Darwin and Evolutionary Psychology

Darwin initiated a radically new way of studying behavior.

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Psychology will be based on a new foundation, that of the necessary acquirement of each mental power by gradation.—CHARLES DARWIN, 1859

26 November 1972 is the hundredth anniversary of the publication of Darwin's *The Expression of the Emotions in Man and Animals* (*1*). Like so many of Darwin's works, this acknowledged classic of psychology has been frequently discussed, occasionally read, but rarely understood (*2, 3*). The trouble has been that his writings contain deeper implications that are not at once apparent, even to an attentive and knowledgeable reader. The admiring comments of innumerable specialists—whether they be geologists, barnacle taxonomists, plant physiologists, geneticists, or students of behavior—support the view that Darwin had something going for him. Nobody seems to be sure of what it was, but at least the biased traditional historiography, which presented him as more of a part-time naturalist than an intellect of the first rank, can no longer be taken seriously.

New ideas and new materials are revolutionizing Darwin scholarship. A new attitude toward scientific innovation has provided conceptual frameworks which allow us to treat the development of any science as a natural, intelligible process. When one goes through, as I have done (*4*), the entire Darwinian corpus—something on the order of 10,000 pages if one does not count revisions—one may catch a glimpse of the author's larger enterprise. The works do not stand alone, but form a single, comprehensive system; but nowhere did Darwin state that they were more than separate treatises, and his silence provides something of an enigma.

An invaluable source for the study of Darwin's work is a mass of documents preserved at Cambridge University. Many of these documents are unpublished and many have not been examined, especially the notes and marginalia. From Darwin's published works it is reasonably apparent that he was deeply interested in psychology. In the light of additional evidence, one can substantiate this view, and add that it was fundamental to his system.

Darwin was born on 12 February 1809. Upon finishing his training for the ministry, he circumnavigated the globe as unpaid "Naturalist" on H.M.S. *Beagle,* a voyage that lasted from 27 December 1831 to 2 October 1836. Not long after his return from the voyage he became an evolutionist and began to search for a mechanism that might account for the evolutionary process. In July 1837, he began to record his thoughts on evolution in a series of notebooks "on transmutation of species" (*5*). One may trace the gradual overthrow of the traditional conception of the natural economy (*6*). But not until he had read Malthus' *Essay on the Principle of Population* was Darwin's theory complete. Only then did he realize that the driving force behind evolution is reproductive competition between members of the same species.

To Darwin, the broader implications of his theory of evolution were apparent virtually from the beginning. He saw that it would transform man's vision of his world, and of himself, from beginning to end. By the time he had reached his 30th birthday, he had worked out the major implications of his theory, and had elaborated, in provisional form, a comprehensive system of evolutionary biology. He labored more than 40 years, in the face of anxiety and ill health, to expound that system. About 20 years after the idea of natural selection first occurred to Darwin, a parallel discovery by Wallace induced him to write, in some haste, *The Origin of Species*; here he presented the theoretical framework of evolution. The details were rendered in a series of specialized treatises on a diversity of subjects. Many of these later works relate, explicitly or implicitly, to psychological topics. Darwin died on 19 April 1882. By then, evolution had been widely accepted, but Darwin's more general message had passed largely unnoticed.

To place Darwin's psychology in its proper theoretical context, one should view him as a truly revolutionary thinker, a man who was seeking to overthrow the traditional conception of the living world. A pair of unpublished notebooks reveal the nature of his ideas and their development. These are his notebooks *M* and *N*, in which he wrote down speculations and memoranda (*7*). The first bears dates from 15 July 1838 to 2 October 1838. The second continues to the spring of the next year; they span, therefore, the period in which Darwin invented the hypothesis of natural selection. They include much discussion of "metaphysics," a term that more or less corresponds to our "psychology." In 1838 psychology had only begun to lose its connections with philosophy.

