all. Depending on circumstances, survival and reproduction can be promoted equally well through the avoidance of predators, more efficient breeding, and improved co-operation with others.³

In recent years there have been several much-publicized controversies over the pace of evolution and the universal occurrence of adaptation.⁴ These uncertainties should not obscure the key facts about organic evolution: that it occurs as a universal process among all kinds of organisms thus far carefully examined, that the dominant driving force is natural selection, and that the observed major patterns of

² See the following widely used textbooks: J. Roughgarden, Theory of Population Genetics and Evolutionary Ecology: An Introduction (New York: Macmillan, 1979); D. L. Hartl, Principles of Population Genetics (Sunderland, Mass.: Sinauer Associates, 1980); R. M. May (ed.), Theoretical Ecology: Principles and Applications, 2nd edn (Sunderland, Mass.: Sinauer Associates, 1981); J. R. Krebs and N. B. Davies (eds), Behavioural Ecology: An Evolutionary Approach, 2nd edn (Sunderland, Mass.: Sinauer Associates, 1984).

³ Reviews of the various modes of selection, including forms that direct individuals away from competitive behaviour, can be found in E. O. Wilson, *Sociobiology: The New Synthesis* (Cambridge, Mass.: Belknap Press of Harvard University Press, 1975); G. F. Oster and E. O. Wilson, *Caste and Ecology in the Social Insects* (Princeton University Press, 1978); S. A. Boorman and P. R. Levitt, *The Genetics of Altruism* (New York: Academic Press, 1980); D. S. Wilson, *The Natural Selection of Populations and Communities* (Menlo Park, Calif.: Benjamin/Cummings, 1980).

⁴ For example, the debate over 'punctuated equilibrium' versus 'gradualism' among palaeontologists and geneticists. For most biologists, the issue is not the mechanism of evolution but the conditions under which evolution sometimes proceeds rapidly and sometimes slows to a crawl. There is no difficulty in explaining the variation in rates. On the contrary, there is a surplus of plausible explanations, virtually all consistent with Neo-Darwinian theory, but insufficient data to choose among them. See, for example, S. J. Gould and N. Eldredge, 'Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered', *Paleobiology* **3** (1977), 115–151; and J. R. G. Turner, '"The hypothesis that explains mimetic resemblance explains evolution": the gradualist-saltationist schism', in M. Grene (ed.), *Dimensions of Darwinism* (Cambridge University Press, 1983), 129–169.

change are consistent with the known principles of molecular biology and genetics. Such is the view held by the vast majority of the biologists who actually work on heredity and evolution.⁵ To say that not all the facts have been explained, to point out that forces and patterns may yet be found that are inconsistent with the central theory—healthy doubts present in any scientific discipline—is by no means to call into question the prevailing explanation of evolution. Only a demonstration of fundamental inconsistency can accomplish that much, and nothing short of a rival explanation can bring the existing theory into full disarray.

There are no such crises. Even Motoo Kimura, the principal architect of the 'neutralist' theory of genetic diversity—which proposes that most evolution at the molecular level happens through random factors—allows that 'classical evolution theory has demonstrated beyond any doubt that the basic mechanism for adaptive evolution is natural selection acting on variations produced by changes in chromosomes and genes. Such considerations as population size and structure, availability of ecological opportunities, change of environment, lifecycle "strategies", interaction with other species, and in some situations kin or possibly group selection play a large role in our understanding of the process."⁶

(4) Human evolution appears to conform entirely to the modern synthesis of evolutionary theory as just stated. We know now that human ancestors broke from a common line with the great apes as recently as six or seven million years ago, and that at the biochemical level we are today closer relatives of the chimpanzees than the chimpanzees are of gorillas.⁷ Furthermore, all that we know about human fossil history, as well as variation in genes and chromosomes among individuals and the key events in the embryonic assembly of the nervous system, is consistent with the prevailing view that natural selection has served as the principal agent in the origin of humanity.

It is true that until recently information on the brain and human evolution was sparse. But knowledge is accelerating, at least as swiftly as the remainder of natural science, about a doubling every ten to fifteen years. Several key developments, made principally during the past twenty years, will prove important to our overall argument for a naturalistic ethic developed as an applied science.

⁵ See footnote 2.

⁶ M. Kimura, *The Neutral Theory of Molecular Evolution* (Cambridge University Press, 1983).

⁷ C. G. Sibley and J. E. Ahlquist, 'The Phylogeny of the Hominoid Primates, as Indicated by DNA-DNA Hybridization', *Journal of Molecular Evolution* **20** (1984), 2–15.

The number of human genes identified by biochemical assay or pedigree analysis is at the time of writing 3,577, with approximately 600 placed to one or the other of the twenty-three pairs of chromosomes.⁸ Because the rate at which this number has been accelerating (up from 1,200 in 1977), most of the entire complement of 100,000 or so structural genes may be characterized to some degree within three or four decades.

