4 Natural Selection and the Human Brain: Darwin *vs.* Wallace

IN THE SOUTH transept of Chartres cathedral, the most stunning of all medieval windows depicts the four evangelists as dwarfs sitting upon the shoulders of four Old Testament prophets—Isaiah, Jeremiah, Ezekiel, and Daniel. When I first saw this window as a cocky undergraduate in 1961, I immediately thought of Newton's famous aphorism—"if I have seen farther, it is by standing on the shoulders of giants"—and imagined that I had made a major discovery in unearthing his lack of originality. Years later, and properly humbled for many reasons, I learned that Robert K. Merton, the celebrated sociologist of science from Columbia University, had devoted an entire book to pre-Newtonian usages of the metaphor. It is titled, appropriately, *On The Shoulders of Giants.* In fact, Merton traces the bon mot back to Bernard of Chartres in 1126 and cites several scholars who believe that the windows of the great south transept, installed after Bernard's death, represent an explicit attempt to capture his metaphor in glass.

Although Merton wisely constructs his book as a delightful romp through the intellectual life of medieval and Renaissance Europe, he does have a serious point to make. For Merton has devoted much of his work to the study of multiple discoveries in science. He has shown that almost all major ideas arise more than once, independently and often virtually at the same time—and thus, that great scientists are embedded in their cultures, not divorced from them. Most

great ideas are "in the air," and several scholars simultaneously wave their nets.

One of the most famous of Merton's "multiples" resides in my own field of evolutionary biology. Darwin, to recount the famous tale briefly, developed his theory of natural selection in 1838 and set it forth in two unpublished sketches of 1842 and 1844. Then, never doubting his theory for a moment, but afraid to expose its revolutionary implications, he proceeded to stew, dither, wait, ponder, and collect data for another fifteen years. Finally, at the virtual insistence of his closest friends, he began to work over his notes, intending to publish a massive tome that would have been four times as long as the *Origin of Species*. But, in 1858, Darwin received a letter and manuscript from a young naturalist, Alfred Russel Wallace, who had independently constructed the theory of natural selection while lying ill with malaria on an island in the Malay Archipelago. Darwin was stunned by the detailed similarity. Wallace even claimed inspiration from the same nonbiological source—Malthus' *Essay on Population*. Darwin, in great anxiety, made the expected gesture of magnanimity, but devoutly hoped that some way might be found to preserve his legitimate priority. He wrote to Lyell: "I would far rather burn my whole book, than that he or any other man should think that I have behaved in a paltry spirit." But he added a suggestion: "If I could honorably publish, I would state that I was induced now to publish a sketch . . . from Wallace having sent me an outline of my general conclusions." Lyell and Hooker took the bait and came to Darwin's rescue. While Darwin stayed home, mourning the death of his young child from scarlet fever, they presented a joint paper to the Linnaean Society containing an excerpt from Darwin's 1844 essay together with Wallace's manuscript. A year later, Darwin published his feverishly compiled "abstract" of the longer work—the *Origin of Species*. Wallace had been eclipsed.

Wallace has come down through history as Darwin's shadow. In public and private, Darwin was infallibly decent and generous to his younger colleague. He wrote to Wallace in 1870: "I hope it is a satisfaction to you to reflect—

and very few things in my life have been more satisfactory to me—that we have never felt any jealousy towards each other, though in one sense rivals." Wallace, in return, was consistently deferential. In 1864, he wrote to Darwin: "As to the theory of Natural Selection itself, I shall always maintain it to be actually yours and yours only. You had worked it out in details I had never thought of, years before I had a ray of light on the subject, and my paper would never have convinced anybody or been noticed as more than an ingenious speculation, whereas your book has revolutionized the study of Natural History, and carried away captive the best men of the present age."