We must abandon the popular myth that Darwin was not interested in philosophy, that he abhorred speculation, and that he always kept to the facts. The documents clearly show that Darwin's ideas about psychology relate to traditional philosophy. He concerned himself with the sources of knowledge and of morals, for example. For the question of where these come from, the "older metaphysicians" had only two basic answers. We had to possess an innate knowledge, say, of the good, or else to derive it from experience. Thus one may categorize traditional philosophers as nativists or empiricists, Plato against Locke, for example. To such notions these philosophers added varying amounts of supernaturalism. An evolutionary outlook rendered their answers obsolete. The mental faculties were the products of nature, and God was a superfluous hypothesis. The phenomena of behavior could be looked upon as molded by racial experience,

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but experience which was innate so far as the individual was concerned. In his notebook *M*, Darwin wrote: "Plato . . . says in *Phaedo* that our *'necessary ideas'* arise from the preexistence of the soul, are not derived from experience. —read monkeys for preexistence" (*8*, p. 128). By implication psychology was transformed into a natural science: "Origin of man now proved.—Metaphysics must flourish.—He who understands baboon would do more toward metaphysics than Locke" (*8*, p. 84). Of equal importance, Darwin saw that the theory of evolution could serve as a powerful analytical instrument: "To study metaphysics as they have been studied appears to me like struggling at astronomy without mechanics.—Experience shows the problem of the mind cannot be solved by attacking the citadel itself.—the mind is function of body.—we must find some *stabile* foundation to argue from" (*9*, p. 5).

In spite of his philosophical interests, Darwin was an empiricist when it came to substantiating his views. His annotations and reading lists show that he knew the literature on a vast range of subjects, and he corresponded with numerous specialists. To this foundation he added a great deal of his own research. He was anything but an armchair scholar when he could help it. His work on psychology understandably dealt with the familiar objects of his household and his garden: plants, insects, earthworms, babies, and domesticated animals. The beginnings of this research can be seen in notebooks *M* and *N*, where the underlying philosophical notions are often stated explicitly. I will now consider various psychological topics that Darwin covered, and show how they relate to the early notebooks.

The Phylogeny of Behavior

Darwin was the first investigator to reconstruct the evolutionary history of behavior using modern comparative methods. He based many of his conclusions on observations of plants. In his book *On the Movements and Habits of Climbing Plants* he showed that the ability of plants to climb progressed from simple, undirected movements to various more elaborate mechanisms (*10*). His *Insectivorous Plants* treated early stages in the evolution of sensation and response to stimulation (*11*). A book on *The Power of Movement in Plants* dealt with simple orientation movements (*12*). More complicated behavioral adaptation was discussed in his book on earthworms (*13*). Now I turn to the early notebooks. He asks "have plants any notion of cause and effect?" (*9*, p. 13). Again, "Has an oyster necessary notion of space—plant though it moves doubtless has not" (*9*, p. 14). The following suggests obvious links with traditional "associationist" psychologies: "The memory of plants must be association.—a certain round of actions taking place every day & closing of the leaves, comes from want of stimulus, after certain other actions, & hence becomes associated with them.—The establishment of this principle of Association will help my theory of sensitive plants" (*9*, p. 50). I hasten to add that Darwin's experiments refuted many of his speculations.

Emotional Expression

The quotation given earlier about struggling at astronomy without mechanics was taken from a discussion on emotional expression. Evidently Darwin was commenting on a solid advance in methodology, one that psychologists now accept as a basic working principle. Overt behavior provides the appropriate source of evidence about whatever it may be that lies beyond; modern behaviorism adopts much the same position. In his autobiography Darwin remarks that he was interested in refuting the view of Charles Bell that "various muscles had been specially created for the sake of expression" (*14*, p. 95). But he tells us that he first read Bell in 1840, whereas he had been systematically investigating the topic of expression for some time (*1; 14*, p. 95). *The Expression of the Emotions* was no ad hoc rebuttal, but it did nonetheless attack one of the metaphysical assumptions of traditional psychology. Bell's view of things was permeated with teleology. He treated behavior, like everything else, as if it had been produced by an intelligent agent and with one thing existing for another's benefit. Thus Bell thought that emotional expressions are there in order to tell us what our feelings are (*15*). Teleological thought habits of this sort are still with us, especially in the behavioral and social sciences. It is only natural to assume that simply because emotional expressions reveal something to another organism, they must have a communicative function. Likewise, psychologists have habitually treated signals as if the organisms emitting them had to be aware of the fact that they were communicating: motives have been confused with functions. Only recently has Darwin's antithetical position on this matter been substantiated (*3*). His view was that some expressions are what we might call signals, some are not, and that when they first originated, before they began to evolve, none were signals. At first they were useless or had another adaptive significance. Thus, according to Darwin's view, a sneer would be derived from a baring of teeth which originally made it easier to bite; only later did it get used in communication. In his early notebooks Darwin concerned himself with the role of communication, but he later de-emphasized its role for the same reason we do. As a rule, true signals are emitted only when an audience is likely to be present. But, as may be seen from the color with which a flower attracts a bee, signals need not be motivated at all.