Hundreds of the known genes affect behaviour. The great majority do so simply by their effect on general processes of tissue development and metabolism, but a few have been implicated in more focused behavioural traits. For example, a single allele (a variant of one gene), prescribes the rare Lesch–Nyhan syndrome, in which people curse uncontrollably, strike out at others with no provocation, and tear at their own lips and fingers. Another allele at a different chromosome position reduces the ability to perform on certain standard spatial tests but not on the majority of such tests.⁹ Still another allele, located tentatively on chromosome 15, induces a specific learning disability.¹⁰

These various alterations are of course strong and deviant enough to be considered pathological. But they are also precisely the kind usually discovered in the early stages of behavioural genetic analysis for any species. *Drosophila* genetics, for example, first passed through a wave of anatomical and physiological studies directed principally at chromosome structure and mechanics. As in present-day human genetics, the first behavioural mutants discovered were broadly acting and conspicuous, in other words those easiest to detect and characterize. When behavioural and biochemical studies grew more sophisticated, the cellular basis of gene action was elucidated in the case of a few behaviours, and the new field of *Drosophila* neurogenetics was born. The hereditary bases of subtle behaviours such as orientation to light and learning were discovered somewhat later.¹¹

We can expect human behavioural genetics to travel along approximately the same course. Although the links between genes and behaviour in human beings are more numerous and the processes involving cognition and decision making far more complex, the whole is

⁸ We are grateful to Victor A. McKusick for providing the counts of identified and inferred human genes up to 1984.

⁹ G. C. Ashton, J. J. Polovina and S. G. Vandenberg, 'Segregation Analysis of Family Data for 15 Tests of Cognitive Ability', *Behaviour Genetics* **9** (1979), 329–347.

¹⁰ S. D. Smith, W. J. Kimberling, B. F. Pennington and H. A. Lubs, 'Specific Reading Disability: Identification of an Inherited Form through Linkage Analysis', *Science* **219** (1982), 1345–1347.

¹¹ See J. C. Hall and R. J. Greenspan, 'Genetic Analysis of Drosophila Neurobiology', Annual Review of Genetics 13 (1979), 127–195.

nevertheless conducted by cellular machinery precisely assembled under the direction of the human genome (that is, genes considered collectively as a unit). The techniques of gene identification, applied point by point along each of the twenty-three pairs of chromosomes, is beginning to make genetic dissection of human behaviour a reality.

Yet to speak of genetic dissection, a strongly reductionist procedure, is not to suggest that the whole of any trait is under the control of a single gene, nor does it deny substantial flexibility in the final product. Individual alleles (gene-variants) can of course affect a trait in striking ways. To take a humble example, the possession of a single allele rather than another on a certain point on one of the chromosome pairs causes the development of an attached earlobe as opposed to a pendulous earlobe. However, it is equally true that a great many alleles at different chromosome positions must work together to assemble the entire earlobe. In parallel fashion, one allele can shift the likelihood that one form of behaviour will develop as opposed to another, but many alleles are required to prescribe the ensemble of nerve cells, neurotransmitters, and muscle fibres that orchestrate the behaviour in the first place. Hence classical genetic analysis cannot by itself explain all of the underpinnings of human behaviour, especially those that involve complex forms of cognition and decision making. For this reason behavioural development viewed as the interaction of genes and environment should also occupy centre stage in the discussion of human behaviour. The most important advances at this level are being made in the still relatively young field of cognitive psychology.¹²

(5) With this background, let us move at once to the central focus of our discussion: morality. Human beings, all human beings, have a sense of right and wrong, good and bad. Often, although not always, this 'moral awareness' is bound up with beliefs about deities, spirits, and other supersensible beings. What is distinctive about moral claims is that they are prescriptive; they lay upon us certain obligations to help and to co-operate with others in various ways. Furthermore, morality is taken to transcend mere personal wishes or desires. 'Killing is wrong' conveys more than merely 'I don't like killing'. For this reason, moral statements are thought to have an objective referent, whether the Will of a Supreme Being or eternal verities perceptible through intuition.

Darwinian biology is often taken as the antithesis of true morality. Something that begins with conflict and ends with personal reproduction seems to have little to do with right and wrong. But to reason along such lines is to ignore a great deal of the content of modern evolutionary biology. A number of causal mechanisms—already well confirmed in

¹² See, for example, the recent analysis by J. R. Anderson, *The Architecture of Cognition* (Cambridge, Mass.: Harvard University Press, 1983).

the animal world—can yield the kind of co-operation associated with moral behaviour. One is so-called 'kin selection'. Genes prescribing co-operation spread through the populations when self-sacrificing acts are directed at relatives, so that they (not the co-operators) are benefited, and the genes they share with the co-operators by common descent are increased in later generations. Another such co-operationcausing mechanism is 'reciprocal altruism'. As its name implies, this involves transactions (which can occur between non-relatives) in which aid given is offset by the expectation of aid received. Such mutual assistance can be extended to a whole group, whose individual members contribute to a general pool and (as needed) draw from the pool.¹³

