II

THE UNITY OF KNOWLEDGE

ALTHOUGH THE TWO GREAT BRANCHES OF LEARNING, SCIENCE AND THE HUMANITIES, ARE RADICALLY DIFFERENT IN THE WAY THEY DESCRIBE OUR SPECIES, THEY HAVE RISEN FROM THE SAME WELLSPRING OF CREATIVE THOUGHT.

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The New Enlightenment

We've considered thus far the biological origins of human nature, and from this information the idea that a large part of human creativity is generated by the inevitable and necessary conflict between the individual and group levels of natural selection. The implied unity in the explanation leads us to the next leg of the journey I suggest. It is the concept that science and the humanities share the same foundation, in particular that the laws of physical cause and effect can somehow ultimately account for both. You will likely recognize this proposition. Western culture has already traveled this way. It was called the Enlightenment.

During the seventeenth and eighteenth centuries, the idea of the Enlightenment ruled the Western intellectual world. At that time it was a juggernaut; in the minds of many it even seemed to be the destiny of the human species. Scholars appeared on track to explain both the Universe and the meaning of humanity by the laws of science, the latter called at that time natural philosophy. The great branches of learning, Enlightenment scholars believed, can be unified by a continuous network of cause and effect. Then, when built from reality and reason alone, cleansed of superstition, all of knowledge might come together to form what in 1620 Francis Bacon, greatest of the Enlightenment's forerunners, termed "the empire of man."

The Enlightenment quest was driven by the belief that entirely on their own, human beings can know all that needs to be known, and in knowing understand, and in understanding gain the power to choose more wisely than ever before.

By the early 1800s, however, the dream faltered and Bacon's empire retreated. There were two reasons. First, although scientists were generating discoveries at an exponential pace, they were nowhere close to meeting the expectations of the more optimistic Enlightenment thinkers. Second, this shortfall allowed the founders of the Romantic tradition of literature, including some of the greatest poets of all time, to reject the presumptions of the Enlightenment worldview and seek meaning in other, more private venues. Science had no way, and it never would, to touch what people deeply feel and express only through the creative arts. Reliance on scientific knowledge, many believed and their contemporary successors continue to believe, beggars the human potential.

For the next two centuries and to the present day, science and the humanities went their own ways. Physicists of course no less continue to enjoy playing in string quartets, and novelists write books that marvel at the wonders uncovered by science. But the two cultures—as they came to be called by the middle of the twentieth century—were considered by most to be separated by a permanent chasm built into the mind, perhaps intrinsic to the nature of existence itself.

In any case there was simply no time during the long eclipse of the Enlightenment to think of unification. In order to accommodate the rising flood of information, scientific disciplines were dividing into specialties at a near-bacterial rate—fast then faster and then even faster. The creative arts for their part continued to flower with brilliant and idiosyncratic expressions of the human imagination. There was very little interest in trying to reignite what was perceived as an antique and hopeless philosophical quest. Yet the Enlightenment was never proved to be impossible. It was not dead. It was just stalled.

Is there any value in resuming the quest now, and any chance of achieving it? Yes, because enough is known today to make it more attainable than during its first flowering. And yes, because the solutions of so many problems of modern life hinge on solutions for the clash of competing religions, the ambiguities of moral reasoning, the inadequate foundations of environmentalism, and (the big one) the meaning of humanity itself.

Studying the relation between science and the humanities should be at the heart of liberal education everywhere, for students of science and the humanities alike. That's not going to be easy to achieve, of course. Among the fiefdoms of academia and punditry there exists a great variation in acceptable ideology and procedure. Western intellectual life is ruled by hard-core specialists. At Harvard University, for example, where I taught for four decades, the dominant criterion in the selection of new faculty was preeminence or the promise of preeminence in a specialty. Starting with the deliberations of department-level search committees, then recommendations to the dean of the faculty of arts and sciences, and at last the final decision by the president of Harvard, who was assisted by an ad hoc committee drawn from both within and outside the university, the pivotal question asked was, "Is the candidate the best in the world in his research specialty?" On teaching, it was almost always an easygoing, "Is the candidate adequate?" The guiding philosophy overall was that the assembly of a sufficient number of such world-class specialists would somehow coalesce into an intellectual superorganism attractive to both students and financial backers.

The early stages of a creative thought, the ones that count, do not arise from jigsaw puzzles of specialization. The most successful scientist thinks like a poet—wide-ranging, sometimes fantastical—and works like a bookkeeper. It is the latter role that the world sees. When writing a report for a technical journal or speaking at a conference of fellow specialists, the scientist avoids metaphor. He is careful never to be accused of rhetoric or poetry. A very few loaded words may be used, if kept to the introductory paragraphs and the discussion following the presentation of data, and if added to clarify the meaning of a technical concept, but they are never used for the primary purpose of stirring emotion. The language of the author must at all times be restrained and obedient to logic based on demonstrable fact.