This genuine affection and mutual support masked a serious disagreement on what may be the fundamental question in evolutionary theory—both then and today. How exclusive is natural selection as an agent of evolutionary change? Must all features of organisms be viewed as adaptations? Yet Wallace's role as Darwin's subordinate alter ego is so firmly fixed in popular accounts that few students of evolution are even aware that they ever differed on theoretical questions. Moreover, in the one specific area where their public disagreement is a matter of record—the origin of human intellect—many writers have told the story backwards because they failed to locate this debate in the context of a more general disagreement on the power of natural selection.

All subtle ideas can be trivialized, even vulgarized, by portrayal in uncompromising and absolute terms. Marx felt compelled to deny that he was a marxist, while Einstein contended with the serious misstatement that he meant to say "all is relative." Darwin lived to see his name appropriated for an extreme view that he never held—for "Darwinism" has often been defined, both in his day and in our own, as the belief that virtually all evolutionary change is the product of natural selection. In fact Darwin often complained, with uncharacteristic bitterness, about this misappropriation of his name. He wrote in the last edition of the *Origin* (1872): "As my conclusions have lately been much misrepresented, and it has been stated that I attribute the

modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.' This has been of no avail. Great is the power of steady misrepresentation."

However, England did house a small group of strict selectionists—"Darwinians" in the misappropriated sense—and Alfred Russel Wallace was their leader. These biologists did attribute all evolutionary change to natural selection. They viewed each bit of morphology, each function of an organ, each behavior as an adaptation, a product of selection leading to a "better" organism. They held a deep belief in nature's "rightness," in the exquisite fit of all creatures to their environments. In a curious sense, they almost reintroduced the creationist notion of natural harmony by substituting an omnipotent force of natural selection for a benevolent deity. Darwin, on the other hand, was a consistent pluralist gazing upon a messier universe. He saw much fit and harmony, for he believed that natural selection holds pride of place among evolutionary forces. But other processes work as well, and organisms display an array of features that are not adaptations and do not promote survival directly. Darwin emphasized two principles leading to nonadaptive change: (1) organisms are integrated systems and adaptive change in one part can lead to nonadaptive modifications of other features ("correlations of growth" in Darwin's phrase); (2) an organ built under the influence of selection for a specific role may be able, as a consequence of its structure, to perform many other, unselected functions as well.

Wallace stated the hard hyper-selectionist line—"pure Darwinism" in his terms—in an early article of 1867, calling it "a necessary deduction from the theory of natural selection."

> None of the definite facts of organic selection, no special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species, can exist but which must now be, or once have been, useful to the individuals or races which possess them.

Indeed, he argued later, any apparent nonutility must only reflect our faulty knowledge—a remarkable argument since it renders the principle of utility impervious to disproof a priori: "The assertion of 'inutility' in the case of any organ . . . is not, and can never be, the statement of a fact, but merely an expression of our ignorance of its purpose or origin."

All the public and private arguments that Darwin pursued with Wallace centered upon their differing assessments of the power of natural selection. They first crossed swords on the issue of "sexual selection," the subsidiary process that Darwin had proposed in order to explain the origin of features that appeared to be irrelevant or even harmful in the usual "struggle for existence" (expressed primarily in feeding and defense), but that could be interpreted as devices for increasing success in mating—elaborate antlers of deer, or tail feathers of the peacock, for example. Darwin proposed two kinds of sexual selection—competition among males for access to females, and choice exercised by females themselves. He attributed much of the racial differentiation among modern humans to sexual selection, based upon different criteria of beauty that arose among various peoples. (His book on human evolution—*The Descent of Man* (1871)—is really an amalgam of two works: a long treatise on sexual selection throughout the animal kingdom, and a shorter speculative account of human origins, relying heavily upon sexual selection.)