Sociobiologists (evolutionists concerned with social behaviour) speak of acts mediated by such mechanisms as 'altruistic'. It must be recognized that this is now a technical biological term, and does not necessarily imply conscious free giving and receiving. Nevertheless, the empirical evidence suggests that co-operation between human beings was brought about by the same evolutionary mechanisms as those just cited. To include conscious, reflective beings is to go beyond the biological sense of altruism into the realm of genuine nonmetaphorical altruism. We do not claim that people are either unthinking genetic robots or that they co-operate only when the expected genetic returns can be calculated in advance. Rather, human beings function better if they are deceived by their genes into thinking that there is a disinterested objective morality binding upon them, which all should obey. We help others because it is 'right' to help them and because we know that they are inwardly compelled to reciprocate in equal measure. What Darwinian evolutionary theory shows is that this sense of 'right' and the corresponding sense of 'wrong', feelings we take to be above individual desire and in some fashion outside biology, are in fact brought about by ultimately biological processes.

Such are the empirical claims. How exactly is biology supposed to exert its will on conscious, free beings? At one extreme, it is possible to conceive of a moral code produced entirely by the accidents of history. Cognition and moral sensitivity might evolve somewhere in some imaginary species in a wholly unbiased manner, creating the organic equivalent of an all-purpose computer. In such a blank-slate species, moral rules were contrived some time in the past, and the exact historical origin might now be lost in the mists of time. If proto-humans evolved in this manner, individuals that thought up and followed rules ensuring an ideal level of co-operation then survived and reproduced, and all others fell by the wayside.

However, before we consider the evidence, it is important to realize

¹³ See footnote 3.

8

that any such even-handed device must also be completely gene-based and tightly controlled, because an exact genetic prescription is needed to produce perfect openness to any moral rule, whether successful or not. The human thinking organ must be indifferently open to a belief such as 'killing is wrong' or 'killing is right', as well as to any consequences arising from conformity or deviation. Both a very specialized prescription and an elaborate cellular machinery are needed to achieve this remarkable result. In fact, the blank-slate brain might require a cranial space many times that actually possessed by human beings. Even then a slight deviation in the many feedback loops and hierarchical controls would shift cognition and preference back into a biased state. In short, there appears to be no escape from the biological foundation of mind.

It can be stated with equal confidence that nothing like all-purpose cognition occurred during human evolution. The evidence from both genetic and cognitive studies demonstrates decisively that the human brain is not a *tabula rasa*. Conversely, neither is the brain (and the consequent ability to think) genetically determined in the strict sense. No genotype is known that dictates a single behaviour, precluding reflection and the capacity to choose from among alternative behaviours belonging to the same category. The human brain is something in-between: a swift and directed learner that picks up certain bits of information quickly and easily, steers around others, and leans toward a surprisingly few choices out of the vast array that can be imagined.

This quality can be made more explicit by saying that human thinking is under the influence of 'epigenetic rules', genetically based processes of development that predispose the individual to adopt one or a few forms of behaviours as opposed to others. The rules are rooted in the physiological processes leading from the genes to thought and action.¹⁴ The empirical heart of our discussion is that we think morally because we are subject to appropriate epigenetic rules. These predispose us to think that certain courses of action are right and certain courses of action are wrong. The rules certainly do not lock people blindly into certain behaviours. But because they give the illusion of objectivity to morality, they lift us above immediate wants to actions which (unknown to us) ultimately serve our genetic best interests.

The full sequence in the origin of morality is therefore evidently the following: ensembles of genes have evolved through mutation and

¹⁴ The evidence for biased epigenetic rules of mental development is summarized in C. J. Lumsden and E. O. Wilson, *Genes, Mind, and Culture* (Cambridge, Mass.: Harvard University Press, 1981) and *Promethean Fire: Reflections on the Origin of Mind* (Cambridge, Mass.: Harvard University Press, 1983).

selection within an intensely social existence over tens of thousands of years; they prescribe epigenetic rules of mental development peculiar to the human species; under the influence of the rules certain choices are made from among those conceivable and available to the culture; and finally the choices are narrowed and hardened through contractual agreements and sanctification.

In a phrase, societies feel their way across the fields of culture with a rough biological map. Enduring codes are not created whole from absolute premises but inductively, in the manner of common law, with the aid of repeated experience, by emotion and consensus, through an expansion of knowledge and experience guided by the epigenetic rules of mental development, during which people sift the options and come to agree upon and to legitimate certain norms and directions.¹⁵

(6) Only recently have the epigenetic rules of mental development and their adaptive roles become accepted research topics for evolutionary biology. It should therefore not be surprising that to date the best understood examples of epigenetic rules are of little immediate concern to moral philosophers. Yet what such examples achieve is to draw us from the realm of speculative philosophy into the centre of ongoing scientific research. They provide the stepping stones to a more empirical basis of moral reasoning.