The exact opposite is the case in poetry and the other creative arts. There metaphor is everything. The creative writer, composer, or visual artist conveys, often obliquely by abstraction or deliberate distortion, his own perceptions and the feelings he hopes to evoke—about something, about anything, real or imagined. He seeks to bring forth in an original way some truth or other about the human experience. He tries to pass what he creates directly along the channel of human experience, from his mind to your mind. His work is judged by the power and beauty of its metaphors. He obeys a dictum ascribed to Picasso: art is the lie that shows us the truth.

Wildly searching, sometimes shocking in effect, the creative arts and much of the humanities scholarship analyzing them are nonetheless in an important sense just the same old story, with the same themes, the same archetypes, the same emotions. We readers don't care. We're addicted to anthropocentricity, bound to a bottomless fascination with ourselves and others of our kind. Even the best-educated live on an ad libitum diet of novels, movies, concerts, sports events, and gossip all designed to stir one or more of the relatively small range of emotions that diagnose *Homo sapiens*.

Our stories about animals require human-like emotions and behavior understandable with well-worn guidebooks of human nature. We use endearing animal caricatures, including even those of tigers and other ferocious predators, to teach children about other people.

We are an insatiably curious species—provided the subjects are our personal selves and people we know or would like to know. The behavior goes far back beyond our species in the evolution of the primate family tree. It has been observed, for example, that when caged monkeys are allowed to look outside at a variety of other objects, their first choice for attention is other monkeys.

The function of anthropocentricity—fascination about ourselves—is the sharpening of social intelligence, a skill in which human beings are the geniuses among all Earth's species. It arose dramatically in concert with the evolution of the cerebral cortex during the origin of *Homo sapiens* from the African australopith prehumans. Gossip, celebrity worship, biographies, novels, war stories, and sports are the stuff of modern culture because a state of intense, even obsessive concentration on others has always enhanced survival of individuals and groups. We are devoted to stories because that is how the mind works—a never-ending wandering through past scenarios and through alternative scenarios of the future.

If gods of the ancient Greek tradition were watching, they would view human error the way we do in comedies and tragedies, but they might also feel empathy by viewing our foibles as flaws forced on us by Darwinian necessity. There is a parallel to gods and their human puppets in people watching kittens at play. The animals use three basic maneuvers suited to their future role as predators: to stalk and leap on a trailing string is practice for catching mice; to leap up to the string above and seize it with paws clapped together is for birds; and to scoop at a string near the feet is for fish or small prey at their feet. It's all amusing to us, but vital to them as a sharpening of survival skills.

Science builds and tests competitive hypotheses from partial evidence and imagination in order to generate knowledge about the real world. It is totally committed to fact without reference to religion or ideology. It cuts paths through the fever swamp of human existence.

You have of course heard of these qualities. But science has additional properties that distinguish it from the humanities. Of these the most important is the concept of the continuum. The idea of variation of entity and process occurring continuously in one, two, or more dimensions is so routine in most of physics and chemistry as to require no explicit mention. Continua include such familiar gradients as temperature, velocity, mass, wave length, particle spin, pH, and carbon-based molecular analogs. They become less obvious in molecular biology, where only a few basic variations in structure work to explain the function and reproduction of cells. They reappear forcefully in evolutionary biology and evolution-based ecology, which address the differing adaptations of millions of species to their respective environments. And they have returned with even greater flair and drama in studies of exoplanets.

Some nine hundred such planets had been discovered prior to the partial shutdown of the Kepler space telescope in 2013, the shutdown due to the malfunction of an aiming device. The Kepler images were amazing even to generations who regarded flybys and soft landings on other planets in the Solar System as routine. They are also immensely important, the equivalent of a seaman's first glimpse of a new continent's coastline, and a shout of, Land! Land!, where none might have existed. An estimated hundred billion star systems make up the Milky Way galaxy, and astronomers believe that all are orbited by an average of at least one planet. A small but still substantial fraction are likely to harbor life-forms—even if the organisms are only microbes living under extremely hostile conditions.

The exoplanets (planets in other star systems) of the galaxy form a continuum. Astronomers have newly observed or at least inferred a bestiary of exoplanets more varied than anything previously imagined. There exist giant gas planets resembling Jupiter and Saturn, some hugely larger in volume. There are smaller rocky planets like our own, tiny specks orbiting at the right distance from the mother star to support life, fundamentally different from rocky planets at other distances (as Mercury and Venus are fatally near to the Sun and planetlike Pluto fatally far away). There exist planets that do not rotate, others that travel close to the mother star and then far away and back again in elliptical orbits. There probably exist orphaned rogue planets, thrown loose from the gravitational pull of their mother stars, drifting through outer space. Some of the exoplanets also have an entourage of one or more moons. In addition to great and continuous variation in size, location, and orbit, there are comparable gradients in the chemical composition of the body and atmosphere of the planets and their moons, derived from the particularities of their origin.