Sexual Selection

Sexual selection, one of the least understood of Darwin's ideas, relates very closely to the matter of teleology. Among the most serious misinterpretations of Darwin's theory is the view that selection will lead to an organism's acting "in the interests of the species." One might get this impression from reading imprecise statements, and from the fact that anything which furthers the survival of the individual should tend to preserve the race. But Darwin explained evolution as the result of differential success in reproductive competition between members of the same species. Hence, especially as a result of what he called sexual selection, features could evolve which actually harmed the species. The combat between stags over does, and the extravagant displays of peacocks before pea hens, Darwin interpreted as maneuvers through which the successful males gained a monopoly over the females. But the species would gain no advantage, for the number of offspring would remain the same; in deed, it would decrease if effort were diverted from caring for the young to fighting for mates.

The history of Darwin's theory of sexual selection has been one of uncomprehending controversy. The biological literature, even that still being accepted as authoritative, abounds in efforts to show that sexual selection really has some other meaning, but most of such efforts may be dismissed

as attempts to salvage teleology. There have been two main opinions concerning the time at which Darwin first developed his theory of sexual selection and the reason for his devoting so much effort to it. Traditionally it was claimed that sexual selection was intended to account for certain facts that could not be explained by natural selection. My own view has been that by showing how pure reproductive competition would produce what was adaptive to the individual but maladaptive for the species, sexual selection would at once refute the teleological interpretation of the natural economy and provide a critical test of the selection theory in general. In addition, a female choosing between potential mates acts rather like a breeder determining which animals among a group of domestic animals should reproduce. From a conceptual point of view, sexual selection could very easily have been derived from artificial selection. In fact we can find early traces of Darwin's thought on such matters in the midst of a discussion on the evolution of the esthetic faculties, where he remarks: "Suppose Pea-hen admires peacock's tail as much as we do" (*16*). Thus, an analogy with man's production, by selective breeding, of beautiful domesticated animals, led to the discovery of comparable phenomena in other species.

Darwin's notebooks and his publications, especially a book entitled *The Descent of Man, and Selection in Relation to Sex*, are full of clever ideas about how reproductive competition of the purely sexual kind might have affected the evolution of human behavior (*17*).

> He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body, but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. Courage, pugnacity, perseverence, strength and size of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour, or form; and these powers of the mind manifestly depend on the development of the brain.

It seems odd, considering the acknowledged fact that so much of human behavior is sexual behavior, that psychologists have virtually ignored Darwin's theory of reproductive competition. But of even greater importance, perhaps, is the point that psychology can contribute as much to the study of evolution as it can learn from it. An understanding of how the nervous system operates should lead to many useful hypotheses. The nervous system is a major force in determining the course of evolution.

Instincts

Much contemporary discussion in the psychological and zoological literature has to do with the nature of instinct. Contemporary polemics have largely to do with the relative importance of heredity and environment. Darwin concerned himself with this issue, but his basic contribution lay elsewhere. His goal was to overthrow the teleological conception of instinct. In the older literature "instinct" was often contrasted with another concept, sometimes called reason, sometimes called intelligence. The latter terms could designate anything from the most elemental forms of learning to the highest manifestations of reflective thought processes. Instincts were complex behavior patterns, unlearned and yet adaptive. They seemed to be rational, and the only way to explain them was as the result of God's miraculous powers (*9*, p. 36). In his personal copy of Müller's *Physiology* Darwin marked the following passage: "The expression of Cuvier with reference to instinct is very correct. He says, that animals in their acts of instinct are impelled by an innate idea, —as it were, by a dream" (*18*).