One of the most fully explored epigenetic rules concerns the constraint on colour vision that affects the cultural evolution of colour vocabularies. People see variation in the *intensity* of light (as opposed to colour) the way one might intuitively expect to see it. That is, if the level of illumination is raised gradually, from dark to brightly lit, the transition is perceived as gradual. But if the *wavelength* is changed gradually, from a monochromatic purple all across the visible spectrum to a monochromatic red, the shift is not perceived as a continuum. Rather, the full range is thought to comprise four basic colours (blue, green, yellow, red), each persisting across a broad band of wavelengths and giving way through ambiguous intermediate colour through narrow bands on either side. The physiological basis of this beautiful deception is partly known. There are three kinds of cones in the retina and four kinds of cells in the lateral geniculate nuclei of the visual

¹⁵ A new discipline of decision-making is being developed in cognitive psychology based upon the natural means—one can correctly say the epigenetic rules—by which people choose among alternatives and reach agreements. See, for example, A. Tversky and D. Kahneman, 'The Framing of Decisions and the Psychology of Choice', *Science* **211** (1981), 453–458; and R. Axelrod, *The Evolution of Cooperation* (New York: Basic Books, 1984).

pathways leading to the optical cortex. Although probably not wholly responsible, both sets of cells play a role in the coding of wavelength so that it is perceived in a discrete rather than continuous form. Also, some of the genetic basis of the cellular structure is known. Colourblindness alleles on two positions in the X-chromosome cause particular deviations in wavelength perception.

The following experiment demonstrated the effect of this biological constraint on the formation of colour vocabularies. The native speakers of twenty languages from around the world were asked to place their colour terms in a standard chart that displays the full visible colour spectrum across varying shades of brightness. Despite the independent origins of many of the languages, which included Arabic, Ibidio, Thai, and Tzeltal, the terms placed together fall into four distinct clusters corresponding to the basic colours. Very few were located in the ambiguous intermediate zones.

A second experiment then revealed the force of the epigenetic rule governing this cultural convergence. Prior to European contact the Dani people of New Guinea possessed a very small colour vocabulary. One group of volunteers was taught a newly invented Dani-like set of colour terms placed variously on the four principal hue categories (blue, green, yellow, red). A second group was taught a similar vocabulary placed off centre, away from the main clusters formed by other languages. The first group of volunteers, those given the 'natural' vocabulary, learned about twice as quickly as those given the off-centre, less natural terms. Dani volunteers also selected these terms more readily when allowed to make a choice between the two sets.¹⁶

So far as we have been able to determine, all categories of cognition and behaviour investigated to the present time show developmental biases. More precisely, whenever development has been investigated with reference to choice under conditions as free as possible of purely experimental influence, subjects automatically favoured certain choices over others. Some of these epigenetic biases are moderate to very strong, as in the case of colour vocabulary. Others are relatively weak. But all are sufficiently marked to exert a detectable influence on cultural evolution.

Examples of such deep biases included the optimum degree of redundancy in geometric design; facial expressions used to denote the basic emotions of fear, loathing, anger, surprise, and happiness; descending degrees of preference for sucrose, fructose, and other sugars; the particular facial expressions used to respond to various distasteful substances; and various fears, including the fear-of-strangers response

¹⁶ E. Rosch, 'Natural Categories', Cognitive Psychology 4 (1973), 328–350.

in children. One of the most instructive cases is provided by the phobias. These intense reactions are most readily acquired against snakes, spiders, high places, running water, tight enclosures, and other ancient perils of mankind for which epigenetic rules can be expected to evolve through natural selection. In contrast, phobias very rarely appear in response to automobiles, guns, electric sockets, and other truly dangerous objects in modern life, for which the human species has not yet had time to adapt through genetic change.

Epigenetic rules have also been demonstrated in more complicated forms of mental development, including language acquisition, predication in logic, and the way in which objects are ordered and counted during the first steps in mathematical reasoning.¹⁷

We do not wish to exaggerate the current status of this area of cognitive science. The understanding of mental development is still rudimentary in comparison with that of most other aspects of human biology. But enough is known to see the broad outlines of complex processes. Moreover, new techniques are constantly being developed to explore the physical basis of mental activity. For example, arousal can be measured by the degree of alpha wave blockage, allowing comparisons of the impact of different visual designs. Electroencephalograms of an advanced design are used to monitor moment-by-moment activity over the entire surface of the brain. In a wholly different procedure, radioactive isotopes and tomography are combined to locate sites of enhanced metabolic activity. Such probes have revealed the areas of the brain used in specific mental operations, including the recall of melodies, the visualization of notes on a musical staff, and silent reading and counting.¹⁸ There seems to be no theoretical reason why such techniques cannot be improved eventually to address emotions, more complex reasoning, and decision-making. There is similarly no reason why metabolic activity of the brain cannot be mapped in chimpanzees and other animals as they solve problems and initiate action, permitting the comparison of mental activity in human beings with that in lower species.

But what of morality? We have spoken of colour perception, phobias, and other less value-laden forms of cognition. We argue that moral reasoning is likewise moulded and constrained by epigenetic rules. Already biologists and behavioural scientists are moving directly into that area of human experience producing the dictates of right and wrong. Consider the avoidance of brother-sister incest, a negative

¹⁷ The epigenetic rules of cognitive development analysed through the year 1980 are reviewed by C. J. Lumsden and E. O. Wilson, op. cit.