Astronomers, being normal humans as well as scientists, are as awed as the rest of us by their discoveries. The discoveries affirm that Earth is not the center of the Universe—we've known that since Copernicus and Galileo—but just how far from the center has been hard to imagine. The tiny blue speck we call home is proportionately no more than that, a mote of stardust near the edge of our galaxy among a hundred billion or more galaxies in the universe. It occupies just one position in a continuum of planets, moons, and other planetlike heavenly bodies that we have just begun to understand. It would be becoming of us to speak modestly of our status in the cosmos. Let me offer a metaphor: Earth relates to the Universe as the second segment of the left antenna of an aphid sitting on a flower petal in a garden in Teaneck, New Jersey, for a few hours this afternoon.

With botany and entomology thus fleetingly brought to mind, it is appropriate to introduce another continuum, the diversity of life in Earth's biosphere. At the time of this writing (in 2013) there are 273,000 known species of plants in the living flora of Earth, a number expected to rise to 300,000 as more expeditions take to the field. The number of all known species of organisms on Earth, plants, animals, fungi, and microbes, is about 2 million. The actual number, combining known and unknown, is estimated to be at least three times that number, or more. The roster of newly described species is about 20,000 a year. The rate will certainly grow, as a multitude of still poorly explored tropical forest fragments, coral reefs, seamounts, and uncharted ridges and canyons of the deep ocean floor become better known. The number of described species will accelerate even faster with exploration of the largely unknown microbial world, now that the technology needed for the study of extremely small organisms has become routine. There will come to light strange new bacteria, archaeans, viruses, and picozoans that still swarm unseen everywhere on the surface of the planet.

As the census of species proceeds, other continua of biodiversity are being mapped. They include the unique biology of each living species and the long, winding processes of evolution that created it. Part of the end product is the gradient of size across a dozen orders of magnitude. It ranges from the blue whale and African elephant down to superabundant photosynthetic bacteria and scavenging picozoans of the sea, the latter so small they cannot be studied with ordinary light microscopy.

Of all the continua mapped by science, the most relevant to the humanities are the senses, which are extremely limited in our species. Vision is based in *Homo sapiens* on an almost infinitesimal sliver of energy, four hundred to seven hundred nanometers in the electromagnetic spectrum. The rest of the spectrum, saturating the Universe, ranges from gamma rays trillions of times shorter than the human visual segment to radio waves trillions of times longer. Animals live within their own slivers of continua. Below four hundred nanometers, for example, butterflies find pollen and nectar in flowers by the patterns of ultraviolet light reflected off the petals—patterns and colors unseen by us.

Where we see a yellow or red blossom, the insects see an array of spots and concentric circles in light and dark.

Healthy people believe intuitively that they can hear almost every sound. However, our species is programmed to detect only twenty to twenty thousand hertz (cycles of air compression per second). Above that range, flying bats broadcast ultrasonic pulses into the night air and listen for the echoes to dodge obstacles and snatch moths and other insects on the wing. Below the human range, elephants rumble complex messages in exchanges back and forth with other members of their herd. We walk through nature like a deaf person on the streets of New York, sensing only a few vibrations, able to interpret almost nothing.

Human beings have one of the poorest senses of smell of all the organisms on Earth, so weak that we have only a tiny vocabulary to express it. We depend heavily on similes such as "lemony" or "acidic" or "fetid." In contrast, the vast majority of other organisms, ranging in kind from bacteria to snakes and wolves, rely on odor and taste for their very existence. We depend on the sophistication of trained dogs to lead us through the olfactory world, tracking individual people, detecting even the slightest trace of explosives and other dangerous chemicals.

Our species is almost wholly unconscious of certain other kinds of stimuli without the use of instruments. We detect electricity solely by a tingle, a shock, or a flash of light. In contrast, there exist a variety of freshwater eels, catfish, and elephant-nose fish, confined to murky water where, deprived of vision, they live instead in a galvanic world. They generate charged fields around their bodies with trunk muscle tissue that has been modified by evolution into organic batteries. With the aid of electric shadows in the pattern of charges, the fish avoid obstacles around them, locate prey, and communicate with others of the same species. Yet another part of the environment beyond the reach of humans is Earth's magnetic field, used by some migratory birds to guide them during their long-distance journeys.

The exploration of continua allows humanity to measure the dimensions of the real cosmos, from the infinite ranges of size, distance, and quantity, in which we and our little planet exist. The scientific enterprise suggests where to look for previously unexpected phenomena, and how to perceive the whole of reality by a measurable webwork of cause-and-effect explanation. By knowing the position of each phenomenon in the relevant continua—relevant continua in ordinary parlance being the variable of each system—we have learned the chemistry of the surface of Mars; we know approximately how and when the first tetrapods crawled out of ponds onto the land; we can predict conditions in both the infinitesimal and near-infinite by the unified theory of physics; and we can watch blood flow and nerve cells in the human brain light up during conscious thought. In time, likely no more than several decades, we will be able to explain the dark matter of the Universe, the origin of life on Earth, and the physical basis of human consciousness during changes of mood and thought. The invisible is seen, the vanishingly small weighed.