Darwin's own research on instincts was focused on the Hymenoptera (ants, bees, and wasps). There were several reasons for this, some more apparent than others. For one thing, several lineages of Hymenoptera had evolved societies, a topic to which I shall return. For another, and this was a point he stressed in *The Origin of Species*, the instincts of the neuter members of these societies could have evolved by a special kind of natural selection, but not by inherited habit (a viable alternative in those days). But these were later developments, and for the stimulus that initiated this idea we have to go back to the notebooks. Darwin writes: "Waterhouse says far more instincts in *all* Hymenoptera, than in other orders (study Kirby with this view) therefore there is Instinctual development in one order, as there is intellectual in human" (*8*, p. 98). He would seem to have been looking at the two modes of behavior as exhibiting diversification, not just progress, and this was a typically Darwinian attitude. In his theory of natural selection Darwin recognizes the importance of variation and of organic diversity. The history of life reflects as much an adaptive radiation, with behavior of different kinds having evolved in different ecological situations, as it does a progressive elaboration of better organisms with nervous systems increasingly like our own. Psychologists today are becoming increasingly dissatisfied with a "comparative" psychology that treats "the white rat" as if it were the mere prototype of "the college sophomore" (*19*). Much of what purports to be evolutionary psychology is really a warmed over version of the medieval *scala naturae* which arranged all beings in a scale from highest to lowest (God, angels, men, brutes, plants . . .) (*20*).

If we turn to Darwin's personal copy of "Kirby" [that is, Kirby and Spence (*21*)], a treatise on entomology, we find it heavily annotated, often with exclamation points which evidently indicated contempt. His negative reactions mainly had to do with the theological effusions; actually he relied very heavily on this work for factual materials. On the other hand, his annotations of it show that much of his research on insect behavior was designed to refute the sort of teleological views that Kirby and Spence repeatedly express. They marveled at the skill with which bees make cells of wax, saying that "the construction of a bee-hive is a miracle which overwhelms our faculties" (*21*). Darwin, in *The Origin of Species*, demonstrated that, impressive as it was, the process whereby bees construct their cells could be reduced to some very simple principles (*22*). Kirby and Spence also made much of the slave-making habit of certain ants; these views were again rebutted in *The Origin of Species*, where Darwin presented some of his original observations (*23*). In a posthumous work published by Romanes, Darwin took issue with the view of Kirby and Spence that bumblebees eat their mothers' eggs to prevent overpopulation (*24*).

> Can the instinct which leads the female spider savagely to attack and devour the male after pairing with him be of service to the species? The carcase of her husband no doubt nourishes her; and without some better explanation can be given, we are thus reduced to the grossest utilitarianism, compatible, it must be confessed, with the theory of natural selection.

Because competition between individuals was the mechanism that accounted for Darwin's theory of evolution, it could produce instincts which subserved the needs of the individual, but not the needs of the species. Darwin ultimately saw that competition between families would have results comparable to the results of competition between single organisms, and on this basis he explained the evolution of instincts in the neuter castes of social insects (*22*, pp. 237–240). But his marginalia in Kirby and Spence show that he struggled at great length with this problem, trying to see if inherited habit or ancestral reversion would explain the situation. This brings me, however, to my next topic.

Evolution of Morals

If the hypothesis of natural selection is both sufficient and true, it is impossible for a genuinely disinterested or "altruistic" behavior pattern to evolve. Naturally this fact suggests that many traditional notions about ethics are wrong. True to form, Darwin treated such matters extensively in *The Descent of Man* (*17*, chaps. 4 and 5). He affirms that a "moral sense" has in fact evolved. But since it furthers the competitive ability of the individual and his family, an "altruistic" act is really a form of ultimate self-interest. This is true even though we derive pleasure from helping others without realizing the ultimate significance of our acts. (That we like sugar does not reveal the nutritional reason for our liking it.) Teleological methods here again have led psychologists to confuse motives with adaptive significance.