¹⁸ N. A. Lassen, D. H. Ingvar and E. Skinhøj, 'Brain Function and Blood Flow', *Scientific American* 239 (1978), 62–71.

choice made by the great majority of people around the world. By incest in this case is meant full sexual attraction and intercourse, and not merely exploratory play among children. When such rare matings do occur, lowered genetic fitness is the result. The level of homozygosity (a matching of like genes) in the children is much higher, and they suffer a correspondingly greater mortality and frequency of crippling syndromes due to the fact that some of the homozygous pairs of genes are defective. Yet this biological cause and effect is not widely perceived in most societies, especially those with little or no scientific knowledge of heredity. What causes the avoidance instead is a sensitive period between birth and approximately six years. When children this age are exposed to each other under conditions of close proximity (both 'use the same potty', as one anthropologist put it) they are unable to form strong sexual bonds during adolescence or later. The inhibition persists even when the pairs are biologically unrelated and encouraged to marry. Such a circumstance occurred, for example, when children from different families were raised together in Israeli kibbutzim and in Chinese households practising minor marriages.¹⁹

A widely accepted interpretation of the chain of causation in the case of brother-sister incest avoidance is as follows. Lowered genetic fitness due to inbreeding led to the evolution of the juvenile sensitive period by means of natural selection; the inhibition experienced at sexual maturity led to prohibitions and cautionary myths against incest or (in many societies) merely a shared feeling that the practice is inappropriate. Formal incest taboos are the cultural reinforcement of the automatic inhibition, an example of the way culture is shaped by biology. But these various surface manifestations need not be consulted in order to formulate a more robust technique of moral reasoning. What matters in this case is the juvenile inhibition: the measures of its strength and universality, and a deeper understanding of why it came into being during the genetic evolution of the brain.

Sibling incest is one of several such cases showing that a tight and formal connection can be made between biological evolution and cultural change. Models of sociobiology have now been extended to include the full co-evolutionary circuit, from genes affecting the direction of cultural change to natural selection shifting the frequencies of these genes, and back again to open new channels for cultural evolution. The models also predict the pattern of cultural diversity resulting from a given genotype distributed uniformly through the human

¹⁹ A. P. Wolf and C. S. Huang, *Marriage and Adoption in China*, 1845– 1945 (Stanford University Press, 1980); J. Shepher, *Incest: A Biosocial View* (New York: Academic Press, 1983); P. L. van den Berghe, 'Human Inbreeding Avoidance: Culture in Nature', *The Behavioural and Brain Sciences* 6 (1983), 91–123. species. It has just been seen how the avoidance of brother-sister incest arises from a strong negative bias and a relative indifference to the preferences of others. The quantitative models incorporating these parameters yield a narrow range of cultural diversity, with a single peak at or near complete rejection on the part of the members of most societies. A rapidly declining percentage of societies possess higher rates of acceptance. If the bias is made less in the model than the developmental data indicate, the mode of this frequency curve (that is, the frequency of societies whose members display different percentages of acceptance) shifts from one end of the acceptance scale towards its centre. If individuals are considerably more responsive to the preferences of others, the frequency curve breaks into two modes.²⁰

Such simulations, employing the principles of population genetics as well as methods derived from statistical mechanics, are still necessarily crude and applicable only to the simplest forms of culture. But like behavioural genetics and the radionuclide-tomography mapping of brain activity, they give a fair idea of the kind of knowledge that is possible with increasing sophistication in theory and technique. The theory of the co-evolution of genes and culture can be used further to understand the origin and meaning of the epigenetic rules, including those that affect moral reasoning.

This completes the empirical case. To summarize, there is solid factual evidence for the existence of epigenetic rules—constraints rooted in our evolutionary biology that affect the way we think. The incest example shows that these rules, directly related to adaptive advantage, extend into the moral sphere. And the hypothesis of morality as a product of pure culture is refuted by the growing evidence of the co-evolution of genes and culture.

This perception of co-evolution is, of course, only a beginning. Prohibitions on intercourse with siblings hardly exhaust the human moral dimension. Philosophical reasoning based upon more empirical information is required to give a full evolutionary account of the phenomena of interest: philosophers' hands reaching down, as it were, to grasp the hands of biologists reaching up. Surely some of the moral premises articulated through ethical inquiry lie close to real epigenetic rules. For instance, the contractarians' emphasis on fairness and justice looks much like the result of rules brought about by reciprocal altruism, as indeed one distinguished supporter of that philosophy has already noted.²¹

²⁰ C. J. Lumsden and E. O. Wilson, op. cit. See also the précis of *Genes*, *Mind*, and *Culture* and commentaries on the book by twenty-three authors in *The Behavioural and Brain Sciences* 5 (1982), 1-37.

²¹ J. Rawls, A Theory of Justice (Cambridge, Mass.: Harvard University Press, 1971), 502-503.