The notion of sexual selection is not really contrary to natural selection, for it is just another route to the Darwinian imperative of differential reproductive success. But Wallace disliked sexual selection for three reasons: it compromised the generality of that peculiarly nineteenth-cen-

tury view of natural selection as a battle for life itself, not merely for copulation; it placed altogether too much emphasis upon the "volition" of animals, particularly in the concept of female choice; and, most importantly, it permitted the development of numerous, important features that are irrelevant, if not actually harmful, to the operation of an organism as a well-designed machine. Thus, Wallace viewed sexual selection as a threat to his vision of animals as works of exquisite craftsmanship, wrought by the purely material force of natural selection. (Indeed, Darwin had developed the concept largely to explain why so many differences among human groups are irrelevant to survival based upon good design, but merely reflect the variety of capricious criteria for beauty that arose for no adaptive reason among various races. Wallace did accept sexual selection based upon male combat as close enough to the metaphor of battle that controlled his concept of natural selection. But he rejected the notion of female choice, and greatly distressed Darwin with his speculative attempts to attribute all features arising from it to the adaptive action of natural selection.)

In 1870, as he prepared the *Descent of Man,* Darwin wrote to Wallace: "I grieve to differ from you, and it actually terrifies me and makes me constantly distrust myself. I fear we shall never quite understand each other." He struggled to understand Wallace's reluctance and even to accept his friend's faith in unalloyed natural selection: "You will be pleased to hear," he wrote to Wallace, "that I am undergoing severe distress about protection and sexual selection; this morning I oscillated with joy towards you; this evening I have swung back to [my] old position, out of which I fear I shall never get."

But the debate on sexual selection was merely a prelude to a much more serious and famous disagreement on that most emotional and contentious subject of all—human origins. In short, Wallace, the hyper-selectionist, the man who had twitted Darwin for his unwillingness to see the action of natural selection in every nuance of organic form, halted abruptly before the human brain. Our intellect and morality, Wallace argued, could not be the product of natural selection; therefore, since natural selection is evolution's only way, some higher power—God, to put it directly—must have intervened to construct this latest and greatest of organic innovations.

If Darwin had been distressed by his failure to impress Wallace with sexual selection, he was now positively aghast at Wallace's abrupt about-face at the finish line itself. He wrote to Wallace in 1869: "I hope you have not murdered too completely your own and my child." A month later, he remonstrated: "If you had not told me, I should have thought that [your remarks on Man] had been added by some one else. As you expected, I differ grievously from you, and I am very sorry for it." Wallace, sensitive to the rebuke, thereafter referred to his theory of human intellect as "my special heresy."

The conventional account of Wallace's apostasy at the brink of complete consistency cites a failure of courage to take the last step and admit man fully into the natural system—a step that Darwin took with commendable fortitude in two books, the *Descent of Man* (1871) and the *Expression of the Emotions* (1872). Thus, Wallace emerges from most historical accounts as a lesser man than Darwin for one (or more) of three reasons, all related to his position on the origins of human intellect: for simple cowardice; for inability to transcend the constraints of culture and traditional views of human uniqueness; and for inconsistency in advocating natural selection so strongly (in the debate on sexual selection), yet abandoning it at the most crucial moment of all.

I cannot analyze Wallace's psyche, and will not comment on his deeper motives for holding fast to the unbridgeable gap between human intellect and the behavior of mere animals. But I can assess the logic of his argument, and recognize that the traditional account of it is not only incorrect, but precisely backwards. Wallace did not abandon natural selection at the human threshold. Rather, it was his peculiarly rigid view of natural selection that led him, quite consistently, to reject it for the human mind. His position never

varied—natural selection is the only cause of major evolutionary change. His two debates with Darwin—sexual selection and the origin of human intellect—represent the same argument, not an inconsistent Wallace championing selection in one case and running from it in the other. Wallace's error on human intellect arose from the inadequacy of his rigid selectionism, not from a failure to apply it. And his argument repays our study today, since its flaw persists as the weak link in many of the most "modern" evolutionary speculations of our current literature. For Wallace's rigid selectionism is much closer than Darwin's pluralism to the attitude embodied in our favored theory today, which, ironically in this context, goes by the name of "Neo-Darwinism."