So, what has this explosive growth of scientific knowledge to do with the humanities? *Everything*. Science and technology reveal with increasing precision the place of humanity, here on Earth and beyond in the cosmos as a whole. We occupy a microscopic space in each of the relevant continua that might have produced a species of human-grade intelligence anywhere, here and on other planets. Our ancestral species, traced further and further back through a series of ever more primitive life-forms, are all lucky lottery winners that stumbled their way through the labyrinth of evolution.

We are a very special species, perhaps the chosen species if you prefer, but the humanities by themselves cannot explain why this is the case. They don't even pose the question in a manner that can be answered. Confined to a small box of awareness, they celebrate the tiny segments of the continua they know, in minute detail and over and over again in endless permutations. These segments alone do not address the origins of the traits we fundamentally possess—our overbearing instincts, our moderate intelligence, our dangerously limited wisdom, even, critics will insist, the hubris of our science.

The first Enlightenment was undertaken more than four centuries ago when science and the humanities both were elementary enough to make their symbiosis look feasible. It became possible with the opening of the global sea routes by Western Europe from the late fifteenth century onward. The circumnavigation of Africa and the discovery of the New World led to new, global trade routes and expanded military conquest. The new, global reach was a turning point in history that placed a premium on knowledge and invention. Now we are launched into a new cycle of exploration—infinitely richer, correspondingly more challenging, and not by coincidence increasingly humanitarian. It is within the power of the humanities and the serious creative arts within them to express our existence in ways that begin at last to realize the dreams of the Enlightenment.

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The All-Importance of the Humanities

You might think this odd coming from a data-driven biologist, but I believe that the extraterrestrials created by the confabulations of science fiction serve us in an important way: they improve reflection on our own condition. When made as fully plausible as science allows, they help us to predict the future. Real aliens would tell us, I believe, that our species possesses one vital possession worthy of their attention. It is not our science and technology, as you might think. It is the humanities.

These imagined yet plausible aliens have no desire to please or elevate our species. Their relation to us is benevolent, the same as our own toward wildlife grazing and stalking in the Serengeti. Their mission is to learn all they can from the singular species that achieved civilization on this planet. Wouldn't that have to be the secrets of our science? No, not at all. We have nothing to teach them. Keep in mind that nearly everything that can be called science is less than five centuries old. Because scientific knowledge has been more or less doubling according to discipline (such as physical chemistry and cell biology) every one or two decades for the past two centuries, it follows that what we know is by geological standards brand-new. Technological applications are also in an early stage of evolution. Humanity entered our present global, hyperconnected technoscientific era only two decades ago—less than an eyeblink in the starry message of the cosmos. By chance alone, and given the multibillion-year age of the galaxy, the aliens reached our present-day, still-infantile level millions of years ago. It could have been as much as a hundred million years ago. What then can we teach our extraterrestrial visitors? Put another way, what could Einstein as a toddler have taught a professor of physics? Nothing at all. For the same reason our technology would be vastly inferior. If that were not so, we would be the extraterrestrial visitors and they the planetary aboriginals.

So what could the hypothetical aliens learn from us that has any value to them? The correct answer is the humanities. As Murray Gell-Mann once remarked of the field he has pioneered, theoretical physics consists of a small number of laws and a great many accidents. The same is true, a fortiori, of all the sciences. The origin of life occurred over three and a half billion years ago. The subsequent diversification of the primordial organisms into species of microbes, fungi, plants, and animals is only one history that could have occurred out of a near-infinitude of histories. The extraterrestrial visitors would know this, from robot probes and the principles of evolutionary biology. They could not immediately fathom Earth's full history of organic evolution, with its extinctions, replacements, and dynastic rise and fall of major groups—cycads, ammonoids, dinosaurs. But with their super-efficient fieldwork and DNA-sequencing and proteonomic technology, they would quickly learn Earth's fauna and flora at the present moment, and the nature and ages of the forerunners, and calculate patterns in space and time of life's evolutionary history. It's all a matter of science. The aliens would soon know all that we know called science, and much more, as though we had never existed.

In a closely parallel manner during the human history of the past hundred thousand years or so, a small number of human Ur-cultures arose, then gave birth to the thousands of daughter cultures. Many of these persist today, each with its one language or dialect, religious beliefs, and social and economic practices. Like species of plants and animals splintering across the geological ages, they have continued to evolve, alone, or divided into two more cultures, perhaps fused in part, and some have just disappeared. Of the nearly seven thousand languages currently spoken worldwide, 28 percent are used by fewer than a thousand people, and 473 are on the edge of extinction, spoken only by a handful of elderly people. Measured this way, recorded history and prehistory before it present a kaleidoscopic pattern similar to that of species formation during organic evolution—yet different in major ways from it.