(7) We believe that implicit in the scientific interpretation of moral behaviour is a conclusion of central importance to philosophy, namely that there can be no genuinely objective external ethical premises. Everything that we know about the evolutionary process indicates that no such extrasomatic guides exist. Let us define ethics in the ordinary sense, as the area of thought and action governed by a sense of obligation-a feeling that there are certain standards one ought to live up to. In order not to prejudge the issue, let us also make no further assumptions about content. It follows from what we understand in the most general way about organic evolution that ethical premises are likely to differ from one intelligent species to another. The reason is that choices are made on the basis of emotion and reason directed to these ends, and the ethical premises composed of emotion and reason arise from the epigenetic rules of mental development. These rules are in turn the idiosyncratic products of the genetic history of the species and as such were shaped by particular regimes of natural selection. For many generations-more than enough for evolutionary change to occur-they favoured the survival of individuals who practised them. Feelings of happiness, which stem from positive reinforcers of the brain and other elements that compose the epigenetic rules, are the enabling devices that led to such right action.

It is easy to conceive of an alien intelligent species evolving rules its members consider highly moral but which are repugnant to human beings, such as cannibalism, incest, the love of darkness and decay, parricide, and the mutual eating of faeces. Many animal species perform some or all of these things, with gusto and in order to survive. If human beings had evolved from a stock other than savanna-dwelling, bipedal, carnivorous man-apes we might do the same, feeling inwardly certain that such behaviours are natural and correct. In short, ethical premises are the peculiar products of genetic history, and they can be understood solely as mechanisms that are adaptive for the species that possess them. It follows that the ethical code of one species cannot be translated into that of another. No abstract moral principles exist outside the particular nature of individual species.

It is thus entirely correct to say that ethical laws can be changed, at the deepest level, by genetic evolution. This is obviously quite inconsistent with the notion of morality as a set of objective, eternal verities. Morality is rooted in contingent human nature, through and through.

Nor is it possible to uphold the true objectivity of morality by believing in the existence of an ultimate code, such that what is considered right corresponds to what is truly right—that the thoughts produced by the epigenetic rules parallel external premises.²² The

²² This is the argument proposed by R. Nozick in *Philosophical Explanations* (Cambridge, Mass.: Belknap Press of Harvard University Press, 1981) in order to escape the implications of sociobiology.

evolutionary explanation makes the objective morality redundant, for even if external ethical premises did not exist, we would go on thinking about right and wrong in the way that we do. And surely, redundancy is the last predicate that an objective morality can possess. Furthermore, what reason is there to presume that our present state of evolution puts us in correspondence with ultimate truths? If there are genuine external ethical premises, perhaps cannibalism is obligatory.

(8) Thoughtful people often turn away from naturalistic ethics because of a belief that it takes the good will out of co-operation and reduces righteousness to a mechanical process. Biological 'altruism' supposedly can never yield genuine altruism. This concern is based on a half truth. True morality, in other words behaviour that most or all people can agree is moral, does consist in the readiness to do the 'right' thing even at some personal cost. As pointed out, human beings do not calculate the ultimate effect of every given act on the survival of their own genes or those of close relatives. They are more than just gene replicators. They define each problem, weigh the options, and act in a manner conforming to a well-defined set of beliefs—with integrity, we like to say, and honour, and decency. People are willing to suppress their own desires for a while in order to behave correctly.

That much is true, but to treat such qualifications as objections to naturalistic ethics is to miss the entire force of the empirical argument. There is every reason to believe that most human behaviour does protect the individual, as well as the family and the tribe and, ultimately, the genes common to all of these units. The advantage extends to acts generally considered to be moral and selfless. A person functions more efficiently in the social setting if he obeys the generally accepted moral code of his society than if he follows moment-by-moment egocentric calculations. This proposition has been well documented in the case of pre-literate societies, of the kind in which human beings lived during evolutionary time. While far from perfect, the correlation is close enough to support the biological view that the epigenetic rules evolved by natural selection.²³

It should not be forgotten that altruistic behaviour is most often directed at close relatives, who possess many of the same genes as the altruist and perpetuate them through collateral descent. Beyond the circle of kinship, altruistic acts are typically reciprocal in nature, performed with the expectation of future reward either in this world or afterward. Note, however, that the expectation does not necessarily employ a crude demand for returns, which would be antithetical to true morality. Rather, I expect you (or God) to help me because it is right for you (or God) to help me, just as it was right for me to help you (or

²³ See footnote 16.

obey God). The reciprocation occurs in the name of morality. When people stop reciprocating, we tend to regard them as outside the moral framework. They are 'sociopathic' or 'no better than animals'.

The very concept of morality—as opposed to mere moral decisions taken from time to time—imparts efficiency to the adaptively correct action. Moral feeling is the shortcut taken by the mind to make the best choices quickly. So we select a certain action and not another because we feel that it is 'right', in other words, it satisfies the norms of our society or religion and thence, ultimately, the epigenetic rules and their prescribing genes. To recognize this linkage does not diminish the validity and robustness of the end result. Because moral consistency feeds mental coherence, it retains power even when understood to have a purely material basis.