One value of Darwin's approach is that it helps to avoid this version of what William James called the "psychologist's fallacy." Darwin's understanding of such matters, however, was a fairly late development in his own work, for it depended upon his having a solid grasp of selective mechanisms. Darwin's interest in morals arose quite early, before he had read Malthus. He remarked that the theory of evolution "would make a man a predestinarian of a new kind, because he would tend to be an atheist" (*8*, p. 74). Again, "the mind of man is no more perfect, than instincts of animals to all & changing contingencies, or bodies of either—descent then, is the origin of our evil passions!!—The Devil under form of Baboon is our grandfather!—" (*8*, p. 122). We should remember that in the traditional view of things, moral behavior had to be innate, or learned, or the product of reason; and it seemed to involve a supernatural order. Darwin saw that morality and immorality alike are the results of a natural process. They had been generated by a kind of racial experience.

In the early notebooks we find the beginnings of naturalistic observations on the behavior of apes and children, much of it concerned with morals. Reflecting on a baboon who concealed her misbehavior from her keeper, Darwin wondered whether she was afraid of being punished, or if, perhaps, she experienced a feeling of shame (*8*, p. 140). Darwin kept notes on one of his children, some of which he published many years later (*25*). He decided that behavior indicating a sense of guilt arose spontaneously, on the grounds that his son showed it, but had never been punished. Of course, we rightly call for more evidence, but we should not forget that Darwin was a pioneer, investigating an important topic with a completely new approach. Moral philosophers of the old school frequently asserted that a system of rewards and punishments was necessitated by the fact that right conduct comes from without. The problem is still with us, as is the a priori approach to its solution.

Psychological research affected Darwin's thinking in ways that one would hardly have expected. For example, it led him to analyze social phenomena, with important results. In his *Autobiography*, Darwin says that he read Malthus "for amusement" (*14*, p. 83). Evidently what he really meant was that he read "metaphysical books" during the hours he could not devote to other scientific work (*14*, p. 69). Actually, from the context of his notebooks, it is clear that he read Malthus as part of his systematic inquiries into the evolution of morals.

Ontogeny of Behavior

For Darwin, the problems of instinct and of embryology were closely linked together. Traditionally, both had been viewed with much the same frame of reference, but with different interpretations. The genesis of an embryo and of a behavior pattern alike had seemed to partake of the miraculous. A divine order, immanent or transcendent, might be posited. And nativist and empiricist psychologies had their analogues in preformation and epigenesis (*26*). The Darwinian solution was to view evolution as a change in developmental mechanisms, with natural selection (and other mechanisms of adaptation) disposing of any need to invoke supernatural agencies. Darwin's studies on human infants can be traced back to his notebook *M*; some of these studies are treated in *The Expression of the Emotions* (*1*). Not surprisingly, Darwin's views on the relationship between behavioral ontogeny and phylogeny were quite sophisticated. He did not treat children as if they represented our full-grown ancestors. That is to say, unlike many who have dealt with the same subject, he was not a naive recapitulationist. A child, like a caterpillar, is an organism in his own right, adapted to his own ecological niche. And, contrary to what teleologists from Aristotle down to the present day have assumed, children do not exist in order that the universe will be populated by adults. But the stamp of history could nonetheless be seen in Darwin's interpretation of infant behavior. He speculated that a "Child does not sneer, because no young animal has canine teeth" (*27*).

Domesticated animals also provided useful subjects for his studies. Darwin noted that white, blue-eyed cats are deaf. He experimented with normal young kittens, which also have blue eyes, and found out that these were deaf too. A failure of the developmental mechanism in these cats had led to an imperfect sensory apparatus (*28*). Darwin foresaw that by analyzing behavior in terms of developmental mechanics, much of psychology could be reduced to physiology. Some changes in behavior are due to inherited modifications in the structure of the nervous system.