Wallace advanced several arguments for the uniqueness of human intellect, but his central claim begins with an extremely uncommon position for his time, one that commands our highest praise in retrospect. Wallace was one of the few nonracists of the nineteenth century. He really believed that all human groups had innately equal capacities of intellect. Wallace defended his decidedly unconventional egalitarianism with two arguments, anatomical and cultural. He claimed, first of all, that the brains of "savages" are neither much smaller nor more poorly organized than our own: "In the brain of the lowest savages, and, as far as we know, of the prehistoric races, we have an organ . . . little inferior in size and complexity to that of the highest type." Moreover, since cultural conditioning can integrate the rudest savage into our most courtly life, the rudeness itself must arise from a failure to use existing capacities, not from their absence: "It is latent in the lower races, since under European training native military bands have been formed in many parts of the world, which have been able to perform creditably the best modern music."

Of course, in calling Wallace a nonracist, I do not mean to imply that he regarded the cultural practices of all peoples as equal in intrinsic worth. Wallace, like most of his contemporaries, was a cultural chauvinist who did not doubt the evident superiority of European ways. He may

have been bullish on the capability of "savages," but he certainly had a low opinion of their life, as he mistook it: "Our law, our government, and our science continually require us to reason through a variety of complicated phenomena to the expected result. Even our games, such as chess, compel us to exercise all these faculties in a remarkable degree. Compare this with the savage languages, which contain no words for abstract conceptions; the utter want of foresight of the savage man beyond his simplest necessities; his inability to combine, or to compare, or to reason on any general subject that does not immediately appeal to his senses."

Hence, Wallace's dilemma: all "savages," from our actual ancestors to modern survivors, had brains fully capable of developing and appreciating all the finest subtleties of European art, morality and philosophy; yet they used, in the state of nature, only the tiniest fraction of that capacity in constructing their rudimentary cultures, with impoverished languages and repugnant morality.

But natural selection can only fashion a feature for immediate use. The brain is vastly overdesigned for what it accomplished in primitive society; thus, natural selection could not have built it:

> A brain one-half larger than that of the gorilla would . . . fully have sufficed for the limited mental development of the savage; and we must therefore admit that the large brain he actually possesses could never have been solely developed by any of those laws of evolution, whose essence is, that they lead to a degree of organization exactly proportionate to the wants of each species, never beyond those wants. . . . Natural selection could only have endowed savage man with a brain a few degrees superior to that of an ape, whereas he actually possesses one very little inferior to that of a philosopher.

Wallace did not confine this general argument to abstract intellect, but extended it to all aspects of European "refine-

ment," to language and music in particular. Consider his views on "the wonderful power, range, flexibility, and sweetness of the musical sounds producible by the human larynx, especially in the female sex."

> The habits of savages give no indication of how this faculty could have been developed by natural selection, because it is never required or used by them. The singing of savages is a more or less monotonous howling, and the females seldom sing at all. Savages certainly never choose their wives for fine voices, but for rude health, and strength, and physical beauty. Sexual selection could not therefore have developed this wonderful power, which only comes into play among civilized people. It seems as if the organ had been prepared in anticipation of the future progress in man, since it contains latest capacities which are useless to him in his earlier condition.

Finally, if our higher capacities arose before we used or needed them, then they cannot be the product of natural selection. And, if they originated in anticipation of a future need, then they must be the direct creation of a higher intelligence: "The inference I would draw from this class of phenomena is, that a superior intelligence has guided the development of man in a definite direction, and for a special purpose." Wallace had rejoined the camp of natural theology and Darwin remonstrated, failed to budge his partner, and finally lamented.

The fallacy of Wallace's argument is not a simple unwillingness to extend evolution to humans, but rather the hyper-selectionism that permeated all his evolutionary thought. For if hyper-selectionism is valid—if every part of every creature is fashioned for and only for its immediate use—then Wallace cannot be gainsaid. The earliest Cro-Magnon people, with brains bigger than our own, produced stunning paintings in their caves, but did not write symphonies or build computers. All that we have accomplished since then is the product of cultural evolution based on a

brain of unvarying capacity. In Wallace's view, that brain could not be the product of natural selection, since it always possessed capacities so far in excess of its original function.