For the same reason there is little to fear from moral relativism. A common argument raised against the materialist view of human nature is that if ethical premises are not objective and external to mankind, the individual is free to pick his own code of conduct regardless of the effect on others. Hence philosophy for the philosophers and religion for the rest, as in the Averrhoist doctrine. But our growing knowledge of evolution suggests that this is not at all the case. The epigenetic rules of mental development are relative only to the species. They are not relative to the individual. It is easy to imagine another form of intelligent life with non-human rules of mental development and therefore a radically different ethic. Human cultures, in contrast, tend to converge in their morality in the manner expected when a largely similar array of epigenetic rules meet a largely similar array of behavioural choices. This would not be the case if human beings differed greatly from one another in the genetic basis of their mental development.

Indeed, the materialist view of the origin of morality is probably less threatening to moral practice than a religious or otherwise nonmaterialistic view, for when moral beliefs are studied empirically, they are less likely to deceive. Bigotry declines because individuals cannot in any sense regard themselves as belonging to a chosen group or as the sole bearers of revealed truth. The quest for scientific understanding replaces the hajj and the holy grail. Will it acquire a similar passion? That depends upon the value people place upon themselves, as opposed to their imagined rulers in the realms of the supernatural and the eternal.

Nevertheless, because ours is an empirical position, we do not exclude the possibility that some differences might exist between large groups in the epigenetic rules governing moral awareness. Already there is related work suggesting that the genes can cause broad social differences between groups—or, more precisely, that the frequency of genes affecting social behaviour can shift across geographic regions.

An interesting example now being investigated is variation in alcohol consumption and the conventions of social drinking. Alcohol (ethanol) is broken down in two steps, first to acetaldehyde by the enzyme alcohol dehydrogenase and then to acetic acid by the enzyme acetaldehyde dehydrogenase. The reaction to alcohol depends substantially on the rate at which ethanol is converted into these two products. Acetaldehyde causes facial flushing, dizziness, slurring of words, and sometimes nausea. Hence the reaction to drinking depends substantially on the concentration of acetaldehyde in the blood, and this is determined by the efficiency of the two enzymes. The efficiency of the enzymes depends in turn on their chemical structure, which is prescribed by genes that vary within populations. In particular, two alleles (gene forms) are known for one of the loci (chromosome sites of the genes) encoding alcohol dehydrogenase, and two are known for a locus encoding acetaldehyde dehydrogenase. These various alleles produce enzymes that are either fast or slow in converting their target substances. Thus one combination of alleles causes a very slow conversion from ethanol to acetic acid, another the reverse, and so on through the four possibilities.

Independent evidence has suggested that the susceptibility to alcohol addiction is under partial genetic control. The tendency now appears to be substantially although not exclusively affected by the combination of genes determining the rates of ethanol and acetaldehyde conversion. Individuals who accumulate moderate levels of acetaldehyde are more likely to become addicted than those who sustain low levels. The propensity is especially marked in individuals who metabolize both ethanol and acetaldehyde rapidly and hence are more likely to consume large quantities to maintain a moderate acetaldehyde titre.

Differences among human populations also exist. Most caucasoids have slow ethanol and acetaldehyde conversion rates, and thus are able to sustain moderately high drinking levels while alone or in social gatherings. In contrast, most Chinese and Japanese convert ethanol rapidly and acetaldehyde slowly and thus built up acetaldehyde levels quickly. They reach intoxication levels with the consumption of a relatively small amount of alcohol.

Statistical differences in prevalent drinking habits are well known between the two cultures, with Europeans and North Americans favouring the consumption of relatively large amounts of alcohol during informal gatherings and eastern Asiatics favouring the consumption of smaller amounts on chiefly ceremonial occasions. The divergence would now seem not to be wholly a matter of historical accident but to stem from biological differences as well. Of course a great deal remains

to be learned concerning the metabolism of alcohol and its effects on behaviour, but enough is known to illustrate the potential of the interaction of varying genetic material and the environment to create cultural diversity.²⁴

It is likely that such genetic variation accounts for only a minute fraction of cultural diversity. It can be shown that a large amount of the diversity can arise purely from the statistical scatter due to differing choices made by genetically identical individuals, creating patterns that are at least partially predictable from a knowledge of the underlying universal bias.²⁵ We wish only to establish that, contrary to prevailing opinion in social theory but in concert with the findings of evolutionary biology, cultural diversity can in some cases be enhanced by genetic diversity. It is wrong to exclude *a priori* the possibility that biology plays a causal role in the differences in moral attitude among different societies. Yet even this complication gives no warrant for extreme moral relativism. Morality functions within groups and now increasingly across groups, and the similarities between all human beings appear to be far greater than any differences.

The last barrier against naturalistic ethics may well be a lingering belief in the absolute distinction between *is* and *ought*. Note that we say 'absolute'. There can be no question that *is* and *ought* differ in meaning, but this distinction in no way invalidates the evolutionary approach. We started with Hume's own belief that morality rests ultimately on sentiments and feelings. But then we used the evolutionary argument to discount the possibility of an objective, external reference for morality. Moral codes are seen instead to be created by culture under the biasing influence of the epigenetic rules and legitimated by the illusion of objectivity. The more fully this process is understood, the sounder and more enduring can be the agreements.