Cultural evolution is different because it is entirely a product of the human brain, an organ that evolved during prehuman and Paleolithic times through a very special form of natural selection called gene-culture coevolution (where genetic evolution and cultural evolution each affect the trajectory of the other). The brain's unique capability, lodged primarily in the memory banks of the frontal cortex, arose from the tenure of *Homo habilis* two million to three million years ago until the global spread of its descendant *Homo sapiens* sixty thousand years ago. To understand cultural evolution from the outside looking in, as opposed to the inside looking out, the way we do it, requires interpreting all of the intricate feelings and constructions of the human mind. It requires intimate contact with people and knowledge of countless personal histories. It describes the way a thought is translated into a symbol or artifact. All this the humanities do. They are the natural history of culture, and our most private and precious heritage.

There is another cardinal reason for treasuring the humanities. Scientific discovery and technological advance have a life cycle. In time, after reaching an immense size and unimaginable complexity, they will certainly slow and stabilize at a much lower level of growth. Within the span of my own career as a published scientist across half a century, the number of discoveries per researcher per year has declined dramatically. Teams have grown larger, with ten or more coauthors on technical papers now a commonplace. The technology required to make a scientific discovery in most disciplines has become much more complex and expensive, and the new technology and statistical analysis required for scientific research more advanced.

Not to worry. By the time the process has set in, likely in this century, the role of science and high technology will, as expected, be beneficent and far more pervasive than now. But—and this is the most important part—science and technology will also be the same everywhere, for every civilized culture, subculture, and person. Sweden, the United States, Bhutan, and Zimbabwe will share the same information. What will continue to evolve and diversify almost infinitely are the humanities.

For the next few decades, most major technological advances are likely to occur in what is often denoted BNR: biotechnology, nanotechnology, and robotics. In pure science the secular grails now sought along the broad frontier include the deduction of how life originated on Earth, along with the creation of artificial organisms, gene substitution and surgically precise modification of the genome, discovery of the physical nature of consciousness, and, not least, the construction of robots that can think faster and work more efficiently than humans in most blue-collar and white-collar labor. At the present time these envisioned advances are the stuff of science fiction. But not for long. Within a few decades they will be reality.

And the cards are now on the table, faceup. First on the agenda is the correction of the more than a thousand genes for which rare mutant alleles have been identified as the cause of hereditary diseases. The method of choice will be gene substitution, replacing the mutant allele with a normal one. Although still in the earliest, mostly untested stage, it promises eventually to replace amniocentesis, which allows first a readout of the embryonic chromosome structure and genetic code, then therapeutic abortion to avoid disability or death. Many people object to therapeutic abortions, but I doubt that many would object to gene substitution, which can be compared with replacement of a defective heart valve or diseased kidney.

An even more advanced form of a volitional evolution, albeit indirect in cause, is the homogenization ongoing among the world populations by increased emigration and interracial marriage. The result is a massive redistribution of *Homo sapiens* genes. Genetic variation between populations is declining, genetic variation within populations is increasing, and, as an overall result, the genetic variation of the species as a whole is also increasing—the last dramatically so. These trends create a dilemma of volitional evolution likely to catch the attention of even the most myopic political think tanks in a few decades. Do we wish to guide the evolution of diversity in order to increase the frequency of desirable traits? Or increase it still more? Or finally—this will almost certainly be the short-term decision—just leave it alone and hope for the best?

Such alternatives are not science fiction, and they are not frivolous. On the contrary, they are linked to yet another biology-based dilemma that has already entered public discussion, ranking with contraceptives in high school and evolution-free textbooks in Texas. It is this: With more and more decision making and work done by robots, what will be left for humans to do? Do we really want to compete biologically with robot technology by using brain implants and genetically improved intelligence and social behavior? This choice would mean a sharp departure away from the human nature we have inherited, and a fundamental change in the human condition.

Now we are talking about a problem best solved within the humanities, and one more reason the humanities are all-important. While I'm at it, I hereby cast a vote for existential conservatism, the preservation of biological human nature as a sacred trust. We are doing very well in science and technology. Let's agree to keep it up, and move both along even faster. But let's also promote the humanities, that which makes us human, and not use science to mess around with the wellspring of this, the absolute and unique potential of the human future.

6

The Driving Force of Social Evolution

Few questions in biology are as important as the evolutionary origin of instinctive social behavior. To find the correct answer is to explain one of the great transitions in levels of biological organization, from the organism to the superorganism—from one ant, say, to an organized colony of ants, and from a solitary primate to an organized society of human beings.

The most complex forms of social organization are made from high levels of cooperation. They are furthered with altruistic acts performed by at least some of the colony members. The highest level of cooperation and altruism is that of eusociality, in which some colony members surrender part or all of their personal reproduction in order to increase reproduction by the "royal" caste specialized for that purpose.