Genetics of Behavior

Because Darwin's work on inheritance was not in all respects successful, his many enduring contributions are habitually overlooked. The genetics of behavior as an academic discipline hardly existed 20 years ago, although its precursors have a long history. Darwin was thinking about the inheritance of handwriting patterns and other traits in the 1830's. Every geneticist concerned with behavior should read Darwin's *Variation of Animals and Plants under Domestication*.

From a modern point of view Darwin's evolutionary genetics must be considered defective in one important

respect. He believed in the inheritance of acquired characteristics and in inherited habit arising from originally intelligent behavior. This sort of mechanism he thought existed in addition to natural selection. For him it was possible that both might have to be taken into account, and this complicated his researches. Our work is now much easier.

It has been widely assumed that this Lamarckian element in Darwin's theory was a later development—an effort to explain away ad hoc facts which seemed a threat to his theory of natural selection. He did indeed place more emphasis on these other mechanism's in his later works, but this was only because he had already dealt with natural selection. Actually, Darwin took the inheritance of acquired habits for granted from a very early period (*9*, p. 7). That he should have done so makes sense, if one considers his general outlook. He treated the organism as a material system which could be modified through interactions with the environment. But he never really resolved to his own satisfaction just what these interactions were.

The history of the assimilation of Darwinism is the history of the failure to assimilate Darwinism. But Darwin's contribution to psychology was neither understood nor accepted, and only now are we beginning to realize what that contribution was. An adequate treatment of what happened to Darwin's psychology would require, in addition to an extensive discussion of psychological technicalities (see *4*), an examination of the sociology of knowledge (see *29*). These subjects cannot be fully discussed here but it is possible to convey a general impression of what seems to have occurred.

Darwin was not a conventional thinker. Albeit a man of his times, he was not constrained by the acceptances of his society. Bound to no single field of knowledge, but master of many, he did not have to think in a fashion dictated by professional training or the needs of a specialty. Neither, at least in the privacy of his study, did he have to conform to the superstition that scientists must repress every impulse to apprehend the larger connection among things, and that they must keep to the "facts." The Darwin of the notebooks stands in stark contrast to the Darwin of his works read without attention to their implicit message. Many readers may think that Darwin was "breaking the rules" in his flights of speculation. But the fact is that as a consequence of much thought about biogeography, esthetics, morals, economics, and various other topics he developed the theory of natural selection. Genius does not obey the rules, it ordains them.

As a thinker who synthesized ideas on a broad scale, Darwin was able to envision his theory as one comprehensive system. And as the inventor of that theory, he mastered it with a depth of understanding and a knowledge of detail which has never been equaled. He alone could grasp the magnitude of his accomplishment, while everybody else had to content themselves with a partial and imperfect view of it. A philosopher such as John Dewey could see that Darwin had rendered teleology untenable; only a first-rate scientist could transform that same insight into an effective program of research. A zoologist would naturally understand that behavior and morphology alike must be treated from an historical point of view; it took a sophisticated evolutionary theorist to see that the record manifests the mechanism. A psychologist might realize that in the light of selection theory, sex had to be viewed in a new light; only a great ecologist could see where the Malthusian economics fits in.

To all this should be added the radical departure from the Western intellectual tradition that was implicit in Darwin's new cosmology. A world populated by organisms striving to no end but rather playing ridiculous sexual games, a world in which the brain is an extension of the gonads, and where killing one's brother is a virtue, so long as it furthers one's mother's reproductive success, simply cannot be reconciled with the old way of thinking. Darwin may be considered the Newton of biology; it was he who showed how all the phenomena of life can be related to one comprehensive theory. As such, his role in history has been well acknowledged. Equally we might recognize him as the Galileo of psychology; the subject need not be treated like astronomy without mechanics. Indeed to a considerable extent his views have suffered a comparable fate. Darwin's heresy affected not just the physical universe, but the moral one. That new kind of predestinarianism of which he wrote could hardly have attained an immediate and universal following. Fortunately, insight has its way of being heard no matter how long prejudice attempts to silence it.

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