Thus the explanation of a phenomenon such as biased colour vision or altruistic feelings does not lead automatically to the prescription of the phenomenon as an ethical guide. But this explanation, the *is* statement, underlies the reasoning used to create moral codes. Whether a behaviour is deeply ingrained in the epigenetic rules, whether it is adaptive or non-adaptive in modern societies, whether it is linked to other forms of behaviour under the influence of separate developmental rules: all these qualities can enter the foundation of the moral codes. Of equal importance, the means by which the codes are created, entailing the estimation of consequences and the settling upon contractual

²⁴ E. Jones and C. Aoki, 'Genetic and Cultural Factors in Alcohol Use' (submitted to *Science*).

²⁵ C. J. Lumsden and E. O. Wilson, op. cit., who show the way to predict cultural diversity caused by random choice patterns in different societies.

arrangements, are cognitive processes and real events no less than the more elementary elements they examine.

(9) No major subject is more important or relatively more neglected at the present time than moral philosophy. If viewed as a pure instrument of the humanities, it seems heavily worked, culminating a long and distinguished history. But if viewed as an applied science in addition to being a branch of philosophy, it is no better than rudimentary. This estimation is not meant to be derogatory. On the contrary, moral reasoning offers an exciting potential for empirical research and a new understanding of human behaviour, providing biologists and psychologists join in its development. Diverse kinds of empirical information, best obtained through collaboration, are required to advance the subject significantly. As in twentieth-century science, the time of the solitary scholar pronouncing new systems in philosophy seems to have passed.

The very weakness of moral reasoning can be taken as a cause for optimism. By comparison with the financial support given other intellectual endeavours directly related to human welfare, moral philosophy is a starveling field. The current expenditure on healthrelated biology in the United States at the present time exceeds three billion dollars. Support has been sustained at that level or close to it for over two decades, with the result that the fundamental processes of heredity and much of the molecular machinery of the cell have been elucidated. And yet a huge amount remains to be done: the cause of cancer is only partly understood, while the mechanisms by which cells differentiate and assemble into tissues and organs are still largely unknown. In contrast, the current support of research on subjects directly related to moral reasoning, including the key issues in neurobiology, cognitive development, and sociobiology, is probably less than one per cent of that allocated to health-related biology. Given the complexities of the subject, it is not surprising that very little has been learned about the physical basis of morality—so little, in fact, that its entire validity can still be questioned by critics. We have argued that not only is the subject valid, but it offers what economists call increasing returns to scale. Small absolute increments in effort will yield large relative returns in concrete results. With this promise in mind, we will close with a brief characterization of several of the key problems of ethical studies as we see them.

First, only a few processes in mental development have been worked out in enough detail to measure the degree of bias in the epigenetic rules. The linkage from genes to cellular structure and thence to forms of social behaviour is understood only partially. In addition, a curious disproportion exists: the human traits regarded as most positive, including altruism and creativity, have been among the least analysed

empirically. Perhaps they are protected by an unconscious taboo, causing them to be regarded as matters of the 'spirit' too sacred for material analysis.

Second, the interactive effects of cognition also remain largely unstudied. Among them are hierarchies in the expression of epigenetic rules. An extreme example is the suppression of preference in one cognitive category when another is activated. This is the equivalent of the phenomenon in heredity known as epistasis. We know in a very general way that certain desires and emotion-laden beliefs take precedence over others. Tribal loyalty can easily dominate other social bonds, especially when the group is threatened from the outside. Individual sacrifice becomes far more acceptable when it is believed to enhance future generations. The physical basis and relative quantitative strengths of such effects are almost entirely unknown.

Third, there is an equally enticing opportunity to create a comparative ethics, defined as the study of conceivable moral systems that might evolve in other intelligent species. Of course it is likely that even if such systems exist, we will never perceive them directly. But that is beside the point. Theoretical science, defined as the study of all conceivable worlds, imagines non-existent phenomena in order to classify more precisely those that do exist. So long as we confine ourselves to one rather aberrant primate species (our own), we will find it difficult to identify the qualities of ethical premises that can vary and thus provide more than a narrow perspective in moral studies. The goal is to locate human beings within the space of all possible moral systems, in order to gauge our strengths and weaknesses with greater precision.

Fourth, there are pressing issues arising from the fact that moral reasoning is dependent upon the scale of time. The trouble is that evolution gave us abilities to deal principally with short-term moral problems. ('Save that child!' 'Fight that enemy!') But, as we now know, short-term responses can easily lead to long-term catastrophes. What seems optional for the next ten years may be disastrous thereafter. Cutting forests and exhausting non-renewable energy sources can produce a healthy, vibrant population for one generation-and starvation for the next ten. Perfect solutions probably do not exist for the full range of time in most categories of behaviour. To choose what is best for the near future is relatively easy. To choose what is best for the distant future is also relatively easy, providing one is limited to broad generalities. But to choose what is best for both the near and distant futures is forbiddingly difficult, often drawing on internally contradictory sentiments. Only through study will we see how our short-term moral insights fail our long-term needs, and how correctives can be applied to formulate more enduring moral codes. University of Guelph and Harvard University