As I've pointed out, there are two competing theories of the origin of advanced social organization. One is the standard theory of natural selection. It has proved correct across a broad range of social and nonsocial phenomena, improving in precision since the origin of modern population genetics in the 1920s and modern synthesis of evolutionary theory in the 1930s. It is based on the principle that the unit of heredity is the gene, which typically acts as part of a network of genes, and the target of natural selection is the trait prescribed by the gene. For example, an unfavorable mutant gene in humans is that which prescribes cystic fibrosis. The gene is rare because its phenotype cystic fibrosis is selected against—it lowers longevity and reproduction. Examples of favorable mutant genes are those that prescribe adult lactose tolerance. After originating in dairying populations in Europe and Africa, the phenotype prescribed by the mutated genes made milk available as a reliable adult food, and thereby increased the comparative longevity and reproduction of the people possessing them.

A gene for a trait that affects a group member's longevity and reproduction relative to other members in the same group is said to be subject to individual-level natural selection. A gene for a trait entailing cooperation and other forces of interaction with fellow group members may or may not be subject to individual-level selection. In either case it is also likely to affect longevity and reproduction of the group as a whole. Because groups compete with other groups, in both conflict and their relative efficiency in resource extraction, their differing traits are subject to natural selection. In particular, the genes prescribing interactive (hence social) traits are subject to group-level selection.

Here is a simplified scenario of evolution according to the standard theory of natural selection. A successful thief furthers his own interests and those of his offspring, but his actions weaken the remainder of the group. Any genes proscribing his psychopathic behavior will increase within the group from one generation to the next—but, like a parasite causing a disease in an organism, his activity weakens the rest of the group—and eventually the thief himself. At the opposite extreme, a valiant warrior leads his group to victory, but in doing so is killed in battle, leaving few or no offspring. His genes for heroism are lost with him, but the remainder of the group, and the heroism genes they share, benefit and increase.

The two levels of natural selection, individual and group, illustrated by these extremes, are in opposition. They will in time lead to either a balance of the opposing genes or an extinction of one of the two kinds altogether. Their action is summarized in this maxim: selfish members win within groups, but groups of altruists best groups of selfish members.

The theory of inclusive fitness, in opposition to the standard theory of natural selection, and with it the established principles of population genetics, treats the individual group member, not its individual genes, as the unit of selection. Social evolution arises from the sum of all the interactions of the individual with each of the other group members in turn, multiplied by the degree of hereditary kinship between each pair. All the effects of this multiplicity of interactions on the individual, both positive and negative, make up its inclusive fitness.

Although the controversy between natural selection and inclusive fitness still flickers here and there, the assumptions of the theory of inclusive fitness have proved to be applicable only in a few extreme cases unlikely to occur on Earth or any other planet. No example of inclusive fitness has been directly measured. All that has been accomplished is an indirect analysis called the regressive method, which unfortunately has itself been mathematically invalidated. The use of the individual or group as the unit of heredity, rather than the gene, is an even more fundamental error.

At this point, prior to developing the theories further, it will be instructive to take a specific example in the evolution of social behavior and see how it is treated respectively by each approach.

The life cycle of ants has always been a favorite of inclusive fitness theorists as offering proof of the role of kinship and the validity of inclusive fitness. Many ant species have the following life cycle: their colonies reproduce by releasing virgin queens and males from the nest. After mating, the queens do not return home, but disperse to establish new colonies on their own. The males die within hours. The virgin queens are much larger than the males, and colonies invest a correspondingly larger fraction of their resources to their production.

The inclusive fitness explanation of the size difference between the sexes, introduced in the 1970s by the biologist Robert Trivers, is as follows. The means of sex determination in ants is peculiar, such that sisters are more closely related to one another than they are to their brothers (providing the queens mate with only one male). Because the workers raise the young, Trivers continued, and because they favor sisters over brothers, they invest more in virgin queens than in males. The colony, with workers in control, accomplish this end by making the queens individually much larger in size. This process deduced with inclusive fitness theory is called indirect natural selection.

The standard population genetics model, in contrast, posits direct natural selection and tests it with direct observation in the field and laboratory. The larger size of the virgin queen is necessary, as all entomologists know, because of the way she starts a new colony. She digs a nest, seals herself in, and raises the first brood of workers on her large bodily reserves of fat and metabolized wing muscles. The male is small because its only function is to mate. After achieving insemination, it dies. (Queens live on in a few species, incidentally, for more than twenty years.) The roundabout inclusive fitness explanation for investments according to gender is therefore wrong.

The assumption of inclusive fitness theory that workers control the colony's allocation, a crucial point in this reasoning, is also wrong. Using the valve on her spermatheca, the bag-like organ in which the sperm are stored, the queen determines the sex of the offspring born. If a sperm is released to fertilize an egg in the queen's ovary, a female is born. If no sperm is released, the egg is not fertilized, and from the unfertilized egg a male is born. Thereafter, a complex of factors, only some of which are under worker control, determine which female eggs and larvae will become queens.