But hyper-selectionism is not valid. It is a caricature of Darwin's subtler view, and it both ignores and misunderstands the nature of organic form and function. Natural selection may build an organ "for" a specific function or group of functions. But this "purpose" need not fully specify the capacity of that organ. Objects designed for definite purposes can, as a result of their structural complexity, perform many other tasks as well. A factory may install a computer only to issue the monthly pay checks, but such a machine can also analyze the election returns or whip anyone's ass (or at least perpetually tie them) in tic-tack-toe. Our large brains may have originated "for" some set of necessary skills in gathering food, socializing, or whatever; but these skills do not exhaust the limits of what such a complex machine can do. Fortunately for us, those limits include, among other things, an ability to write, from shopping lists for all of us to grand opera for a few. And our larynx may have arisen "for" a limited range of articulated sound needed to coordinate social life. But its physical design permits us to do more with it, from singing in the shower for all to the occasional diva.

Hyper-selectionism has been with us for a long time in various guises; for it represents the late nineteenth century's scientific version of the myth of natural harmony—all is for the best in the best of all possible worlds (all structures well designed for a definite purpose in this case). It is, indeed, the vision of foolish Dr. Pangloss, so vividly satirized by Voltaire in *Candide*—the world is not necessarily good, but it is the best we could possibly have. As the good doctor said in a famous passage that predated Wallace by a century, but captures the essence of what is so deeply wrong with his argument: "Things cannot be other than they are. . . . Everything is made for the best purpose. Our noses were made to carry spectacles, so we have spectacles. Legs were clearly intended for breeches, and we wear them." Nor is Panglossianism dead today—not when so

many books in the pop literature on human behavior state that we evolved our big brain "for" hunting and then trace all our current ills to limits of thought and emotion supposedly imposed by such a mode of life.

Ironically then, Wallace's hyper-selectionism led right back to the basic belief of the creationism that it meant to replace—a faith in the "rightness" of things, a definite place for each object in an integrated whole. As Wallace wrote, quite unfairly, of Darwin:

> He whose teachings were at first stigmatized as degrading or even atheistical, by devoting to the varied phenomena of living things the loving, patient, and reverent study of one who really had faith in the beauty and harmony and perfection of creation, was enabled to bring to light innumerable adaptations, and to prove that the most insignificant parts of the meanest living things had a use and a purpose.

I do not deny that nature has its harmonies. But structure also has its latent capacities. Built for one thing, it can do others—and in this flexibility lies both the messiness and the hope of our lives.

5 | Darwin's Middle Road

"WE BEGAN TO sail up the narrow strait lamenting," narrates Odysseus. "For on the one hand lay Scylla, with twelve feet all dangling down; and six necks exceeding long, and on each a hideous head, and therein three rows of teeth set thick and close, full of black death. And on the other mighty Charybdis sucked down the salt sea water. As often as she belched it forth, like a cauldron on a great fire she would seethe up through all her troubled deeps." Odysseus managed to swerve around Charybdis, but Scylla grabbed six of his finest men and devoured them in his sight—"the most pitiful thing mine eyes have seen of all my travail in searching out the paths of the sea."

False lures and dangers often come in pairs in our legends and metaphors—consider the frying pan and the fire, or the devil and the deep blue sea. Prescriptions for avoidance either emphasize a dogged steadiness—the straight and narrow of Christian evangelists—or an averaging between unpleasant alternatives—the golden mean of Aristotle. The idea of steering a course between undesirable extremes emerges as a central prescription for a sensible life.

The nature of scientific creativity is both a perennial topic of discussion and a prime candidate for seeking a golden mean. The two extreme positions have not been directly competing for allegiance of the unwary. They have, rather, replaced each other sequentially, with one now in the as-