For half a century, while data were still relatively scarce, the theory of inclusive fitness was the prevailing explanation of the origin of advanced social behavior. It began in 1955 with a simple mathematical model by the British geneticist J. B. S. Haldane. His argument was in the following form (which I've altered here a bit to make it intuitively easier). Imagine that you are a childless bachelor standing on a riverbank. Looking out over the water, you see that your brother has fallen in and is drowning. The river that day is raging, and you're a poor swimmer, so you know that if you jump in and save him, you yourself will probably drown. So the rescue requires altruism on your part. But (Haldane said) it does not also require altruism on the part of your genes, including those responsible for making you altruistic. The reason is the following. Because the man is your brother, half of his genes are identical to yours. So you jump in, save him, and sure enough, you drown. Now you're gone, but half of your genes are saved. All your brother has to do in order to make up the loss in genes is to have two additional children. The genes are the unit of selection; the genes are what count in evolution by natural selection.

In 1964, another British geneticist, William D. Hamilton, expressed Haldane's concept in a general formula, which came to be known in later years as the Hamilton inequality. It said that a gene prescribing altruism, such as that of the heroic brother, will increase if the benefit in number of offspring to the recipient exceeds the cost in offspring to the altruist. However, this advantage to the altruist will be effective only if the recipient and the altruist are closely related. The degree of kinship is the fraction of genes that are shared by the altruist and recipient due to their common descent: one-half between siblings, one-eighth between first cousins, and so on in a rapidly declining rate as the degree of kinship becomes more distant. The process later came to be called kin selection. It seemed, at least from this line of reasoning, that close kinship is the key to the biological origin of altruism and cooperation. Hence close kinship is a primary factor of advanced social evolution.

On the surface, kin selection seemed at first to be a reasonable explanation for the origin of organized societies. Consider any group of individuals that have come together in one manner or another but remain unorganized—a fish school, for example, a flock of birds, or a local population of ground squirrels. The group members, let us say, are able to distinguish not just their own offspring, leading to evolution of parental care by standard (Darwinian) natural selection. Suppose they also recognize collateral relatives related by common descent such as siblings and cousins. Allow further that mutations occur that induce individuals to favor close collateral relatives over distant relatives or nonrelatives. An extreme case would be Haldane's heroism biased toward a brother. The result would be nepotism, resulting in a Darwinian advantage over others in the group. But where does that lead an evolving population? As the collateral-favoring genes spread, the group would change into an ensemble not of competing individuals and their offspring, but of an ensemble of parallel competing extended families. To achieve group-wide altruism, cooperation, and division of labor, in other words organized societies, requires a different level of natural selection. That level is group selection.

Also in 1964, Hamilton took the kinship principle one step further by introducing the concept of inclusive fitness. The social individual lives in a group, and it interacts with other members of the group. The individual participates in kin selection with each of the other group members with which it interacts. The added effect it has on its own genes passed into the next generation is its inclusive fitness: the sum of all the benefits and costs, discounted by the degree of kinship with each other group member. With inclusive fitness the unit of selection had passed subtly from the gene to the individual.

At first I found the theory of inclusive fitness, winnowed down to a few cases of kin selection that might be studied in nature, enchanting. In 1965, a year after Hamilton's article, I defended the theory at a meeting of the Royal Entomological Society of London. Hamilton himself was at my side that evening. In my two books formulating the new discipline of sociobiology, *The Insect Societies* (1971) and *Sociobiology: The New Synthesis* (1975), I promoted kin selection as a key part of the genetic explanation of advanced social behavior, treating it as equal in importance to caste, communication, and the other principal subjects that make up sociobiology. In 1976 the eloquent science journalist Richard Dawkins explained the idea to the general public in his best-selling book *The Selfish Gene*. Soon kin selection and some version of inclusive fitness were installed in textbooks and popular articles on social evolution. During the following three decades a large volume of general and abstract extensions of the theory of kin selection was tested, especially in ants and other social insects, and purportedly found proof in studies on rank orders, conflict, and gender investment.

By 2000 the central role of kin selection and its extensive inclusive fitness had approached the stature of dogma. It was a common practice for writers of technical papers to acknowledge the truth of the theory, even if the content of the data to be presented were only distantly relevant to it. Academic careers had been built upon it by then, and international prizes awarded.

Yet the theory of inclusive fitness was not just wrong, but fundamentally wrong. Looking back today, it is apparent that by the 1990s two seismic flaws had already appeared and begun to widen. Extensions of the theory itself were growing increasingly abstract, hence remote from the empirical work that continued to flourish elsewhere in sociobiology. At the same time the empirical research devoted to the theory remained limited to a small number of measurable phenomena. Writings on the theory mostly in the social insects were repetitive. They offered more and more about proportionately fewer topics. The grand patterns of ecology, phylogeny, division of labor, neurobiology, communication, and social physiology remained virtually untouched by the asseverations of the inclusive theorists. Much of the popular writing devoted to it was not new but affirmative in tone, declaring how great the theory was yet to become.

Inclusive fitness theory, fondly called IF theory for short by its defenders, was showing increasing signs of senescence. By 2005 questions about its soundness were being openly expressed, especially among leading experts on the details of the biology of the ants, termites, and other eusocial insects, as well as a few theoreticians bold enough to seek alternative explanations of the origin and evolution of eusociality. The researchers most committed to IF theory either ignored these deviations or summarily dismissed them. By 2005 they had gained enough representation in the anonymous peer review system to hinder publication of contrary evidence and opinions in leading journals. For example, a keystone early support of inclusive fitness theory, cited in textbooks, was the prediction of overrepresentation of the Hymenoptera (bees, wasps, ants) among eusocial animal species. When after a time one investigator pointed out that new discoveries had nullified the prediction, he was told, in effect, “We already knew that.” They did know that, but hadn't done more than just drop the subject. The “Hymenoptera hypothesis” was not wrong; it had just become “irrelevant.” When a senior investigator used field and laboratory studies to show that primitive termite colonies compete with one another and grow in part by the fusion of unrelated workers, the data were rejected on grounds that the conclusion did not adequately take into account inclusive fitness theory.

Why did an outwardly arcane topic of theoretical biology excite such fierce partisanship? Because the problem it addresses is of fundamental importance, and the stakes in trying to solve it had become exceptionally high. Furthermore, inclusive fitness was beginning to resemble a house of cards. To pull even one out risked collapsing the whole. Pulling cards, however, was worth the price to reputation. There existed in the air the promise of a paradigm shift, a rare event in evolutionary biology.

In 2010, the dominance of inclusive fitness theory was finally broken. After struggling as a member of the small but still muted contrarian school for a decade, I joined two Harvard mathematicians and theoretical biologists, Martin Nowak and Corina Tarnita, for a top-to-bottom analysis of inclusive fitness. Nowak and Tarnita had independently discovered that the foundational assumptions of inclusive fitness theory were unsound, while I had demonstrated that the field data used to support the theory could be explained equally well, or better, with direct natural selection—as in the sex-allocation case of ants just described.

Our joint report was published on August 26, 2010, as the cover article of the prestigious journal *Nature*. Knowing the controversy involved, the *Nature* editors had proceeded with unusual caution. One of them familiar with the subject and the mode of mathematical analysis came from London to Harvard to hold a special meeting with Nowak, Tarnita, and myself. He approved, and the manuscript was next examined by three anonymous experts. Its appearance, as we expected, caused a Vesuvian explosion of protest—the kind cherished by journalists. No fewer than 137 biologists committed to inclusive fitness theory in their research or teaching signed a protest in a *Nature* article published the following year. When I repeated part of my argument as a chapter in the 2012 book *The Social Conquest of Earth*, Richard Dawkins responded with the indignant fervor of a true believer. In his review for the British magazine *Prospect*, he urged others not to read what I had written, but instead to cast the entire book away, "with great force," no less.

Yet no one since that time has refuted the mathematical analysis by Nowak and Tarnita, or my argument favoring the standard theory over inclusive fitness theory in the interpretation of field data.

In 2013 Nowak and I were joined by another mathematical biologist, Benjamin Allen, in a still deeper expansion of the ongoing analysis. (Tarnita had moved to Princeton, where she was busy adding field research to her mathematical modeling.) In late 2013 we published the first in a planned series of refereed articles. Because of the need for exactitude, and the material that these articles contain that may be relevant to the history and philosophy of the subject, I've taken the step of providing a simplified summary of the first one in the appendix of this book.

Now at last we can return to a key question in a more open spirit of inquiry: What was the driving force in the origin of human social behavior? The prehumans of Africa approached the threshold of advanced social organization in a manner parallel to that in the lower animals but attained it in a very different manner. As brain size more than doubled, the bands used intelligence based on vastly improved memory. Where primitively social insects evolved division of labor with narrow instincts that play upon categories of social organization in each group, such as larvae and adults, nurses and foragers, the earliest humans operated with variable instinct-driven behavior that made use of detailed knowledge of each group member by all the others.

The creation of groups from personal and intimate mutual knowledge was the unique achievement of humanity. While similarity of genomes by kinship was an inevitable consequence of group formation, kin selection was not the cause. The extreme limitations of kin selection and the phantom-like properties of inclusive fitness apply equally to humans and to eusocial insects and other animals. The origin of the human condition is best explained by the natural selection for social interaction—the inherited propensities to communicate, recognize, evaluate, bond, cooperate, compete, and from all these the deep warm pleasure of belonging to your own special group. Social intelligence enhanced by group selection made *Homo sapiens* the first fully dominant species in Earth's history.